BESTÄUBERGEMEINSCHAFTEN AUF SUBVENTIONIERTEN BLÜHFLÄCHEN

-BIODIVERSITÄT, KONNEKTIVITÄT UND RESSOURCENVERFÜGBARKEIT-

Dissertation
zur
Erlangung des Doktorgrades
der Naturwissenschaftlichen Fakultät
der Justus-Liebig-Universität Gießen

vorgelegt von
Daniela Warzecha
geboren in Frankfurt am Main, Deutschland

Gießen, Dezember 2021

Eingereicht am: 17. Dezember 2021

Erstgutachter: Prof. Dr. Volkmar Wolters
Zweitgutachter: Prof. Dr. Tim Diekötter

Tag der Disputation am: 14. März 2022

INHALTSVERZEICHNIS

INHALTSVERZEICHNIS

VORWORT

VORWORT

Die Zerstörung von Lebensräumen als Folge von Landnutzung generell und die Intensivierung der Landwirtschaft im Besonderen haben zu einem starken Rückgang der Diversität geführt (Foley *et al.* 2005). Die Nachricht über den alarmierenden Rückgang von Fluginsekten in Naturschutzgebieten (Hallmann *et al.* 2017) hat die Problematik in das breitere Licht der Öffentlichkeit gerückt. Besonders gefährdet scheinen dabei Hautflügler wie etwa Wildbienen zu sein (Sánchez-Bayoa & Wyckhuys 2019). Durch ihre starke Bindung an Blüten reagieren sie empfindlich auf den Rückgang von Blütenpflanzen, zählen jedoch gleichzeitig zu den wichtigsten Bestäubern von Wild- (Biesmeijer *et al.* 2006; Ollerton *et al.* 2011) und Kulturpflanzen (Klein *et al.* 2007; Winfree 2010; Garibaldi *et al.* 2013). Die Einsaat von Blühflächen innerhalb von Agrarumweltprogrammen soll durch die gesteigerte Verfügbarkeit von Blüten diesem Trend entgegenwirken.

Bisher kommen Studien zur Wirksamkeit dieser Maßnahmen zu unterschiedlichen Ergebnissen (Haaland *et al.* 2011). Während es zu der Situation in der agrarisch geprägten Offenlandschaft noch keinen wissenschaftlichen Konsens gibt, tragen kommunale und private Initiativen dazu bei, dass gerade Wildbienen durch eine gesteigerte Blütenverfügbarkeit in Städten Rückzugsorte oder teils geeignetere Bedingungen als in natürlichen Lebensräumen finden (Baldock *et al.* 2015; Theodorou *et al.* 2020). Ein viel diskutierter, aber bisher wenig untersuchter Faktor ist in diesem Zusammenhang der die Maßnahmen umgebende Landschaftskontext (Tscharntke *et al.* 2012). Denn viele Arten sind nicht nur an ein einziges spezifisches Habitat gebunden, sondern sie sind vielmehr dynamische Multihabitatnutzer. Zudem rückt verstärkt die Zusammensetzung der ausgebrachten Mischungen in den Fokus, um die Effizienz der Unterstützung von definierten Zielarten oder –funktionen zu steigern. Diesen beiden Aspekten soll im Rahmen dieser Arbeit nachgegangen werden.

ZUSAMMENFASSUNG

ZUSAMMENFASSUNG

Die Zerstörung und Fragmentierung von Lebensräumen gehören zu den Hauptreibern des weltweiten Artenrückgangs. Blütenreiche Habitate der Kulturlandschaft sind davon besonders betroffen, so dass sich innerhalb der Agrarumweltprogramme die Anlage von Blühflächen etabliert hat, um durch die gesteigerte Verfügbarkeit von Pollen und Nektar vor allem dem Rückgang blütenbesuchender Insekten entgegenzuwirken. Studien zur Effektivität von Blühflächen kommen jedoch zu widersprüchlichen Ergebnissen. Es liegt nahe, dass bisher wenig berücksichtigte Faktoren jenseits der Habitat Ebene eine entscheidende Rolle spielen. Auch ist über die Dynamiken der Gemeinschaften über die Dauer der Maßnahmen wenig bekannt. Ziel dieser Arbeit ist es daher, zwei bedeutende Stellgrößen für eine standortangepasste Optimierung von Blühflächen näher zu untersuchen: die umgebende Landschaft und die Zusammensetzung der ausgebrachten Blühmischung. Modellorganismen sind Wildbienen und Schwebfliegen, da sie beide eine starke Blütenbindung aufweisen, aber aufgrund ihrer Biologie unterschiedlich auf Landschaftsmuster reagieren.

Die ersten drei Studien (Kapitel II-IV) befassen sich mit dem Einfluss der Landschaft auf die Besiedlung von Blühflächen im Landkreis Marburg-Biedenkopf, Hessen, entlang eines Landschaftskomplexitätsgradienten (Anteil Grünländer und naturnaher Habitatelemente). Die Hälfte der mittels GIS gestützter Landschaftsanalysen ausgewählten Blühflächen lagen in Nachbarschaft zu mindestens einer weiteren Blühfläche („vernetzte“ Blühflächen), die anderen wiesen keine zusätzlichen Blühflächen in einem Radius von 500 m auf („isolierte“ Blühflächen).

Obwohl mit über 320 Insektenarten mittels Transektfängen auf einer Auswahl etablierter Blühflächen überraschend viele unterschiedliche Blütenbesucher in der ersten Studie (Kapitel II) nachgewiesenen wurden, fiel die Hälfte aller Individuen auf die Taxa der Bienen und Schwebfliegen. Trotz dieser guten Ansprache der Zieltaxa waren jedoch nur 2,6 % aller Individuen Wildbienen abseits der Honigbienen und Hummeln. Ordinationen der Blütenbesuchergemeinschaften zeigten, dass sich sowohl der Zeitpunkt der Aufnahme, als auch die umgebende Landschaft auf die Gemeinschaftszusammensetzung auswirken. Die Landschaftskomplexität und die Konnektivität zu benachbarten Blühflächen wirkte sich positiv auf die Wildbienenvielfalt aus, während Schwebfliegen vermehrt auf isolierten Flächen zu finden waren. Für keine andere untersuchte Gruppe außer den Wildbienen konnte ein Effekt der Landschaft gefunden werden.

Dieser Landschaftseffekt wurde in Hinblick auf die Besiedlung durch und die Dynamiken innerhalb der Wildbienen und Schwebfliegen im Rahmen der zweiten Studie (Kapitel III) über drei aufeinanderfolgende Jahre mit Farbschalen auf 33 neu angelegten Blühflächen genauer untersucht. Hierbei wurden mehr als ein Viertel der regionalen Wildbienen und Schwebfliegen nachgewiesen. Erneut zeigten ausschließlich Wildbienen eine deutliche Reaktion auf die Landschaft. So stieg die Alpha-Diversität auf isolierten Flächen mit der Landschaftskomplexität an, während für verknüpfte Flächen ein gegenteiliges Muster zu beobachten war. Jedoch waren die Wildbienen Gemeinschaften benachbarter Flächen in einfachen Landschaften ähnlicher zueinander als in komplexen

Landschaften. Dieser Effekt spiegelte sich auch mit der Komplexität des Pflanzenspektrums wieder. Schwebfliegen reagierten gegenläufig und auf einer höheren taxonomischen Ebene (Pflanzenfamilienvielfalt). Als Resultat der voranschreitenden Sukzession veränderten sich zudem die Gemeinschaftszusammensetzungen über den Untersuchungszeitraum deutlich.

Der Einfluss des Fragmentierungsgrades auf die Besiedlung der Blühflächen zeigte sich auch in der innerartlichen Größenvariabilität häufiger Wildbienenarten (KAPITEL IV). Bei den vier häufigsten in KAPITEL III nachgewiesenen Sandbienenarten der Gattung *Andrena* stieg die intra-spezifische Körpergröße (gemessen als Intertegulardistanz ITD) der beiden mittelgroßen Arten mit dem Grad der Fragmentierung an. Zum einen bestätigt die Studie, dass bei mobilen Arten in fragmentierten Landschaften die im Zusammenhang mit der Ausbreitung relevanten Körperregionen größer ausgebildet sind. Zum anderen deutet die Tatsache, dass die Anzahl der durch *A. flavipes* gesammelten Pollentypen mit der Körpergröße abnahm, auf funktionelle Konsequenzen dieses Mechanismus hin.

Lokale Faktoren hinsichtlich der Zusammensetzung von Blühmischungen als Steuergröße der Attraktivität für umfangreichere Blütenbesuchergemeinschaften sind Gegenstand von KAPITEL V. Für die vier untersuchten Saatmischungen des Hessischen Agrarumweltprogramms zeigten umfangreiche Analysen der Pflanze-Blütenbesucherinteraktionen zwei aufeinanderfolgender Jahre für etwa die Hälfte der 94 vorgefundenen Pflanzenarten (etwa ein Drittel stammte dabei aus der Samenbank) Besuche. Dabei reichen bereits 14 Schlüssel-Pflanzenarten aus, um die gesamte lokale blütenbesuchende Wildbienen- und Schwebfliegengemeinschaft abzudecken, die Top vier Pflanzenarten unterstützten 80 % dieser Blütenbesucher. Obwohl sich die Attraktivität der Blühmischungen zwischen den untersuchten Gruppen unterschied, war das Vorhandensein der Schlüsselpflanzen wichtiger als die Pflanzen-Diversität an sich.

Die vorgestellten Studien belegen anhand des breiten Besucherspektrums der Blühflächen den Bedarf einer Steigerung von Blütenressourcen in der Landschaft. Das Förderpotenzial von Wildbienen hängt dabei entscheidend von der umgebenden Landschaft ab. Durch ihre aufwendige Brutpflege sind sie auf kurze Wege zwischen Nahrungs- und Nisthabitaten angewiesen und profitierten durch die Anlage mehrerer Blühflächen, indem diese zu einer besseren Vernetzung mit bestehenden (Teil-) Lebensräumen beitragen und ihre Erreichbarkeit in fragmentierten Landschaften fördern. Dies könnte den Selektionsdruck auf Individuenebene (Körpergröße) als auch die Gemeinschaftsstruktur reduzieren. Die Berücksichtigung der vorgestellten Ergebnisse für eine standortangepasste Optimierung von Blühflächen kann somit deren Effizienz in modernen Agrarlandschaften steigern. Da Wildbienen jedoch sehr sensibel auf Lebensraumveränderungen reagieren, können Blühflächen eine unterstützende Wirkung nur in Landschaften entfalten, die noch ausreichend naturnahe Habitate aufweisen. Gleichzeitig decken die Pflanzenzusammensetzungen bisheriger Mischungen überwiegend die Bedürfnisse häufiger Arten ab und sind für die Förderung der Mehrheit der Wildbienen nicht ausreichend. Der Erhalt oder die Restaurierung naturnaher Lebensräume sollten daher immer der Schaffung künstlicher und zeitlich begrenzter Strukturen vorgezogen werden.

SUMMARY

SUMMARY

Global decline of biodiversity is caused by multiple and interacting stressors, but loss and fragmentation of habitats are considered as major drivers. Because flower-rich habitats in cultivated landscapes are especially affected, wildflower areas are increasingly initiated within agri-environmental schemes (AES) to promote biological diversity, especially by increasing pollen and nectar availability for flower-visiting insects. However, diversity benefits vary substantially among AES sites and schemes. One hypothesis for this inconsistency is that the effectiveness of flowering AES is modulated by landscape context. Multi-year landscape-ecological studies on the colonization of and species composition in wildflower areas are still scarce. Thus, the aim of this work is to quantify the effects of landscape context and local flower composition of wildflower areas to increase their efficiency for pollinators. Wild bees and hoverflies were chosen as model organisms, as they share a strong dependency on flower resources but show different responses to landscape patterns related to their differing life history strategy.

The first three studies (CHAPTER II-IV) focus on the colonization of wildflower areas in dependence of landscape context (percentage of area covered by permanent grassland and semi-natural habitats) in the county of Marburg-Biedenkopf, Hesse. GIS analyses were used to select wildflower areas which were equally assigned to one of two isolation classes: “isolated” (no additional wildflower areas present within a radius of 500 m) and “connected” (at least one additional wildflower area present within a radius of 500 m).

With over 320 insect species, a surprising high number of flower visitors were recorded during transect surveys on a selection of established flowering areas in the first study (CHAPTER II), however, half of all individuals were bees and hoverflies. Still, only 2.6 % of the specimens recorded were wild bees compared to the majority being honeybees and bumblebees. Ordinations of the flower visitor communities showed that both the time of recording and the surrounding landscape had an impact on the community composition. While wildflower plantings that were accompanied by additional local plantings and embedded within complex landscapes supported a high wild bee diversity, hoverfly richness was higher when no additional plantings were present. No flower-visitor group other than wild bees was affected by the landscape context.

Within study two (CHAPTER III) we examined in more detail the effect of landscape context on the colonization and community dynamics of wild bees and hoverflies in 33 newly established wildflower areas over a period of three consecutive years by using pan traps. We recorded more than 25 % of the wild bee and hoverfly species of Hesse. Again, landscape effects were mostly driven by wild bees. While alpha-diversity increased with landscape complexity in isolated wildflower areas, the opposite pattern was observed for connected areas. However wild bee communities became dissimilar with an increase in the complexity of surrounding landscape structure and plant species composition. Hoverflies showed a contrasting pattern on a higher taxonomic level (plant family richness). The observed species turnover over time and space was high and landscape-context dependent and a result of successional changes in floral composition of wildflower areas.

Beyond pollinator community composition, fragmentation effects similarly affected intraspecific body size variation within common wild bee species (CHAPTER IV). Within the four most frequently occurring mining-bees of the genus *Andrena* from CHAPTER III, the intraspecific body size (measured as the inter-tegular distance (ITD)) of the two medium sized species increased with the degree of landscape fragmentation. On the one hand, the study confirms that highly mobile species respond with an intraspecific increase in size of dispersal related body parts to habitat fragmentation. On the other hand, the fact that the number of pollen types collected by *A. flavipes* decreased with body size indicates functional consequences of this mechanism.

Local factors with regard to the composition of flower mixtures as a control variable of attractiveness for larger flower visitor communities are the subject of CHAPTER V. For the four tested seed mixtures of the Hessian agri-environmental program, extensive analyses of the plant-flower visitor interactions over two consecutive years showed visits for around half of the 94 plant species found (around one third originated from the seedbank). However, 14 key plant species were crucial for the entire local flower-visiting bee and hoverfly community. The four top plants already supported 80 % of flower visitors. Although seed mixtures differed significantly in attracting flower visitors at the plot level and between target taxa, the presence of key plants was more important than plant species diversity per se.

The studies presented confirm the need for an increase in flower resources in the landscape on the basis of the broad spectrum of visitors to the flowering areas. However, to fully realize the potential for promoting wild bees, the establishment of wild flower areas must be adapted to landscape conditions. Wild bees, central-place foragers that must frequently commute between nesting sites and food plants, multiple wildflower areas are clearly beneficial, especially in simple landscapes. Multiple wildflower areas help to increase connectivity of (partial) habitat elements, defragmentate landscapes and by that enable more species to utilize those resources. Further, this could reduce filtering processes at the individual level (intraspecific body size for higher dispersal capacity) and at the community level. Accordingly, adjusting local conditions likely optimizes conservation effectiveness in modern agroecosystems. Because wild bees are sensitive to changes in habitat quality, wildflower areas can only be colonized in landscapes with a sufficient amount of seminatural habitats. In addition, current seed mixtures do not meet the needs of most wild bee species. Therefore, the preservation or restoration of existing habitats should always be preferred to the creation of artificial and temporary structures.

KAPITEL I – ALLGEMEINE EINFÜHRUNG

ALLGEMEINE EINFÜHRUNG

EINLEITUNG

Mit der MacSharry-Agrarreform wurden in den 1990er Jahren Agrarumweltmaßnahmen auf europäischer Ebene in die Gemeinsame Agrarpolitik (GAP) integriert, um den negativen Folgen der intensiven Landwirtschaft auf die Biodiversität entgegenzuwirken (Hodge *et al.* 2015). Eine gängige Maßnahme darin ist die Anlage von Blühflächen mit dem Ziel, die Ressourcenverfügbarkeit für blütenbesuchende Insekten in der landwirtschaftlich geprägten Umgebung zu erhöhen (Haaland *et al.* 2011). Trotz der umfangreichen Bemühungen scheinen jedoch die Agrarumweltmaßnahmen bisher nicht den Artenrückgang aufzuhalten (Pe'er *et al.* 2019). So sind beispielsweise Unterschiede in der Effizienz von Agrarumweltmaßnahmen anscheinend auf den Landschaftskontext (Batáry *et al.* 2011, 2015; Tscharntke *et al.* 2012; Scheper *et al.* 2013), aber auch die verwendeten Blühmischungen (Wood *et al.* 2017) zurück zu führen. Dazu fehlt es jedoch noch weitestgehend an empirischen, mehrjährigen Studien. Ziel dieser Dissertation ist es daher zu untersuchen, wie sich lokale (Zusammensetzung der Blühmischungen) und regionale (Landschaftskomplexität und Konfiguration der Flächen untereinander) Faktoren auf die Besiedlung durch blütenbesuchende Insekten wie Wildbienen und Schwebfliegen auswirken. Betrachtet werden Dynamiken innerhalb dieser Gemeinschaften intra-annuell über die Saison sowie inter-annuell über die Dauer der Maßnahme. Im Fokus stehen insbesondere funktionelle Eigenschaften der Blütenbesucher, die Unterschiede in der Nutzung und Zugänglichkeit der Blühflächen erklären können. Die Ergebnisse sollen im Anschluss dabei helfen, durch standortangepasste Optimierungen die Effizienz von Blühflächen besonders für das sensible Taxon der Wildbienen zu steigern.

Ein globaler Rückgang der Biodiversität wird seit Jahren diskutiert (Butchart *et al.* 2010) und stellt eine der größten Herausforderung unserer Zeit dar (Hallmann *et al.* 2017; Cardoso *et al.* 2020). Obwohl dieser Rückgang durch eine Reihe von teils intergierenden Stressoren angetrieben wird (Brook *et al.* 2008), so werden der Verlust, die Fragmentierung und Degradierung naturnaher Habitate (Potts *et al.* 2010) als Haupttreiber betrachtet (Foley *et al.* 2011; Sánchez-Bayo & Wyckhuys 2019). In Europa ist dies vor allem in Agrarlandschaften zu beobachten, welche in den letzten Jahrzehnten dramatische Veränderungen durchlaufen haben (Meeus 1993; Stoate *et al.* 2001; Dramstad *et al.* 2002). So ist sowohl die agrarwirtschaftlich genutzte Fläche, als auch die Intensität der Bearbeitung in den letzten 60 Jahren dramatisch gestiegen (Rabbinge & van Diepen 2000; Robinson & Sutherland 2002). Als Folge sind naturnahe Habitate wie extensive Grünländer, Heckenzüge oder Ackerrandstreifen, die überlebenswichtige Ressourcen für viele Arten bieten (Marshall & Moonen 2002; Hannon & Siks 2009; Holland *et al.* 2016; Librán-Embid *et al.* 2021), weitgehend verloren gegangen.

Extensiv bewirtschaftete, naturnahe Grünländer zählen weltweit zu den Lebensräumen mit der höchsten Pflanzendiversität (Wilson *et al.* 2012). Jedoch geht nicht nur ihr Flächenanteil stark zurück (Bignal & McCracken 1996), sondern durch die Verwendung von Pestiziden (Geiger *et al.* 2010) und Dünger (Billeter *et al.* 2008) auch ihr Pflanzenreichtum (Wesche *et al.* 2012). Entsprechend sind moderne Agrarsysteme arm an Blütenressourcen (Carvell *et al.* 2006a) und Insekten (Clough *et al.* 2014; Seibold *et al.* 2019). Zwar können Massentrachten wie Raps zumindest über einen kurzen Zeitraum potenziell geeignete Nahrungsressourcen in sonst blütenarmen Landschaften darstellen (Westphal *et al.* 2003; Beyer *et al.* 2021), doch scheint vor allem die Lücke an Pollen- und Nektarpflanzen spät im Jahr besonders gravierend (Scheper *et al.* 2014; Hofman *et al.* 2019). Viele Blütenbesucher wie beispielsweise Bienen und Schwebfliegen sind als adulte Insekten auf Blüten als Nahrungsressource angewiesen und bestäuben während der Aufnahme von Pollen und Nektar die Pflanze (Kevan & Baker 1983). Als Folge hat der Rückgang ausreichender Pflanzenressourcen und geeigneter Habitate besonders bei diesen Taxa zu einer starken Abnahme der Abundanz und des Artenreichtums geführt (Biesmeijer *et al.* 2006; Fitzpatrick *et al*. 2007; Winfree *et al.* 2009; Williams *et al.* 2010; Sánchez-Bayo & Wyckhuys 2019).

Um diesem Rückgang entgegenzuwirken hat sich vor allem die Anlage von Blühflächen innerhalb der Agrarumweltprogramme, mit dem Ziel die Ressourcenverfügbarkeit in der landwirtschaftlich geprägten Umgebung durch finanzielle Unterstützung zu erhöhen, zu einer bevorzugten Maßnahme etabliert (Haaland *et al.* 2011). Zwar resultiert die gesteigerte Blütenverfügbarkeit solcher Maßnahmen im Vergleich zur herkömmlichen Bewirtschaftung in einer höheren Bestäuberdichte und Artenvielfalt (z.B. Carvell *et al.* 2007; Redpath *et al.* 2010; Korpela *et al.* 2013; Wood *et al.* 2015; Buhk *et al.* 2018), jedoch beruhen viele dieser Untersuchungen zum Einfluss von Blühflächen auf die Bestäubergemeinschaft (Carvell 2002; Carvell *et al.* 2004; Heard *et al.* 2007; Wood *et al.* 2015) sowie zur Effizienz der verwendeten Saatmischungen (Pywell *et al.* 2006; Carvell *et al*. 2007) auf der Erfassung von Hummeln. Studien zu den Reaktionen der Gesamtheit der Bestäuber, von denen die Hummeln nur einen funktionell distinkten Teil ausmachen und sich in ihre Lebensweise mitunter stark von den anderen unterscheiden, fehlen hingegen noch weitgehend. Jedoch ist die Berücksichtigung ökologischer Eigenschaften, die etwa über die Nutzung von Blüten bestimmen oder der Aktionsradius einer Art, notwendig, um die Anlage von Blühflächen für ein breites Spektrum an Arten effizient zu gestalten.

Als soziale Arten mit langlebigen Kolonien sind Hummeln auf eine Blütenverfügbarkeit über die ganze Saison angewiesen (Wray & Elle 2015), zumal sie Pollen- und Nektarvorräte nur für wenige Tage anlegen (Brian 1954; Shelly *et al.* 1991). Während sie dafür zwar sämtliche Blüten nutzen, deren Pollen und Nektar sie erreichen können (Westrich 2019) und damit ein breites Spektrum an Pflanzen (Fussell & Corbet 1992), bevorzugen langrüsslige Arten jedoch tiefkelchige Blüten (Fussell & Corbet 1992; Carvell *et al.* 2006b). Die Mehrheit der übrigen Wildbienen und Schwebfliegen besitzt kurze Rüssel, weshalb sie vor allem leicht zugängliche Blüten besuchen (Kevan & Baker 1983; Scheper *et al.* 2021). Zudem zeigen rund ein Drittel der nestbauenden solitären Wildbienen eine Spezialisierung auf den Pollen bestimmter Pflanzenfamilien oder gar -arten (Westrich 2019), und ihr Vorkommen ist an Bestände dieser Pflanzen gebunden. Vor diesem Hintergrund ist es schwierig Präferenzen aus Versuchen zu Saatmischungen auf solitäre Wildbienen und Schwebfliegen, die einen weitaus diverseren Teil der Bestäubergemeinschaft ausmachen, zu übertragen, wie Studien aus England belegen (Wood *et al.* 2017).

Wurden Ressourcenansprüche, die sich nicht nur auf die lokale Nahrungsverfügbarkeit beziehen, für die Effizienz von Agrarumweltmaßnahmen bisher wenig beachtet, so wird die Bedeutung der umgebenden Landschaft immer deutlicher (Heller & Zavaleta, 2009; Batáry *et al.* 2011). Der Grund dafür ist, dass die meisten Arten nicht auf ein spezifisches Habitat begrenzt sind, sondern viel mehr dynamische Multihabitat-Nutzer sind. Als „central place foragers“ müssen beispielsweise Bienen regelmäßig zwischen ihren Nist- und Nahrungshabitaten pendeln (Westrich 1996), die häufig in unterschiedlichen Lebensraumelementen liegen (Gathmann & Tscharntke 2002). Diese müssen räumlich eng miteinander vernetzt sein (Kearns & Oliveras 2009; Wright *et al.* 2015), um ohne zu hohen Energieaufwand noch erreichbar zu sein (Zurbuchen *et al.* 2010a). Obwohl andere Bestäubergruppen wie Schwebfliegen sich wegen fehlender Brutpflege in der Landschaft relativ frei ausbreiten können (Jauker *et al.* 2009; Aguirre-Gutiérrez *et al.* 2015), nutzen auch sie unterschiedliche Teillebensräume für Blütenbesuche und die Eiablage.

Trotz vergleichbarer Brutpflegestrategie unterscheidet sich der Aktionsradius von Bienen – und damit verbunden die Reaktion auf Landschaftsfaktoren – stark (Le Feon *et al.* 2010; Winfree 2010). Während er bei Hummeln bis zu mehreren Kilometern betragen kann (Goulson & Stout 2001), weisen die meisten solitären Bienenarten eine geringe Mobilität von 150 – 300 m auf (Zurbuchen *et al.* 2010b; Wright *et al.* 2015). Weniger mobile Arten sind deshalb anfälliger für kleinräumige Veränderungen und reagieren besonders stark durch Artverlust auf den Anstieg intensiv landwirtschaftlich genutzter Flächen (Steffan-Dewenter & Tscharntke 1999; Steffan-Dewenter *et al.* 2002; Le Feon *et al.* 2010; Williams *et al.* 2010) und der damit einhergehenden Habitat-Isolierung (Franzen & Nilsson 2008). Der Aktionsradius ist dabei eng mit der Körpergröße verknüpft (Greenleaf *et al.* 2007), so dass sich mit steigender Habitatfragmentierung die Zusammensetzung lokaler Bienengemeinschaften hin zu größeren Arten verschiebt (Jauker *et al.* 2013). Erreicht der Fragmentierungsgrad blütenreicher Habitate in Agrarlandschaften jedoch einen sehr hohen Wert, werden auch mobilere Bestäuber wie Schwebfliegen negativ beeinflusst (Haslett 1989; Jauker *et al.* 2019).

Während die Vereinfachung und Fragmentierung der Landschaft als Filter gegen Arteigenschaften wie die Körpergröße (Jauker *et al.* 2013; Gámez-Virués *et al.* 2015) und Nahrungsspezialisierung (Gámez-Virués *et al.* 2015) selektiert und Biotopinseln aus naturnahen Habitaten überwiegend Generalisten das Überleben in Agrarlandschaften ermöglichen (Dramstad & Fry 1995; Biesmeijer *et al.* 2006; Jauker *et al.* 2009), ist wenig darüber bekannt, ob sich diese Muster auch bei der Besiedlung von Blühflächen finden. Hierfür fehlt es vor allem an empirischen mehrjährigen landschaftsökologischen Studien, die die Besiedlung und Artenzusammensetzung in Blühflächen untersuchen (siehe jedoch Scheper *et al.* 2015; Neumüller *et al.* 2021). Gleichzeitig scheint die Zusammensetzung von Bestäubergemeinschaften in Agrarlandschaften sehr dynamisch und sowohl über die Zeit (Kremen *et al.* 2002) als auch Regionen (Winfree *et al.* 2018) betrachtet erheblich zu variieren. Entsprechend bestimmt viel mehr eine Rückkopplung aus lokalen und regionalen Prozessen die lokale Gemeinschaftszusammensetzung aus einem regionalen Artenpool (Mittelbach & Schemske 2015) und ist somit auch für die Besiedlung von Blühflächen zu erwarten.

Tatsächlich konnte für Laufkäfer gezeigt werden, dass sich durch die Umwandlung von Ackerland in Blühflächen die Gemeinschaften hin zu ressourceneffizienten Nutzern verschiebt (Baulechner *et al.* 2019) und auch Grabwespen nehmen Blühflächen in der Nähe zu ihren Nisthabitaten als Jagdreviere an (Hoffmann *et al*. 2020). Bisher bleibt jedoch unbeantwortet, wie der Landschaftskontext die Struktur von Bestäubergemeinschaften beeinflusst, die neu angelegte Blühflächen als Nahrungshabitat nutzen, und inwieweit Umweltschutzmaßnahmen effektiv an unterschiedlich strukturierte Landschaften angepasste werden können. So könnte beispielsweise die Anlage mehrerer Blühflächen deren Konnektivität untereinander, sowie die Vernetzung mit bestehenden Habitaten erhöhen (Haaland *et al.* 2011). Ziel der vorliegenden Arbeit ist es deshalb herauszufinden (i) wie die umgebende Landschaft die Besiedlung von Blühflächen durch Bestäuber und hier vor allem Wildbienen- und Schwebfliegen beeinflusst (KAPITEL II, III & IV); (ii) inwieweit die Anlage mehrerer Blühflächen die *Konnektivität* zu bestehenden (Teil-) Lebensräumen und damit ihre Effektivität zur Förderung der *Biodiversität* verstärkt (KAPITEL II & III) und (iii) wie sich die Ansprüche an die *Ressourcenverfügbarkeit* zwischen den untersuchten Bestäubern (KAPITEL V) als auch im Landschaftskontext unterscheiden (KAPITEL III & IV).

HYPOTHESEN

Aus den oben beschriebenen Zielen leitet sich folgende ÜBERGEORDNETE HYPOTHESE ab:

> Die *Biodiversität* auf Blühflächen resultiert aus Prozessen auf lokaler (Ressourcenverfügbarkeit) und regionaler (Landschaftskontext) Ebene in Abhängigkeit von den ökologischen Eigenschaften der betrachteten Taxa. Entsprechend sind unterschiedliche Reaktionen der Großgruppen (Wildbienen und Schwebfliegen), innerhalb von Großgruppen (Gattungen der Wildbienen) und innerhalb dominanter Arten (intraspezifisch) erkennbar.

Im Einzelnen werden folgende SPEZIELLE HYPOTHESEN getestet:

1. Der Landschaftskontext wirkt als Filter auf die Ausbreitungsfähigkeit der Taxa regionaler Artenpools und bestimmt damit über die Besiedlung die Gemeinschaftszusammensetzung innerhalb der Blühflächen.

2. Die Anzahl der Blühflächen steuert auf Landschaftsebene die *Konnektivität* von potenziellen Habitaten und kann als Managementoption adversen Landschaftseffekten entgegenwirken.

3. Mit dem Grad der Spezialisierung der Arten, die eine Blühfläche erreichen, erhöht sich die Bedeutung der Diversifizierung der *Ressourcenverfügbarkeit* auf lokaler Ebene.

UNTERSUCHUNGSREGION UND VERSUCHSDESIGN

Programme zur Förderung der Biodiversität in Agrarlandschaften werden in Deutschland auf Landesebene implementiert (Hartmann *et al.* 2003). Ein Beispiel hierfür ist das in Hessen zwischen 2007 und 2013 gelaufene **H**essische **I**ntegrierte **A**grarumwelt-**P**rogramm (HIAP), welches 2014 in das Hessische Programm für Agrarumwelt- und Landschaftspflege-Maßnahmen (HALM) überging (Regierungspräsidium Gießen 2020). Das Programm des Hessischen Ministeriums für Umwelt, Energie, Landwirtschaft und Verbraucherschutz bietet Landwirten einen finanziellen Ausgleich für zusätzliche Kosten oder Ertragsverzicht in Folge besonders umweltgerechter Landbewirtschaftung. Die Anlage der Blühflächen ist darin über einen Zeitraum von 5 Jahren festgelegt und soll zur Erhaltung und Förderung einer vielfältigen Flora und Fauna beitragen. Hierbei wird auf ehemals landwirtschaftlich genutzten Flächen einmalig eine standortangepasste Pflanzenmischung eingesät. Während der Vertragslaufzeit darf auf diesen Flächen, außer Bestellmaßnahmen, keine weitere Bearbeitung stattfinden, auch die Verwendung von Dünge- oder Pflanzenschutzmitteln ist verboten.

Die Untersuchungen zu Blühflächen und den verwendeten Blühmischungen innerhalb des HIAPs fanden in Mittelhessen statt. Während das Untersuchungsgebiet der Studien aus Kapitel II bis IV der Landkreis Marburg-Biedenkopf war, wurde der Saatgutversuch aus Kapitel V auf dem Versuchsgut „Oberer Hardthof“ der Justus-Liebig-Universität durchgeführt (Abb.1). Beide Landkreise liegen im gleichen Regierungsbezirk und unterstehen dem Regierungspräsidium Gießen, wodurch eine vergleichbare Entwicklung des ländlichen Raums gegeben ist. Indem sie dem gleichen Naturraum, dem Hessischen Bergland angehören, ist von einem ähnlichen Arteninventar auszugehen. Obwohl der Landkreis Marburg-Biedenkopf insgesamt stark landwirtschaftlich geprägt ist, variiert die Nutzungsintensität auf Landschaftsebene erheblich, so dass sich ein großräumiges Nutzungsmosaik aus intensiv bewirtschafteten Äckern, Wiesen, Weiden, Laub- und Nadelwäldern sowie Brachen in unterschiedlichen Sukzessionsstadien bildet. Zu Beginn der Studie im Jahr 2011 waren 229 Schläge als HIAP-Blühflächen unter Vertrag (davon wurden 35 Flächen im Jahr 2010 und 194 im Jahr 2011 angelegt) und lagen in Landschaftsausschnitten unterschiedlicher Nutzungsintensität. Anhand aktueller Nutzungsdaten, die durch eine Kooperation mit dem Amt für den ländlichen Raum des Landkreises Marburg-Biedenkopf zur Verfügung standen, wurden mit einem Geographischen Informationssystem (GIS) Landschaftssektoren mit einem Radius von 500 m um alle unter Vertrag stehenden Flächen gelegt und die Nutzungsanteile bestimmt. Aus der Gesamtmenge der 194 im Jahr 2011 neuangelegten Blühflächen wurden elf „isolierte“ und elf „vernetzte“ Blühflächen ähnlicher Größe ausgewählt, die jeweils einen Gradienten von 35 % bis 95 % Ackerland in ihrer Umgebung abbilden. Isolierte Flächen weisen keine weitere Blühfläche in einem Radius von 500 m auf. Vernetzte Blühflächen (Fokalflächen) hingegen weisen mindestens eine weitere Blühfläche (Satellitenfläche) in einem Radius von 500 m auf, wobei die zusätzliche Blühfläche in der Gesamtgröße konstant gehalten wurde.

Abb. 1: Lage der zwei Studienregionen in Hessen (hellgrau) bzw. Deutschland sowie der untersuchten Blühflächen (weiß) im Landkreis Marburg-Biedenkopf (dunkelgrau). Eine Detailansicht von je einer isolierten und verknüpften Blühflächen findet sich im Anhang III auf Seite 63.

KAPITELÜBERSICHT

Die folgenden Kapitel, die auf vier in international referierten Journalen publizierten Manuskripten basieren, verdeutlichen die Rolle von Blühflächen für blütenbesuchende Insekten. Sie sollen für ein besseres Verständnis der Funktionsweise ökologischer Prozesse sorgen, um mit deren Berücksichtigung die Umsetzung für einen effizienten Schutz ihrer Besucher zu optimieren.

Kapitel II: Blütenbesuchergemeinschaften – Much more than bees—Wildflower plantings support highly diverse flower-visitor communities from complex to structurally simple agricultural landscapes

Dieses Kapitel behandelt die Verschiebung der Blütenbesuchergemeinschaften auf 14 etablierten Blühflächen auf zeitlicher und räumlicher Ebene. Hierfür wurden zu einem frühen und späten Zeitpunkt der Blühsaison sämtliche Blütenbesucher dieser Blühflächen während Transektgängen erfasst. Die Blühflächen unterschieden sich sowohl im Grad der Vernetzung als auch der Komplexität der sie umgebenden Landschaft. Mit insgesamt 322 blütenbesuchender Insektenarten aus 32 Überfamilien konnte für die untersuchten Blühflächen ein großes Spektrum an Arten erfasst werden, welche die Blühflächen nutzen. Trotz der hohen Diversität an Blütenbesuchern scheinen die Blühflächen von den Zieltaxa wie Bienen und Schwebfliegen allgemein gut angenommen zu werden, denn rund 81 Arten und die Hälfte der Individuen fielen auf diese Gruppen. Dennoch stellten die Wildbienen abseits der Hummel nur rund 9 % der Bienen und lediglich 2,6 % der Gesamtindividuen. Starke zeitliche Unterschiede in der Gemeinschaftszusammensetzung zeigen dabei, dass vor allem Honigbienen vermehrt zum späten Zeitpunkt auf den Flächen beobachtet wurden, wenn andere Blütenressourcen in der Landschaft knapp sind. Die Landschaftskomplexität und die Konnektivität zu benachbarten Blühflächen wirkte sich vor allem auf Wildbienen positiv aus, während Schwebfliegen vermehrt auf isolierten Flächen zu finden waren. Für keine andere untersuchte Gruppe außer den Wildbienen konnte ein Effekt der Landschaft gefunden werden. Vielmehr scheinen Blühflächen in jeder Landschaft eine diverse und funktionell komplementäre Artengemeinschaft zu beherbergen. Hier zeigt sich das Potential von Blühflächen für ein breites Artenspektrum in der Agrarlandschaft, allerdings weniger für Wildbienen. Einige der hier profitierenden Generalisten, wie beispielsweise andere Fliegen als Schwebfliegen, könnten dabei besonders in einfachen Landschaften ökosystemare Dienstleistungen aufrechterhalten, in denen entsprechende Spezialisten bereits verschwunden sind.

Kapitel III: Blühflächen im Landschaftskontext – Spatial configuration and landscape context of flowering fields determine their benefits to pollinator α- and β-diversity

Dieses Kapitel untersucht wie der Landschaftskontext und die Konfiguration von Blühflächen deren Besiedlung durch und die Dynamiken innerhalb der Blütenbesuchergemeinschaften beeinflussen und ob die vermehrte Anlage von funktionell verknüpften Blühflächen einen Mehrwert für die Effizienz dieser Maßnahme liefert. Hierfür wurden auf 33 neu angelegten Blühflächen unterschiedlichen Vernetzungsgrades über einen Zeitraum von drei Jahren Wildbienen und Schwebfliegen mit gelben Farbschalen in Agrarlandschaften entlang eines Komplexitätsgradienten im Landkreis Marburg-Biedenkopf erfasst. Insgesamt konnten mehr als ein Viertel der regionalen Wildbienen und Schwebfliegen nachgewiesen werden, wobei Wildbienen, anders als Schwebfliegen, eine deutliche Reaktion auf die Landschaft zeigten. Während die Alpha-Diversität auf isolierten Flächen mit dem Anteil an umgebenden naturnahen Habitaten anstieg, konnte für verknüpfte Flächen das gegenteilige Muster beobachtet werden. Eine um 50 % höhere Alpha-Diversität auf verknüpften im Vergleich zu isolierten Flächen in einfachen Landschaften lässt auf einen Konzentrationseffekt und bessere Erreichbarkeit durch die stärkere Vernetzung mit anderen Teilhabitaten durch die höhere Anzahl an Blühflächen schließen. Die sinkende Alpha-Diversität auf verknüpften Flächen als Folge der steigenden Landschaftskomplexität lässt hingegen auf einen Verdünnungseffekt und eine Aufspaltung der Artengemeinschaften zwischen den vermehrt verfügbaren Blühflächen schließen. Diese Interpretation wird durch den Vergleich der Gemeinschaftszusammensetzung (gemessen als Beta-Diversität) zwischen benachbarten Blühflächen gestützt. So wurden die Gemeinschaften der Flächen sich unähnlicher, je komplexer das Pflanzenspektrum auf und die Landschaft um die Blühflächen wurde. Die Betrachtung der Gemeinschaften über die Zeit zeigte zudem, dass wir, anders als erwartet, keinen Zuwachs innerhalb der Gemeinschaften nachweisen konnten, sondern sich vielmehr die Gemeinschaftszusammensetzungen über den gesamten Zeitraum sehr dynamisch als Resultat der voranschreitenden Sukzession der Flächen verändert haben. Die Ergebnisse dieses Kapitels zeigen, dass die Anlage mehrerer Blühflächen die Vernetzung mit bestehenden Teillebensräumen fördert und zur Entspannung der Nahrungskonkurrenz beitragen kann. Gleichzeitig eröffnen an die Landschaft angepasste Managementstrategien die Möglichkeiten zur Optimierung von Blühflächen, zeigen aber auch, dass eine einheitliche Empfehlung zur Anlage dieser wenig zielführend ist.

Kapitel IV: Intraspezifische Körpergröße – Intraspecific body size increases with habitat fragmentation in wild bee pollinators.

In Kapitel II konnte gezeigt werden, wie die Vereinheitlichung und Fragmentierung der Landschaft die Blütenbesuchergemeinschaften auf Blühflächen von Habitatspezialisten hin zu Generalisten verschieben kann. Diese Verschiebung ist häufig auch mit einer Verschiebung hin zu größeren Arten verbunden, welche die Distanzen zwischen Habitatfragmenten leichter überwinden können. Dieses Kapitel untersucht, inwieweit dieser Landschaftsfilter auch auf innerartlicher Ebene greift und deren möglichen ökologischen Folgen. Hierfür wurde die Intertegular Distanz (ITD) von Individuen der vier häufigsten Sandbienenarten der 22 zentralen Blühflächen aus Kapitel III (Studie 2) vermessen sowie die Pollenhöschen der häufigsten Art *Andrena flavipes* PANZER (Hymenoptera: Apoidea) untersucht. Es zeigt sich, dass in den lokalen Populationen die Körpergröße der beiden mittelgroßen Arten mit dem Grad der Fragmentierung ansteigt, was auf eine innerartliche Selektion hinweist, die ein größeres Ausbreitungsvermögen begünstigt. Die Pollenanalyse verdeutlicht zudem, dass diese Größenverschiebung auch die ökologischen Funktionen verschieben kann, denn die größeren Individuen einer Population sammelten Pollen von einem deutlich geringeren Pflanzenspektrum als die kleineren Individuen. Diese Ergebnisse legen nahe, dass die Vereinheitlichung und Fragmentierung der Landschaft die Bestäubungsleistung verändern kann, auch ohne den Artenreichtum oder die Komposition erkennbar zu beeinflussen.

Kapitel V: Blühmischungen der HIAP Flächen – Attractiveness of wild-flower mixtures for wild bees and hoverflies depends on some key plant species.

Dieses Kapitel untersucht vier unterschiedlich zusammengesetzte Blühmischungen innerhalb des Hessischen Intergrierten Agrarumweltprogrammes (HIAP) (drei am häufigsten verwendeten der Region und eine besonders artenreiche) auf ihre Attraktivität für Wildbienen und Schwebfliegen. Für das Experiment wurden auf dem Versuchsgut Oberer Hardthof in Gießen in einem randomisierten Blockdesign 28 Versuchsblöcke angelegt und diese mit Kescherfängen über zwei aufeinanderfolgende Jahre beprobt. Über alle Mischungen hinweg konnten insgesamt 94 Pflanzenarten nachgewiesen und für 41 dieser Pflanzen mindestens ein Besuch registriert werden. Anhand der insgesamt 1.835 Blütenbesuchsinteraktionen konnten 14 Schlüssel Pflanzenarten identifiziert werden, die ausreichten, um die gesamte blütenbesuchende Wildbienen- und Schwebfliegengemeinschaft abzudecken. Vielmehr noch unterstützten bereits die Top vier Pflanzenarten 80 % dieser Blütenbesucher. Obwohl sich die Attraktivität der Blühmischungen sowohl auf Plot-Ebene als auch zwischen den untersuchten Gruppen unterschied, war das Vorhandensein der Schlüsselpflanzen deutlich wichtiger als die Pflanzendiversität an sich. Das Kapitel macht deutlich, dass die häufigen Genrealisten unter den Blütenbesuchern bereits mit einfachen Blühmischungen angesprochen werden können. Die Tatsache, dass in den Versuchsplots seltene und spezialisierte Arten jedoch überwiegend fehlten, sowie die gegenteilige Resonanz der beiden untersuchten Gruppen, lässt Spielraum für die weitere Optimierung maßgeschneiderter Mischungen. Gleichzeitig verdeutlicht es, dass neben Nahrungsressourcen auch andere Habitatelemente auf Landschaftsebene das Vorkommen dieser Arten in der Agrarlandschaft beeinflussen und steht somit im Einklang mit den vorherigen Kapiteln.

KAPITEL II –BLÜTENBESUCHERGEMEINSCHAFTEN

MUCH MORE THAN BEES – WILDFLOWER PLANTINGS SUPPORT HIGHLY DIVERSE FLOWER-VISITOR COMMUNITIES FROM COMPLEX TO STRUCTURALLY SIMPLE AGRICULTURAL LANDSCAPES

Ingo Grass, Jörg Albrecht, Frank Jauker, Tim Diekötter, Daniela Warzecha, Volkmar Wolters, Nina Farwig

Erschienen 2016 in *Agriculture, Ecosystems & Environment* 225: 45–53

Agriculture, Ecosystems and Environment 225 (2016) 45–53

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Much more than bees—Wildflower plantings support highly diverse flower-visitor communities from complex to structurally simple agricultural landscapes

Ingo Grass[a,b,*], Jörg Albrecht[c,b], Frank Jauker[d], Tim Diekötter[d,e], Daniela Warzecha[d], Volkmar Wolters[d], Nina Farwig[b]

[a] *Agroecology, Department of Crop Sciences, University of Göttingen, Göttingen, Germany*
[b] *Conservation Ecology, Faculty of Biology, University of Marburg, Marburg, Germany*
[c] *Institute of Nature Conservation, Polish Academy of Sciences, Krakow, Poland*
[d] *Department of Animal Ecology, Justus Liebig University, Giessen, Germany*
[e] *Department of Landscape Ecology, Kiel University, Kiel, Germany*

ARTICLE INFO

Article history:
Received 20 November 2015
Received in revised form 17 March 2016
Accepted 4 April 2016
Available online xxx

Keywords:
Agri-environment scheme (AES)
Ecosystem services
Flower resources
Landscape
Farmland biodiversity
Restoration

ABSTRACT

One goal of wildflower plantings is to promote biodiversity in intensively managed agricultural landscapes. Flower visitors of wildflower plantings encompass many ecologically and economically important species. However, most studies on flower visitors of wildflower plantings have focused on single or few prominent taxa (e.g., wild bees and hoverflies). In contrast, it remains largely unresolved how non-prominent flower visitors of the community are affected by wildflower resources, landscape context and time of the flowering season. We studied highly diverse flower-visitor communities on 14 wildflower plantings varying in flower abundance and richness and their surrounding landscape context within a 500 m radius (percentage arable land, presence of additional wildflower plantings). Flower visitors were sampled in the early (May–June) and late (June–July) flowering season and grouped as follows: managed honeybees, wild bees, hoverflies, all other flower visitors. Strikingly, only 81 (25.1%) of all 322 visiting species (<50.0% of individuals) were bees or hoverflies, and 241 non-prominent 'other' visitor taxa were sampled, encompassing many ecologically and economically important species, e.g., parasitic wasps and non-syrphid Diptera. With the exception of honeybee abundance that was positively related to flower abundance, flower abundance and richness of wildflower plantings affected neither abundance nor richness of any visitor group. While a high amount of surrounding arable land decreased species richness of wild bees, richness of all other groups was unaffected. In contrast to the relatively weak abundance and richness responses at the group-level, we found strong species-specific responses to landscape context, resulting in substantial spatial and temporal turnover in community composition. In the early flowering season, wildflower plantings that were accompanied by additional local plantings and embedded within complex landscapes supported the highest abundances of habitat specialists (e.g. *Bombus* spp.), whereas isolated plantings were predominantly visited by agricultural generalists (e.g. predatory hoverflies and pollen beetles). These compositional differences diminished towards the end of the flowering season. Our study highlights the great conservation potential of wildflower plantings in agricultural landscapes. With the exception of wild bees, wildflower plantings support a high diversity of functionally complementary flower-visitor species from complex to structurally simple agricultural landscapes. These so-far overlooked flower visitors may have the potential to provide complementary ecosystem services and to step-in in agricultural settings where prominent providers have been lost. Assessments of the value of wildflower plantings to biodiversity conservation and agriculture require a shift away from solely focusing on prominent taxa and towards a more holistic appreciation of the entire flower-visitor community.

---

* Corresponding author at: Agroecology, Department of Crop Sciences, University of Göttingen, Göttingen, Germany.
E-mail addresses: ingo.grass@agr.uni-goettingen.de (I. Grass), albrecht@iop.krakow.pl (J. Albrecht), frank.jauker@allzool.bio.uni-giessen.de (F. Jauker), tdiekoetter@ecology.uni-kiel.de (T. Diekötter), daniela.warzecha@allzool.bio.uni-giessen.de (D. Warzecha), volkmar.wolters@allzool.bio.uni-giessen.de (V. Wolters), farwig@staff.uni-marburg.de (N. Farwig).

http://dx.doi.org/10.1016/j.agee.2016.04.001
0167-8809/

1. Introduction

Agricultural intensification is a major threat to global biodiversity (Foley et al., 2005; Sala et al., 2000). The ongoing conversion of heterogeneous landscapes into human-dominated land goes along with the loss of natural and semi-natural habitats and thus resources that are crucial for the persistence of many taxa (Goulson et al., 2015). As a countermeasure, agri-environmental schemes (AES) have been implemented in numerous European countries to maintain and restore biodiversity in agricultural landscapes (Batáry et al., 2011; Kleijn et al., 2006). Although AES target overall biodiversity, a major focus is on pollinators because they can increase yields of adjacent pollinator-dependent crops and return the initial AES establishment costs (Blaauw and Isaacs, 2014b; Garibaldi et al., 2014; Scheper et al., 2015). Accordingly, knowledge of the effectiveness of AES for prominent pollinator groups such as wild bees or hoverflies is increasing (e.g., Carvell et al., 2011; Korpela et al., 2013; Scheper et al., 2015). However, we still know little about whether AES also benefit flower-visiting insects besides these prominent taxa, even though these 'other' flower visitors may represent a much larger share of biodiversity and constitute important ecosystem service providers (e.g., Rader et al., 2016).

The composition of flower visitors on wildflower plantings depends on drivers acting at multiple spatial and temporal scales. At the local scale, the abundance and species richness of flowering plants is most important (Blaauw and Isaacs, 2014a; Scheper et al., 2013). At the landscape scale, the availability of permanent semi-natural habitats is important, because flower visitors generally depend on resources in multiple elements for nesting and foraging (Jauker et al., 2013; Tscharntke et al., 2005). Whether the effects of multiple locally connected wildflower plantings on flower-visitor communities are comparable to those of natural or semi-natural habitats is, however, unknown. Finally, the role of wildflower plantings for flower visitors can change during the flowering season. In the early season, mass-flowering crops can provide highly abundant resources to many flower-visiting species (Riedinger et al., 2015) potentially reducing the importance of wildflower plantings. This pattern could be reversed in the late flowering season when mass-flowering has ceased, yet plantings continue to provide floral resources. Importantly, our knowledge about the importance of these spatial and temporal drivers of the assembly of flower-visitor communities on wildflower plantings is mainly limited to the prominent flower-visitor taxa of wild bees, hoverflies and occasionally butterflies (see e.g., Carvell et al., 2011; Korpela et al., 2013; Scheper et al., 2013, 2015). In contrast, the effects of these drivers for the remaining community of non-prominent flower visitors remains poorly understood.

Here we studied highly diverse flower-visitor communities on 14 wildflower plantings three years after planting establishment. These plantings differed in the abundance and richness of floral resources and the landscape context within a 500 m radius (proportional cover of arable land, presence of other wildflower plantings). We sampled flower visitors early (May–June) and late (June–July) in the flowering season to address the following research questions: First, how large is the proportion of non-prominent flower visitors (i.e., non-bee and non-hoverfly visitors) within the entire flower-visitor community? Second, do non-prominent flower visitors differ from bees and hoverflies in their responses to local, landscape and seasonal effects? Third, how does the overall composition of flower-visitor communities change with local and landscape effects and between the early and late flowering season?

2. Materials and methods

2.1. Study design

We conducted our study in an agricultural area with an extent of approximately 30 km × 25 km in the district Marburg-Biedenkopf, Hesse, central Germany. Forest and grassland make up the predominant semi-natural habitat types in the region. Arable land is dominated by monocultures of wheat, barley, maize and oilseed rape. Between 2010 and 2013 a total of 406 wildflower plantings were established in the district as part of an AES aiming at more sustainable land use and restoration of biodiversity and ecosystem functioning in agricultural landscapes (HIAP 'Hessisches Integriertes Agrarumweltprogramm'—'Hessian integrated agri-environmental program'). As part of HIAP, local farmers were contracted by the state of Hesse for 5 years for the establishment of wildflower plantings on previously cultivated arable land, receiving a compensation of 600 € ha^{-1} $year^{-1}$ (Table A.1 for details on the used wildflower seed mixtures). After establishment all plantings were set aside (no mowing, weeding, etc.) allowing for an undisturbed colonization by species from the regional species pool and a natural succession of plant and flower-visitor communities over the following years. Reaching equilibrium in flower-visitor communities may take several years (Blaauw and Isaacs, 2014b). Thus, we delayed our sampling of flower visitors for three years.

In 2014, we selected 14 of the wildflower plantings established in 2011 (see Table A.2 for site characteristics). Their area ranged from 2278 m^2 to 5027 m^2 (3160 m^2 ± 692 m^2; mean ± SD throughout) and pairwise distances between their centroids ranged from 1.1 km to 30 km (15 km ± 8.2 km). To assess the effects of varying landscape context on flower visitors, the 14 plantings were situated along a landscape-complexity gradient, as measured by the proportion of surrounding arable land in a 500 m radius (Gathmann and Tscharntke, 2002) (range: 25–82% [49% ± 18%]; GIS landcover data from 2013 based on InVeKoS data, ALKIS data and manual mapping of seminatural structures in the field; ground-truthed in 2014). Furthermore, we were interested in whether the establishment of multiple locally connected wildflower plantings results in similar flower-visitor communities as that of single, isolated plantings. Thus, the 14 wildflower plantings were also chosen with respect to the presence of other, smaller wildflower plantings (which were not part of the visitor surveys) within the 500 m radius. We included this information as a binary variable 'presence of additional plantings' with levels 'yes' (at least one more planting present; $n = 8$) or 'no' (no other planting present; $n = 6$). The percentage of surrounding arable land and the presence of other plantings did not co-vary systematically (ANOVA: $F_{1,12} = 0.90$, $P = 0.361$).

We sampled flower visitors between May and July 2014 along two permanent transects of 50 m length and 1 m width established at the edge of each planting. Before a sampling survey, we assessed the abundance and species richness of the flowering plant community of a given transect ("flower abundance" and "flower richness" in the following). We recorded the flower abundance in floral units. Depending on plant family, a floral unit is a single flower or a collection of flowers that an averaged-sized flower visitor covers by walking and without flying (Dicks et al., 2002). Afterwards, two persons simultaneously sampled flower visitors, with one person per transect. During a period of 30 min, each observer slowly walked up and down her 50 m transect and sampled all insect visitors that contacted floral sexual organs of plants with a sweep net, and subsequently killed these with ethyl acetate in a killing jar. Following the 30 min, the observers immediately switched transects, and another 30 min sampling round took place. Thus, on a given survey day each of the 50 m transects was sampled for 1 h in total. Surveys were repeated four times on each wildflower planting during the study period (1 h × 2 transects × 4 surveys × 14 plantings = 112 h sampling in total). All surveys were carried out between 09:30 and 17:00 h on dry and warm days (>15 °C) with low wind speeds. The first two surveys took place between 16th May and 15th June ('early' flowering season), and the latter two between 16th June and 7th July ('late' flowering season). We pooled the data from the two surveys within each season for analyses. We identified 75% of all flower visitors to species level, 85% to genus level and 97% to family level (for simplicity, we refer to morphospecies as species; Table A.3).

Bees (Hymenoptera: Apidae) and hoverflies (Diptera: Syrphidae) are the most frequently studied flower visitors of wildflower plantings, and have been repeatedly emphasized as being among the most important pollinators of many wild and crop plants (Garibaldi et al., 2014; Jauker et al., 2012a; Potts et al., 2010). Thus, we also focussed on these important pollinator groups to evaluate similarities in their responses with those of the remaining flower-visitor community. In addition, we separated honeybees (*Apis mellifera*) from wild bees. As no natural populations of *A. mellifera* exist in our study region all recorded individuals stemmed from apiaries. Consequently, we differentiated between four flower-visitor groups: (1) *A. mellifera*, (2) wild bees, (3) hoverflies and (4) all 'other' non-prominent flower visitors.

2.2. Statistical analyses

2.2.1. Local, landscape and seasonal effects on abundance and richness of flower visitors

We used generalized linear mixed effects models to analyze variation in the abundance and richness of *A. mellifera*, wild bees, hoverflies and all other flower visitors among study sites, respectively. We fitted the same model structure for each response variable, with flower abundance (ln-transformed) and richness of the wildflower plantings, the proportion of surrounding arable land, the presence of additional plantings and season (early vs. late) as fixed effects. We detected no multicollinearity for any of the variable combinations. Study site was included as a random effect to account for the non-independence of the two sampling rounds (early and late flowering season). For all models with abundance as response, we used a negative-binomial distribution with a log-link function to account for overdispersion in the data (Zuur et al., 2009). The models with species richness as response did not show any overdispersion and were fitted using a Poisson distribution, again using a log-link. In all models, the numerical predictors were scaled to zero mean and unit variance to allow for comparison of effect sizes.

2.2.2. Local, landscape and seasonal effects on community composition of flower visitors

In addition to abundance and richness of flower visitors, we analyzed variation in the composition of flower-visitor communities across wildflower plantings and the flowering season. First, we visualized the overall variation in community composition. We assembled one site × species abundance matrix, with sites replicated for the early and late flowering season (28 × 322 entries). Then we Hellinger-transformed this matrix, calculated Bray-Curtis distances between pairs of study sites and plotted a two-dimensional ordination of a non-metric dimensional scaling (NMDS) analysis of the distance matrix.

Second, we used a model-based approach based on multivariate generalized linear models to assess environmental drivers of the variation in community composition across wildflower plantings (Wang et al., 2012). These models do not require a normal distribution of the response variable or a reduction in the multi-dimensionality of community composition data (as is the case when fitting environmental variables on a two-dimensional ordination such as from NMDS). Thus, they are ideally suited to model multivariate abundance data (Wang et al., 2012). These models, however, cannot accommodate multi-level designs (e.g. repeated sampling as in this study). Thus, we assembled two site × species abundance matrices, one for the early and one for late flowering season, respectively, and fitted a model to each. Predictors were the flower abundance (ln-transformed) and richness of wildflower plantings, the proportion of surrounding arable land and the presence of additional plantings. The models were fitted using a negative-binomial error distribution, and significance of predictors was assessed using analysis of deviance based on likelihood ratio tests.

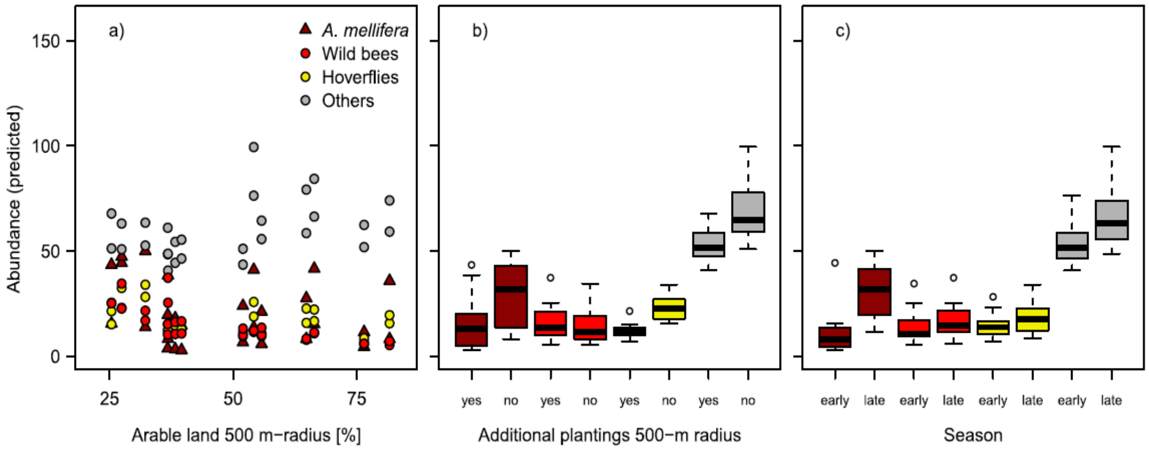


Fig. 1. Abundance of flower visitor groups as a function of (a) the proportion of arable land surrounding wildflower plantings, (b) the presence of additional plantings (yes or no) and (c) time of the flowering season (early or late). Shown are predicted values from generalized linear mixed effects models.

Table 1
Generalized linear mixed-effects models showing the effects of local flower resources (flower abundance and richness of wildflower plantings), landscape context (arable land in 500 m radius and presence of additional plantings) and time of season on the abundance (a) and species richness (b) of flower-visitor groups (*Apis mellifera*, wild bees, hoverflies, all other flower visitors) on the 14 wildflower plantings. Significant predictors ($P < 0.05$) are shown in bold.

	Apis mellifera			Wild bees			Hoverflies			Others		
	Estimate	Z	P	Estimate	Z	P	Estimate	Z	P	Estimate	Z	P
(a) *Response: abundance*												
(Intercept)	1.97	5.38	<0.001	2.54	10.32	<0.001	2.29	11.13	<0.001	3.87	32.92	<0.001
Flower abundance	**0.46**	**2.14**	**0.033**	0.26	1.89	0.058	−0.07	−0.46	0.642	−0.02	−0.18	0.857
Flower richness	0.12	0.97	0.331	−0.03	−0.21	0.834	0.09	0.71	0.480	0.07	0.97	0.330
Arable land	−0.02	−0.09	0.926	−0.34	−1.95	0.051	−0.24	−1.74	0.082	0.05	0.63	0.530
Additional plantings present (yes vs. no)	0.41	1.22	0.221	−0.14	−0.42	0.673	**0.80**	**2.94**	**0.003**	0.23	1.38	0.168
Season (early vs. late)	**1.16**	**3.57**	**<0.001**	0.17	0.73	0.464	0.20	0.91	0.364	0.19	1.77	0.077
(b) *Response: species richness*												
(Intercept)				1.38	7.99	<0.001	1.48	9.81	<0.001	3.24	47.58	<0.001
Flower abundance				0.10	0.85	0.394	0.10	0.95	0.343	0.07	1.43	0.152
Flower richness				−0.04	−0.43	0.666	0.10	1.20	0.232	0.03	0.77	0.441
Arable land				**−0.32**	**−2.60**	**0.010**	−0.03	−0.33	0.739	−0.02	−0.60	0.550
Additional plantings present (yes vs. no)				0.39	1.64	0.100	**0.42**	**2.12**	**0.034**	0.06	0.66	0.512
Season (early vs. late)				−0.18	−1.03	0.303	0.07	0.45	0.655	**−0.22**	**−2.81**	**0.005**

2.2.3. Modelling species-specific responses to landscape context and season

Finally, we predicted non-linear changes in the dominance structure of flower visitors in response to landscape context and time of the flowering season. To this end, we modeled changes in the relative abundances of the 10 most abundant flower-visitor species in the early (representing 44% of all visitors) and late (69%) flowering season, respectively. We used multinomial models with abundances as response and the interaction of surrounding arable land and presence of additional plantings as fixed effects. By including this interaction, we investigated whether the effects of establishing multiple locally connected plantings on flower visitors depended on the surrounding arable land cover. We fitted our multinomial models using function 'manyglm' in package *mvabund*; this function fits a separate generalized linear model to each species in the abundance matrix. We calculated the statistical significance of predictors (and interactions) using likelihood ratio tests comparing models with and without the predictor (interaction) of interest.

All analyses were done in *R* version 3.2.1 (R Development Core Team, 2015), using packages ***lme4*** (Bates et al., 2015), ***glmmADMB*** (Skaug et al., 2016), ***vegan*** (Oksanen et al., 2015), ***mvabund*** (Wang et al., 2015) and ***nnet*** (Venables and Ripley, 2002).

3. Results

From May–July 2014, we recorded 76 flowering plant species along transects of the 14 wildflower plantings (range: 12–38; 21 ± 6; mean ± SD; no significant difference in flower abundance or richness between the early and late flowering season; Table A.3). On 49 of these plant species, we recorded a total of 3165 flower visitors belonging to 322 species (Table A.4). Divided into the above-described flower-visitor groups, these were 588 individuals of *A. mellifera*, 427 individuals representing 41 wild bee species and 470 individuals of 39 hoverfly species. The fourth group – other flower visitors, which were not bees or hoverflies – comprised more than half of all observed individuals (1680 individuals; 53.1%) and a total of 241 species (74.8% of all species) (Fig. A.1). These non-prominent flower visitors comprised nine insect orders, with most species belonging to non-syrphid Diptera (43.5%), non-bee Hymenoptera (15.9%), Coleoptera (15.4%) and Lepidoptera (9.8%) (Fig. A.1).

3.1. Local, landscape and seasonal effects on abundance and richness of flower visitors

Abundance and species richness responses to local resources, landscape context and time of the flowering season differed substantially among the four flower-visitor groups (Fig. 1). Abundance of *A. mellifera* increased with flower abundance and was higher in the late flowering season, but was not related to landscape context (Table 1a; Fig. 1). Abundance of wild bees tended to increase with flower abundance ($P = 0.058$). In addition, there was a marginally negative effect of the proportion of arable land surrounding wildflower plantings on wild bee abundance (Table 1a; Fig. 1a). Hoverfly abundance was not affected by arable land; however, abundances were higher on isolated plantings as compared to those with other plantings in their surroundings (Fig. 1b). The abundance of the remaining flower-visitor community was neither related to variation in landscape context nor to the flower abundance or richness on wildflower plantings (Table 1a).

Neither flower abundance nor richness on the wildflower plantings affected the species richness of any of the flower-visitor groups (Table 1b). However, species richness responses to landscape context and time of the flowering season differed among visitor groups (Fig. 2). Richness of wild bees decreased with increasing amount of arable land in the landscape surroundings (Table 1b; Fig. 2a). Hoverfly richness was not affected by arable land, however, it was higher when no additional plantings were present (Table 1b; Fig. 2b). Landscape context did not affect the species richness of non-prominent flower visitors (Table 1b). While the species richness of wild bees and hoverflies did not vary between the two surveys, the richness of the remaining flower-visitor community was lower in the late as compared to the early flowering season (Table 1b; Fig. 2c).

3.2. Local, landscape and seasonal effects on flower-visitor community composition

Community composition of flower visitors varied considerably with local resources, landscape context and time of the flowering season (Table 2a and b; Fig. 3a). Multivariate generalized linear models indicated strong effects of flower abundance and richness as well as arable land and presence of additional plantings on community composition in the early and late flowering season (Table 2a and b). The variation in flower visitor composition with landscape context and season was also apparent in the two-dimensional ordination of the NMDS analysis (stress: 0.21):

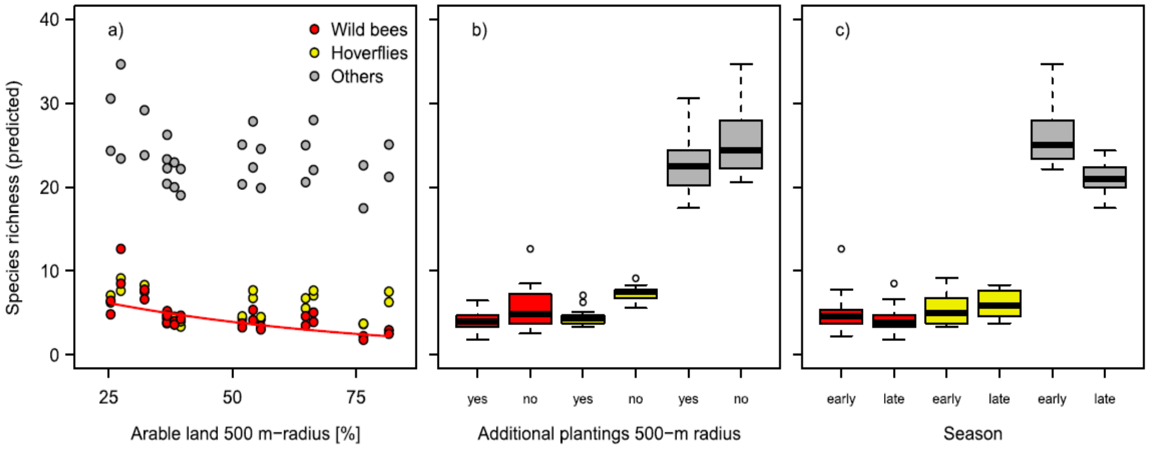


Fig. 2. Species richness of flower visitor groups as a function of (a) the proportion of arable land surrounding wildflower plantings, (b) the presence of additional plantings (yes or no) and (c) time of the flowering season (early or late). Shown are predicted values from generalized linear mixed effects models. The red line in (a) shows the predicted effect of arable land on the richness of wild bees, which was the only flower visitor group to respond to arable land. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

wildflower plantings formed two distinct groups associated with the early and late flowering season (Fig. 3a). Moreover, in the early season but not in the late season, isolated plantings grouped separately from those where at least one other planting was present (Fig. 3a). The most abundant flower visitor species clustered close to the site scores of wildflower plantings of the late flowering season (Fig. 3b).

3.3. Modelling species-specific responses to landscape context and season

Changes in the composition of flower-visitor communities also showed when focussing on the dominance structure of the 10 most abundant species in the early and late flowering season, respectively (Fig. 4). Changes in species' relative abundance resulted from the combined effects of the presence of additional plantings, surrounding arable land and time of season. *A. mellifera* peaked in isolated sites with low influence of arable land in the early flowering season (Fig. 4a); this dominance levelled off in the late season (Fig. 4c). On isolated plantings, the hoverfly *Sphaerophoria* sp. and the pollen beetle *Brassicogethes aeneus* reached high dominance with high proportion of arable land (Fig. 4a). In contrast, wild bees (e.g. *Bombus lapidarius*,*B. terrestris* agg.) reached their highest relative abundance given the presence of other plantings and a low proportion of arable land (Fig. 4b and d); this pattern was particularly pronounced in the early season (Fig. 4b). The presence of additional plantings also benefited the pollen-feeding beetles *Oedemera nobilis* and *Oedemera* sp. and shifted the attraction of *Empis opaca* towards simple landscapes (Fig. 4b).

Table 2
Summary of analysis of deviance (ikelihood ratio test) on multivariate generalized linear model fits with the community composition of flower visitors in (a) the early and (b) late flowering season as response.

Source of variation	Df.diff	Dev	Pr(>Dev)
(a) *Early season—Flower visitors*			
Flower abundance	1	408.3	0.021
Flower richness	1	281.7	0.082
Arable land	1	440.9	0.002
Additional plantings present (yes vs. no)	1	330.8	0.006
(b) *Late season—Flower visitors*			
Flower abundance	1	279.4	0.020
Flower richness	1	222.8	0.034
Arable land	1	230.3	0.017
Additional plantings present (yes vs. no)	1	221.9	0.001

4. Discussion

We found that wildflower plantings support highly diverse flower-visitor communities, encompassing many species that are traditionally outside the focus of conservation measures. The landscape context was of particular importance in structuring these communities. Thereby, landscape effects on well-studied flower-visitor groups (wild bees, hoverflies) were often distinct from effects on non-prominent flower visitors, indicating little transferability from previous studies to so far neglected visitor taxa. Moreover, the community composition changed in the course of the flowering season, which at the species-level again was mediated by the landscape context.

4.1. Harnessing the high biodiversity value of wildflower plantings

In many European countries, wildflower plantings are being implemented as part of agri-environmental schemes to balance the negative effects of intensified agriculture on the environment. Flower-visiting taxa are a main target of wildflower plantings, however, most scientific work so far has focussed on wild bees or hoverflies (e.g., Blaauw and Isaacs, 2014a, 2014b; Garibaldi et al., 2014; Scheper et al., 2013). Here we show that wildflower plantings support not only these prominent groups but also a considerably large number of other flower-visiting species. In fact, over half of all flower-visiting individuals and 74% of all species recorded in this study were neither bees nor hoverflies.

Bees and hoverflies are prominent ecosystem-service providers in agricultural landscapes (Tenhumberg and Poehling, 1995; Jauker et al., 2009; Blaauw and Isaacs, 2014b). However, non-bee or non-hoverfly taxa may provide similar and even complementary ecosystem services. Recently, non-syrphid Diptera have been highlighted as important pollinators of wild and crop plants (Orford et al., 2015). Non-syrphid Diptera made up 43.5% of all

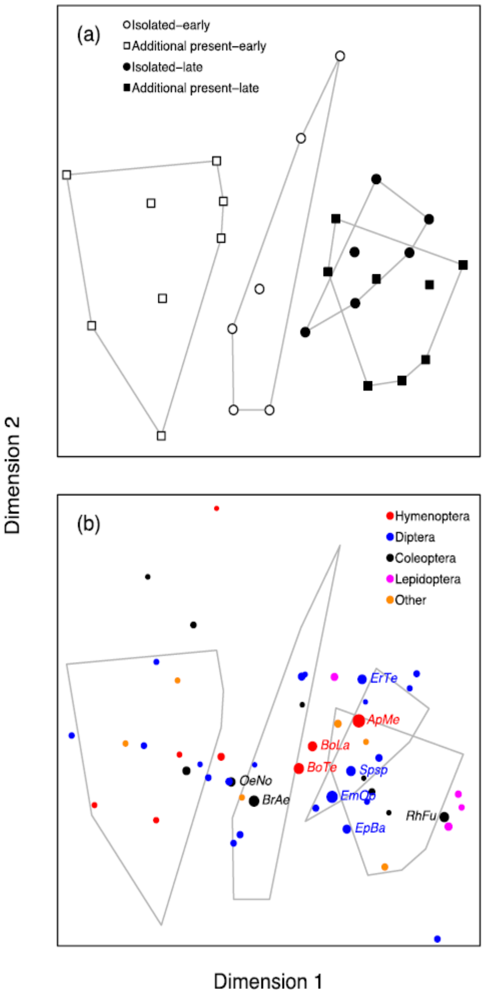


Fig. 3. Changes in the composition of flower-visitor communities on the 14 wildflower plantings. Shown are (a) compositional differences among the 14 wildflower plantings for the early (open symbols) and late (closed symbol) flowering season, as well as on isolated plantings (circles) and those were additional plantings were present in a 500-m radius (squares). Hulls (polygon shapes) indicate treatments of plantings. Species scores (coloured circles) visualize (b) the 50 overall most abundant flower-visitor species, with symbol size proportional to species abundance. The same hulls as in (a) are shown in (b) to indicate associations between species and treatments. Scientific names (abbreviated) of the 10 most abundant flower visitors: ApMe = *Apis mellifera* (588 individuals) EmOp = *Empis opaca* (303), BrAe = *Brassicogethes aeneus* (189), BoTe = *Bombus terrestris* agg. (177), RhFu = *Rhagonycha fulva* (113), Spsp = *Sphaerophoria* sp. (110), BoLa = *Bombus lapidarius* (99), ErTe = *Eristalis tenax* (90), OeNo = *Oedemera nobilis* (71), EpBa = *Episyrphus balteatus* (60).

'other' flower visitor species on our wildflower plantings (Fig. S1). The pollen-loads of these flies are often comparable to those of hoverflies (Orford et al., 2015). In addition, non-syrphid Diptera encompass important predators of crop pests (Scatophagidae, Dolichopodidae, Empididae; Holland et al., 2008), and contribute to decomposition and nutrient cycling (Farwig et al., 2014). Hymenoptera other than bees made up the second most species-rich group of flower visitors. These included in particular parasitoids (Braconidae; Ichneumonidae), which can be important for biocontrol of some crop pests (Thies and Tscharntke, 1999; Pfiffner et al., 2009). Due to the difficulty in identifying the hugely diverse group of these and other non-prominent flower-visitor taxa to species level, our estimates of their species richness are likely very conservative. We suggest that this neglected part of flower-visitor communities needs to receive more attention when debating the role of wildflower plantings for biodiversity conservation and ecosystem services in agricultural landscapes.

4.2. Local and landscape effects on flower-visitor communities

Scarcity of floral resources is the predominant driver of pollinator loss following land-use intensification (Roulston and Goodell, 2011; Scheper et al., 2014). Hence, wildflower plantings could help to slow down pollinator declines and maintain pollination services in agricultural landscapes (Garibaldi et al., 2014; Kremen et al., 2002). Interestingly, we found only weak effects of flower abundance and flower richness of the wildflower plantings on the abundance and richness of visitors in our study. In fact, only *A. mellifera* increased in abundance with higher flower abundance. The richness of flowering species on the wildflower plantings in our study ranged from 12 to 38. Thus, our study indicates that wildflower plantings are consistently attractive to functionally different flower-visiting taxa, even when flower abundance or richness are comparatively low.

Theory predicts that besides local resource availability the structure of the surrounding landscape determines AES effects on biodiversity (Batáry et al., 2011). An increasing number of empirical studies are corroborating this prediction; however, these are often limited to prominent flower-visitor groups such as wild bees, hoverflies or butterflies (e.g., Carvell et al., 2011; Korpela et al., 2013; Scheper et al., 2015). A comparison to non-prominent other flower visitors is often missing. We found that the proportion of arable land surrounding wildflower plantings negatively affects the species richness of wild bees. Moreover, plantings attracted higher richness of hoverflies when no additional plantings were present, which may be explained by concentration effects resulting from their ecological contrast to the agricultural matrix (Scheper et al., 2013). However, we did not find similar effects of landscape context on the species richness of non-bee and non-hoverfly visitors indicating that wildflower plantings support a constantly high-diversity of 'other' flower visitors in any agricultural context.

While the overall richness of non-prominent taxa was relatively constant, the composition of flower-visitor communities showed strong shifts with landscape context. Land-use intensification usually increases the dominance of habitat and resource generalists at the expense of specialists, resulting in the functional homogenization of flower-visitor communities (Grass et al., 2014, 2013; Winfree et al., 2009). We similarly found substantial turnover in the dominance structure of flower-visitor communities that can be explained by interspecific differences in habitat and resource use. For instance, on isolated plantings, *Sphaerophoria* sp. and *B. aeneus* thrived in simple landscapes. Hoverflies such as *Sphaerophoria* sp. often increase in agricultural settings, driven by their larvae feeding on cereal aphids (Jauker et al., 2009). Similarly, mass-flowering oilseed rape can enhance populations of the pollen beetle *B. aeneus*. *A. mellifera* was particularly dominant on isolated plantings (Fig. 4a), reflecting the species' high efficiency in locating spatially isolated but rewarding floral resources. The presence of additional plantings close to our study sites benefited the less mobile pollen-feeding beetles of the genus *Oedemera* and increased the relative abundance of the predatory fly *E. opaca* in structurally simple landscapes (Fig. 4b). *E. opaca* is an important predator of aphids (Holland et al., 2008); multiple locally connected plantings may therefore support biocontrol in crop-dominated landscapes. Establishing multiple plantings similarly led to higher relative abundance of the ecologically and economically important wild bees *B. lapidarius* and *B. terrestris* agg. Notably, this positive effect of multiple plantings was

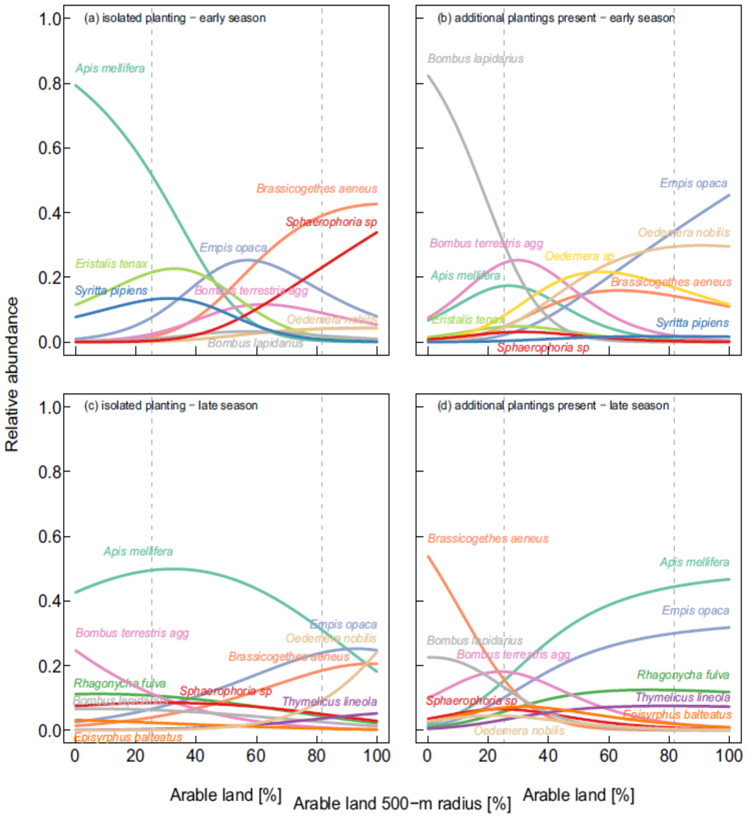


Fig. 4. Predicted changes in the relative abundances of the 10 most abundant flower-visitor species with increasing proportion of surrounding arable land on (a,c) isolated plantings and (b and d) on plantings where additional plantings were present, for the (a and b) early and (c and d) late flowering season. Predictions were based on a multinomial model for each season, with species abundances as response and the interaction of surrounding arable land and location of the wildflower planting as fixed effects. Dashed lines indicate predicted changes in relative abundance outside of the sampled range of arable land. Note that *Oedemera* sp. was among the 10 most dominant species in the early season; however, its predicted relative abundance in panel (a) equals that of *Oedemera nobilis* and is therefore not visible.

particularly pronounced when these were established in structurally complex landscapes (Fig. 4b).

4.3. Seasonal variation in flower-visitor communities

The composition of flower-visitor communities changed in the course of the flowering season. Spillover from the surrounding crop and non-crop habitats into wildflower plantings – and vice versa – may have played an important role (Blitzer et al., 2012). Late-seasonal crop to non-crop spillover is known from pests and pollinators (e.g., Blitzer et al., 2012; Diekötter et al., 2010; Jauker et al., 2012b). Correspondingly, our model predicted increasing relative abundances of the pollen beetle *B. aeneus* in the late flowering season, a serious pest of oilseed rape reducing seed output of wild and crop plants (Parsche et al., 2011). This finding could point to a supportive role of wildflower plantings to pollen beetles in the late flowering season. To our knowledge, no study so far has evaluated disservices of wildflower plantings to agriculture, however, their importance for populations of agricultural pests merits further research. Switches between flower resources similarly may have driven the enhanced abundance of *A. mellifera* in the late flowering season, as the species primarily feeds on mass-flowering crops the early flowering season (Westphal et al., 2008). For species richness, the non-prominent flower visitors were the only group to decline towards the late flowering season, which may be related to differences in life-history traits and resource use (e.g., parasitoids in contrast to wild bees). We also found indication of higher similarity in community composition between isolated plantings and those with additional plantings being present towards the late season (Fig. 3a). Again, species dispersal seems a likely cause; however, in the absence of movement data this remains speculative. It remains to be studied whether spatio-temporal variation in community composition of flower visitors also affects their provisioning of ecosystem services at different times of the season.

4.4. Conclusions

Increasing the availability of floral resources in agricultural landscapes through species-rich wildflower plantings promises to support the abundance and richness of prominent ecosystem service-providers such as wild bees and hoverflies. We show that wildflower plantings also support many overlooked flower-visitor species whose biodiversity by far outweighs that of these two prominent groups. In addition to possibly providing complementarity ecosystem services, non-prominent flower visitors may have the potential to stabilize ecosystem services in agricultural settings where prominent providers have been lost (Rader et al., 2016). We thus suggest that assessments of the value of wildflower plantings to biodiversity conservation and agriculture require a shift away from solely focusing on prominent taxa, towards a more holistic appreciation of the entire flower-visitor community. Conserving these highly diverse communities with wildflower plantings requires a multi-scale perspective that takes into account the different foraging strategies and life histories of consumers.

Acknowledgements

We greatly thank Lara Bau, Stefanie Braun, Stefanie Kaib, Lilith Jeske and Sarah Werner for flower-visitor sampling and identification. Birgit Jauker assisted with species identification. We thank all farmers who participated in HIAP and allowed us access to their lands. Two anonymous reviewers gave very helpful comments on the manuscript. D.W. is funded by the German Federal Environmental Foundation (DBU) in the framework of a PhD. scholarship. I. G. and J.A. acknowledge funding from the foundation of the University of Marburg.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2016.04.001.

References

Batáry, P., Baldi, A., Kleijn, D., Tscharntke, T., 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. Proc. R. Soc. B Biol. Sci. 278, 1894–1902. doi:http://dx.doi.org/10.1098/rspb.2010.1923.

Bates, D.M., Maechler, M., Bolker, B., Walker, S., 2015. lme4: linear mixed-effects models using Eigen and S4. R package version 1, 1–9. doi:http://dx.doi.org/10.1177/009286150103500418.

Blaauw, B.R., Isaacs, R., 2014a. Larger patches of diverse floral resources increase insect pollinator density diversity, and their pollination of native wildflowers. Basic. Appl. Ecol. 15, 701–711.

Blaauw, B.R., Isaacs, R., 2014b. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. J. Appl. Ecol. 51, 890–898. doi:http://dx.doi.org/10.1111/1365-2664.12257.

Blitzer, E.J., Dormann, C.F., Holzschuh, A., Klein, A.-M., Rand, T.A., Tscharntke, T., 2012. Spillover of functionally important organisms between managed and natural habitats. Agric. Ecosyst. Environ. 146, 34–43. doi:http://dx.doi.org/10.1016/j.agee.2011.09.005.

Carvell, C., Osborne, J.L., Bourke, A.F.G., Freeman, N., Pywell, R.F., Heard, M.S., 2011. Bumble bee species' responses to a targeted conservation measure depend on landscape context and habitat quality. Ecol. Appl. 21, 1760–1771.

Dicks, L.V., Corbet, S.A., Pywell, R.F., 2002. Compartmentalization in plant-insect flower visitor webs. J. Appl. Ecol. 71, 32–43.

Diekötter, T., Kadoya, T., Peter, F., Wolters, V., Jauker, F., 2010. Oilseed rape crops distort plant-pollinator interactions. J. Appl. Ecol. 47, 209–214. doi:http://dx.doi.org/10.1111/j.1365-2664.2009.01759.x.

Farwig, N., Brandl, R., Siemann, S., Wiener, F., Müller, J., 2014. Decomposition rate of carrion is dependent on composition not abundance of the assemblages of insect scavengers. Oecologia 175, 1291–1300.

Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.a., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science 309, 570–574. doi:http://dx.doi.org/10.1126/science.1111772.

Garibaldi, L.A., Carvalheiro, L.G., Leonhardt, S.D., Aizen, M., Blaauw, a, Isaacs, B.R., Kuhlmann, R., Kleijn, M., Klein, D., Kremen, A.M., Morandin, C., Scheper, L., Winfree, J., 2014. From research to action: practices to enhance crop yield through wild pollinators. Front. Ecol. Environ. 12, 439–447. doi:http://dx.doi.org/10.1890/130330.

Gathmann, A., Tscharntke, T., 2002. Foraging ranges of solitary bees. J. Anim. Ecol. 71, 757–764. doi:http://dx.doi.org/10.1046/j.1365-2656.2002.00641.x.

Goulson, D., Nicholls, E., Botías, C., Rotheray, E.L., 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. SciencExpress 1–16. doi:http://dx.doi.org/10.1126/science.1255957.

Grass, I., Berens, D.G., Peter, F., Farwig, N., 2013. Additive effects of exotic plant abundance and land-use intensity on plant–pollinator interactions. Oecologia 173, 913–923. doi:http://dx.doi.org/10.1007/s00442-013-2688-6.

Grass, I., Berens, D.G., Farwig, N., 2014. Natural habitat loss and exotic plants reduce the functional diversity of flower visitors in a heterogeneous subtropical landscape. Funct. Ecol. 28, 1117–1126. doi:http://dx.doi.org/10.1111/1365-2435.12285.

Holland, J.M., Oaten, H., Southway, S., Moreby, S., 2008. The effectiveness of field margin enhancement for cereal aphid control by different natural enemy guilds. Biol. Control 47, 71–76. doi:http://dx.doi.org/10.1016/j.biocontrol.2008.06.010.

Jauker, F., Diekötter, T., Schwarzbach, F., Wolters, V., 2009. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landsc. Ecol. 24, 547–555. doi:http://dx.doi.org/10.1007/s10980-009-9331-2.

Jauker, F., Bondarenko, B., Becker, H.C., Steffan-Dewenter, I., 2012a. Pollination efficiency of wild bees and hoverflies provided to oilseed rape. Agric. For. Entomol. 14, 81–87. doi:http://dx.doi.org/10.1111/j.1461-9563.2011.00541.x.

Jauker, F., Peter, F., Wolters, V., Diekötter, T., 2012b. Early reproductive benefits of mass-flowering crops to the solitary bee Osmia rufa outbalance post-flowering disadvantages. Basic Appl. Ecol. 13, 268–276. doi:http://dx.doi.org/10.1016/j.baae.2012.03.010.

Jauker, B., Krauss, J., Jauker, F., Steffan-Dewenter, I., 2013. Linking life history traits to pollinator loss in fragmented calcareous grasslands. Landsc. Ecol. 28, 107–120. doi:http://dx.doi.org/10.1007/s10980-012-9820-6.

Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M., Yela, J.L., 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecol. Lett. 9, 243–254. doi:http://dx.doi.org/10.1111/j.1461-0248.2005.00869.x.

Korpela, E.-L., Hyvönen, T., Lindgren, S., Kuussaari, M., 2013. Can pollination services, species diversity and conservation be simultaneously promoted by sown wildflower strips on farmland? Agric. Ecosyst. Environ. 179, 18–24.

Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. Proc. Natl. Acad. Sci. U. S. A. 99, 16812–16816. doi:http://dx.doi.org/10.1073/pnas.262413599.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2015. vegan: community ecology package. R package version 2 3–1.

Orford, K.A., Vaughan, I.P., Memmott, J., 2015. The forgotten flies: the importance of non-syrphid Diptera as pollinators. Proc. R. Soc. B Biol. Sci. 282 doi:http://dx.doi.org/10.1098/rspb.2014.2934 (20142934).

Parsche, S., Fründ, J., Tscharntke, T., 2011. Experimental environmental change and mutualistic vs. antagonistic plant flower–visitor interactions. Perspect. Plant Ecol. Evol. Syst. 13, 27–35. doi:http://dx.doi.org/10.1016/j.ppees.2010.12.001.

Pfiffner, L., Luka, H., Schlatter, C., Juen, A., Traugott, M., 2009. Impact of wildflower strips on biological control of cabbage lepidopterans. Agric. Ecosyst. Environ. 129, 310–314. doi:http://dx.doi.org/10.1016/j.agee.2008.10.003.

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

R Development Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rader, R., Bartomeus, I., Garibaldi, L.A., et al., 2016. Non-bee insects are important contributors to global crop pollination. Proc. Natl. Acad. Sci. U. S. A. 113, 146–151.

Riedinger, V., Mitesser, O., Hovestadt, T., Steffan-Dewenter, I., Holzschuh, A., 2015. Annual dynamics of wild bee densities: attractiveness and productivity effects of oilseed rape. Ecology 96, 1351–1360. doi:http://dx.doi.org/10.1890/14-1124.1.

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

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E.L., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774. doi:http://dx.doi.org/10.1126/science.287.5459.1770.

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

Scheper, J., Reemer, M., van Kats, R., Ozinga, W.A., van der Linden, G.T.J., Schaminée, J.H.J., Siepel, H., Kleijn, D., 2014. Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. Proc. Natl. Acad. Sci. 111, 17552–17557. doi:http://dx.doi.org/10.1073/pnas.1412973111.

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

Skaug, H., Fournier, D., Bolker, B., Magnusson, A., Nielsen, A., 2016. Generalized Linear Mixed Models using 'AD Model Builder'. R package version 0.8.3. 3.

Tenhumberg, B., Poehling, H.-M., 1995. Syphids as natural enemies of cereal aphids in Germany: aspects of their biology and efficacy in different years and regions. Agric. Ecosyst. Environ. 52, 39–43.

Thies, C., Tscharntke, T., 1999. Landscape structure and biological control in agroecosystems. Science 285, 893–895. doi:http://dx.doi.org/10.1126/science.285.5429.893.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. Ecol. Lett. 8, 857–874. doi:http://dx.doi.org/10.1111/j.1461-0248.2005.00782.x.

Venables, W., Ripley, B., 2002. Modern Applied Statistics with S. Fourth. Springer, New York.

Wang, Y., Naumann, U., Wright, S.T., Warton, D.I., 2012. mvabund—an R package for model-based analysis of multivariate abundance data. Methods Ecol. Evol. 3, 471–474. doi:http://dx.doi.org/10.1111/j.2041-210X.2012.00190.x.

Wang, Y., Naumann, U., Wright, S., Warton, D., 2015. mvabund: statistical methods for analysing multivariate abundance data. R package version 3.10. 4.

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., Woyciechocwski, M., Biesmeijer, J.C., Kunin, W.E., Settele, J., Steffan-Dewenter, I., 2008. Measuring bee diversity in different European habitats and biogeographical regions. Ecol. Monogr. 78, 653–671.

Winfree, R., Aguilar, R., LeBuhn, G., 2009. A meta-analysis of bees' responses to anthropogenic disturbance. Ecology 90, 2068–2076.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York.

ANHANG KAPITEL II

Appendix A. Supplementary data.

Table A.1. Wildflower mixtures used to establish the 14 wildflower plantings investigated in this study. Shown is the share of seeds [%] per wildflower mixture. See Table A.2. for the distribution of the mixtures among study sites.

Seed mixture	Plant species	Family	Share [%]
Mixture 1 (Kranichsteiner Mischung)	*Achillea millefolium*	Asteraceae	0.25
	Anthemis tinctoria	Asteraceae	1.2
	Anthoxanthum odoratum	Poaceae	2.25
	Carum carvi	Apiaceae	2.25
	Centaurea cyanus	Asteraceae	9
	Centaurea jacea	Asteraceae	0.6
	Cichorium intybus	Asteraceae	4.5
	Cynosurus spec.	Poaceae	2.25
	Daucus carotaæ	Apiaceae	1.2
	Fagopyrum esculentum	Polygonaceae	10
	Galium mollugo	Rubiaceae	0.35
	Galium verum	Rubiaceae	0.6
	Helianthus annuus	Asteraceae	9
	Heracleum sphondylium	Apiaceae	0.6
	Hypericum perforatum	Hypericaceae	1.2
	Lathyrus pratensis	Fabaceae	0.1
	Leucanthemum vulgare	Asteraceae	1.2
	Linumæ spec.	Linaceae	2.8
	Malva spec.	Malvaceae	5.95
	Medicago sativa	Fabaceae	5
	Melilotus officinalis	Fabaceae	0.25
	Onobrychis	Fabaceae	6.5
	Pastinaca sativa	Apiaceae	4.5
	Phleum pratense	Poaceae	5
	Poa pratensis	Poaceae	5
	Salvia pratensis	Lamiaceae	3.7
	Secale multicaule	Poaceae	4.7
	Trifolium incarnatum	Fabaceae	2.2
	Trifolium pratense	Fabaceae	5
	Verbascum nigrum	Verbascaceae	0.25
	Verbascum phoeniceum	Verbascaceae	0.6
	Vicia spec.	Viciaceae	2
Mixture 2 (Lebensraum 1)	*Achillea millefolium*	Asteraceae	1
	Anthemis tinctoria	Asteraceae	1
	Artemisia vulgaris	Asteraceae	0.1
	Barbarea vulgaris	Brassicaceae	1
	Borago officinalis	Boraginaceae	0.2
	Carum carvi	Apiaceae	2.5
	Centaurea jacea	Asteraceae	1.8
	Centaurea scabiosa	Asteraceae	0.1
	Cerastium holosteoides	Cariophyllaceae	0.1
	Chrysanthemum segetum	Asteraceae	0.2
	Cichorium intybus	Asteraceae	2.5
	Clinopodium vulgare	Lamiaceae	0.1
	Crepis biennis	Asteraceae	0.1
	Daucus carota	Apiaceae	1.5
	Dipsacus fullonum	Dipsacaceae	1
	Echium vulgare	Boraginaceae	0.8
	Foeniculum vulgare	Apiaceae	5
	Fragopyrum esculentum	Polygonaceae	7.5
	Galium album	Rubiaceae	0.5
	Galium verum	Rubiaceae	0.5
	Helianthus annuus	Asteraceae	5
	Heracleum sphondyllum	Apiaceae	0.4
	Hypericum perforatum	Hypericaceae	0.1
	Leucanthemum ircutianum	Asteraceae	0.5
	Linum usitatissimum	Linaceae	8
	Lotus corniculatus	Fabaceae	2
	Malva mauritanica	Malvaceae	0.5
	Malva moschata	Malvaceae	0.5
	Malva sylvestris	Malvaceae	1
	Malva verticiliata	Malvaceae	0.5
	Medicago lupulina	Fabaceae	2
	Medicago sativa	Fabaceae	7.5
	Oenothera biennis	Onagraceae	0.5
	Onobrychis viciifolia	Fabaceae	15
	Origanum vulgare	Lamiaceae	0.2
	Petroselinum sativum	Apiaceae	1
	Plantago lanceolata	Plantaginaceae	0.5
	Prunella vulgaris	Lamiaceae	0.1
	Reseda luteola	Resedaceae	0.1
	Salvia pratensis	Lamiaceae	0.5
	Sanguisorba minor	Rosaceae	5.8
	Setaria italica	Poaceae	1
	Silene alba	Cariophyllaceae	1.5
	Silene dioica	Cariophyllaceae	0.5
	Silene vulgaris	Cariophyllaceae	1.8
	Silene-flos-cuculi	Cariophyllaceae	0.2
	Silybum marianum	Asteraceae	1
	Tanacetum corymbosum	Asteraceae	0.2
	Tanacetum vulgare	Asteraceae	0.1
	Trifolium hybridum	Fabaceae	0.5
	Trifolium pratense	Fabaceae	5
	Verbascum lychnitis	Verbascaceae	0.1
	Verbascum nigrum	Verbascaceae	0.1
	Verbascum thapsus	Verbascaceae	0.1
	Vicia sativa	Fabaceae	2.8
	Vicia villosa	Fabaceae	5

Seed mixture	Plant species	Family	Share [%]
Mixture 3 (Odin)	*Borago officinalis*	Boraginaceae	1.67
	Brassica spec.	Brassicaceae	3
	Calendula officinalis	Asteraceae	1.67
	Carum carvi	Apiaceae	1.67
	Coriandrum sativum	Apiaceae	1.67
	Daucus carota	Apiaceae	1.67
	Fagopyrum esculentum	Polygonaceae	8
	Helianthus annuus	Asteraceae	8
	Linum usitatissimum	Linaceae	8
	Malva spec.	Malvaceae	4
	Medicago sativa	Fabaceae	5
	Onobrychis	Fabaceae	8
	Ornithopus sativus	Fabaceae	6
	Phacelia spec.	Hydrophyllaceae	2
	Sanguisorbe minor	Rosaceae	1.67
	Trifolium incarnatum	Fabaceae	6
	Trifolium pratense	Fabaceae	6
	Trifolium resupinatum	Fabaceae	6
	Trigonella caerulea	Fabaceae	8
	Trigonella foenum-	Fabaceae	6
	Vicia sativa	Fabaceae	6
Mixture 4 (Wildsaaten Mischung)	*Achillea millefolium*	Asteraceae	1
	Anthemis tinctoria	Asteraceae	1.5
	Borago officinalis	Boraginaceae	4
	Calendula officinalis	Asteraceae	7
	Carum carvi	Apiaceae	4
	Centaurea cyanus	Asteraceae	2
	Chrysanthemum segetum	Asteraceae	4
	Cichorium intybus	Asteraceae	1
	Crepis biennis	Asteraceae	1
	Daucus carota	Apiaceae	3.5
	Dipsacus fullonum	Dipsacaceae	0.5
	Fagopyrum esculentum	Polygonaceae	10
	Foeniculum vulgare	Apiaceae	6
	Galium verum	Rubiaceae	0.5
	Helianthus annuus	Asteraceae	15
	Hypericum perforatum	Hypericaceae	1
	Isatis tinctoria	Asteraceae	1
	Leucanthemum ircutianum	Asteraceae	3
	Linum usitatissimum	Linaceae	5
	Lotus corniculatus	Fabaceae	2
	Malva moschata	Malvaceae	1
	Medicago lupulina	Fabaceae	1
	Medicago sativa	Fabaceae	4
	Melilotus albus	Fabaceae	2
	Oenothera biennis	Onagraceae	1
	Papaver rhoeas	Papaveraceae	1
	Plantago lanceolata	Plantaginaceae	1
	Reseda luteola	Resedaceae	0.5
	Salvia pratensis	Lamiaceae	1
	Sanguisorba minor	Rosaceae	3
	Secale multicaule	Poaceae	4
	Silene alba	Cariophyllaceae	1
	Silene vulgaris	Cariophyllaceae	0.5
	Sinapis arvensis	Brassicaceae	2.8
	Trifolium pratense	Fabaceae	1
	Verbascum lychnitis	Verbascaceae	0.2
	Vicia sativa	Fabaceae	2

Table A.2. Study site characteristics as well as abundance and species richness of the four flower-visitor groups in the early and late flowering season.

							Abundance				Species richness		
Site	Season	Flower abundance	Flower richness	Additional planting	Wildflower mixture	Arable land [500 m]	*Apis mellifera*	Wild bees	Hover-flies	Others	Wild bees	Hover-flies	Others
1	early	1004	14	yes	Mixture 4	0.37	1	2	15	58	2	5	30
1	late	3952	18	yes	Mixture 4	0.37	43	14	14	59	5	8	24
2	early	3475	18	yes	Mixture 3	0.56	0	35	1	49	6	1	22
2	late	6630	15	yes	Mixture 3	0.56	4	4	8	89	2	3	19
3	early	23393	17	no	Mixture 2	0.66	2	17	6	76	8	6	24
3	late	11429	20	no	Mixture 2	0.66	113	15	18	80	7	5	15
4	early	19803	14	no	Mixture 3	0.54	1	5	11	76	3	7	31
4	late	11323	19	no	Mixture 3	0.54	52	12	21	152	2	6	29
5	early	2687	20	no	Mixture 4	0.82	3	5	31	44	2	11	22
5	late	5972	23	no	Mixture 4	0.82	29	11	29	59	3	8	26
6	early	786831	14	no	Mixture 4	0.27	61	17	32	59	11	10	39
6	late	25265	13	no	Mixture 4	0.27	20	32	31	49	13	7	20
7	early	38797	27	yes	Mixture 2	0.25	10	32	6	46	8	5	30
7	late	16479	33	yes	Mixture 2	0.25	21	17	32	72	5	9	26
8	early	5632	9	no	Mixture 1	0.65	1	10	19	47	6	7	28
8	late	3766	17	no	Mixture 1	0.65	4	2	7	93	2	3	18
9	early	755	14	yes	Mixture 3	0.38	3	5	2	52	2	2	20
9	late	3515	16	yes	Mixture 3	0.38	6	20	13	38	3	2	20
10	early	2075	14	yes	Mixture 3	0.76	1	2	6	56	2	3	31
10	late	1148	13	yes	Mixture 3	0.76	57	1	15	58	1	6	15
11	early	15520	12	yes	Mixture 2	0.37	9	44	10	37	3	5	21
11	late	52572	12	yes	Mixture 2	0.37	29	53	6	39	5	4	22
12	early	629	10	yes	Mixture 3	0.40	3	9	9	35	7	1	19
12	late	2771	10	yes	Mixture 3	0.40	3	20	39	77	7	8	24
13	early	13233	19	no	Mixture 4	0.32	11	16	56	70	9	10	30

13	late	19839	19	no	Mixture 4	0.32	81	22	18	31	5	8	18
14	early	6028	16	yes	Mixture 3	0.52	3	5	7	32	5	3	19
14	late	10437	14	yes	Mixture 3	0.52	17	4	8	43	2	7	18

Table A.3. Composition of the flowering plant community on the 14 wildflower plantings (S1–S14) in the early and late flowering season. Shown is the sum of floral units for each plant species as assessed on the two 50 m × 1 m transects per planting.

	Sum of floral units - early flowering season														Sum of floral units - late flowering season													
Plant species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14
Achillea millefolium	0	0	4	0	44	0	10	10	0	0	0	0	189	0	10	0	319	0	1370	9	810	140	0	0	0	0	2125	1
Aegopodium podagraria	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agrimonia eupatoria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	95	0	0	0	0	0	0	0	0	0	0	0	0
Anthemis tinctoria	0	0	0	0	2	0	0	0	0	0	0	0	0	0	94	0	475	122	82	1841	1500	41	0	0	0	0	255	0
Anthriscus caucalis	0	167	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthriscus sylvestris	0	0	1371	0	5	0	169	0	32	0	0	0	0	0	0	0	140	0	0	0	0	0	1	0	0	0	0	0
Aquilegia vulgaris	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Barbarea vulgaris	0	0	94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Campanula persicifolia	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capsella bursa-pastoris	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carum carvi	18	66	49	0	224	0	896	175	365	0	0	0	20	173	0	10	0	0	2	0	84	0	10	0	0	0	0	0
Centaurea cyanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
Centaurea jacea	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	4	0	0	0	308	1	0	0	0	0	0	0
Centaurea scabiosa	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0	0	1	0	0	0	15	0	0	0	0	0	0	0
Cerastium fontanum	13	34	6	0	73	0	5	0	11	10	0	5	129	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cichorium intybus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0
Cirsium arvense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	113	31	54	1975	1	1	0	30	78	79	4	0	0	854
Cirsium vulgare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	4	0	0	0
Crepis biennis	0	0	83	0	0	0	163	0	0	2	0	0	0	0	0	0	3	0	6	0	15	0	0	0	0	9	0	0
Daucus carota	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	248	0	0	462	0	0
Epilobium parviflorum	0	0	0	11	0	0	0	0	0	0	25	46	0	50	8	5	0	66	0	0	0	0	5	3	166	1357	72	1775

Galium aparine	0	290	62	65	2	40	10	0	0	205	8965	0	0	536	42	35	10	55	44	0	20	0	0	0	30080	0	5	435
Galium mollugo	0	0	20375	16660	21	767245	33064	4145	0	0	0	0	245	0	50	0	7500	1161	843	12082	11790	1238	22	0	0	0	5500	0
Galium verum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	130	4575	30	0	200	1182	0	0	0	0	400	0
Geranium dissectum	1	139	0	0	0	0	0	0	0	0	0	0	0	0	0	30	0	0	0	0	0	0	0	0	0	0	0	0
Geum urbanum	0	1	0	16	3	0	0	0	6	4	4	3	11	5	8	2	0	1	0	0	0	0	3	16	3	2	16	21
Hypericum perforatum	0	0	0	0	0	0	0	0	58	0	0	0	0	0	71	69	0	0	332	1367	24	0	2305	0	0	607	574	0
Impatiens glandulifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	76	0	0	0
Isatis tinctoria	0	0	0	0	0	7320	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lamium album	0	1973	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0
Lamium purpureum	7	0	0	0	0	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lapsana communis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0
Leucanthemum vulgare	744	2	5	100	707	11883	410	443	0	0	0	0	8084	0	492	0	0	2	525	3979	20	211	0	0	0	0	2579	0
Lotus corniculatus	0	0	0	0	119	0	1	0	0	0	0	0	104	0	1	0	0	0	183	0	20	0	0	0	0	0	15	0
Lupinus polyphyllus	0	0	0	860	0	0	0	764	0	0	0	0	0	0	0	0	0	25	0	0	0	423	0	0	0	0	0	0
Lychnis flos-cuculi	0	0	0	0	0	0	1016	0	7	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0
Malva moschata	0	0	0	5	51	0	0	0	0	0	0	0	20	0	2094	0	523	731	1739	1998	131	77	0	0	0	0	3296	0
Malva sylvestris	0	0	0	0	0	0	0	0	0	0	51	0	0	10	0	0	0	0	0	0	0	0	0	0	353	0	0	61
Matricaria recutita	0	0	0	0	0	0	0	0	40	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
Medicago lupulina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0
Medicago sativa	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	22	0	127	3	0	1	19	0	0	0
Melilotus albus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	150	0	0	0	3	0	0	0	0	0	0	0	0	0
Mycelis muralis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Myosotis sylvatica	6	57	37	0	3	132	26	27	105	3	45	0	55	149	66	381	70	43	22	1978	38	12	190	18	0	0	34	794
Onobrychis viciifolia	0	0	0	0	0	0	12	0	0	24	0	0	0	3	0	0	0	0	0	0	22	0	0	6	0	0	0	14
Phacelia tanacetifolia	0	0	0	0	0	0	0	0	10	0	1343	0	0	180	0	0	0	0	0	0	0	0	0	0	2634	0	0	84
Plantago lanceolata	86	24	0	0	144	1	1	0	0	0	0	0	764	0	723	4	0	0	303	0	2	0	0	0	0	0	982	0
Prunella vulgaris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0
Ranunculus repens	2	138	35	0	36	0	12	0	38	75	215	370	50	88	0	0	1	0	2	0	0	0	1	48	12	1	0	1
Rubus idaeus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rumex acetosa	20	140	0	0	0	66	0	0	10	28	0	127	831	198	0	4625	60	30	0	0	2	0	0	0	0	30	3176	105
Rumex sanguineus	0	0	0	0	0	0	0	0	0	1329	0	0	0	0	0	0	406	0	0	0	105	26	260	380	0	0	0	96
Salvia pratensis	85	0	0	0	11	1	353	0	0	0	0	0	124	0	0	0	0	0	13	0	15	0	0	0	0	0	20	0

Sanguisorba minor	13	6	109	114	192	91	126	8	55	0	0	43	2	442	0	15	11	5	15	0	56	2	133	2	0	6	0	351
Saxifraga granulata	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scrophularia nodosa	0	0	0	0	0	0	0	0	0	0	38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Silene dioica	0	0	825	0	2	0	671	25	0	0	0	0	127	0	2	0	903	5	0	0	277	50	0	0	0	0	0	0
Silene latifolia	1	0	262	130	669	0	49	35	0	0	0	0	566	0	23	0	402	152	288	209	5	239	0	0	0	0	526	0
Silene vulgaris	5	5	0	30	329	14	1516	0	0	0	0	0	1909	0	2	0	7	0	80	3	460	1	0	0	0	0	261	0
Sinapis arvensis	0	0	0	0	0	1	0	0	0	0	9	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0
Stellaria graminea	0	0	0	0	0	0	246	0	0	0	0	0	0	0	0	0	0	0	0	0	361	0	0	0	0	0	0	0
Tanacetum vulgare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0
Taraxacum sect. Ruderalia	3	1	0	0	0	0	2	0	0	0	5	1	0	3	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Trifolium pratense	0	0	0	5	0	0	2	0	0	1	0	21	1	0	0	0	0	0	1	0	18	0	0	13	0	186	0	0
Trifolium repens	0	0	0	0	0	0	0	0	0	1	0	6	0	0	0	0	0	0	0	0	11	0	0	10	0	111	1	0
Tripleurospermum maritimum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1782	0	0	0	0	0	0	0	0
Urtica dioica	0	400	50	1570	50	0	0	0	14	220	4690	0	0	1865	0	1306	410	2225	66	0	0	90	195	570	19220	0	0	5845
Valeriana officinalis	0	0	0	236	0	0	0	0	0	0	0	0	0	0	0	0	0	129	0	0	0	0	0	0	0	0	0	0
Valerianella locusta	0	0	0	0	0	0	0	0	0	0	0	0	0	2314	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Verbascum lychnitis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0	0	0
Veronica arvensis	0	31	0	0	0	0	0	0	0	0	130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Veronica chamaedrys	0	0	0	0	0	0	10	0	0	165	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Veronica persica	0	0	0	0	0	0	8	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vicia hirsuta	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	54	2	0	0	0	0
Vicia villosa	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0
Viola arvensis	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A.4. Specimen sampled on the transects of the 14 wildflower plantings during flower visitor surveys. MOR = morphotype; ABU = total abundance.

MOR	Order	Suborder	Superfamily	Family	Genus	Scientific name	ABU
A001	Hymenoptera	Apocrita	Apoidea	Apidae	*Apis*	*Apis mellifera*	588
A002	Hymenoptera	Apocrita	Apoidea	Apidae	*Nomada*	*Nomada goodeniana*	2
A003	Hymenoptera	Apocrita	Apoidea	Apidae	*Megachile*	*Megachile alpicola*	1
A004	Hymenoptera	Apocrita	Apoidea	Apidae	*Halictus*	*Halictus maculatus*	2
A005	Hymenoptera	Apocrita	Apoidea	Apidae	*Halictus*	*Halictus tumulorum*	4
A006	Hymenoptera	Apocrita	Apoidea	Apidae	*Halictus*	*Halictus scabiosae*	2
A007	Hymenoptera	Apocrita	Apoidea	Apidae	*Halictus*	*Halictus rubicundus*	1
A008	Hymenoptera	Apocrita	Apoidea	Apidae	*Chelosoma*	*Chelostoma rapunculi*	2
A009	Hymenoptera	Apocrita	Apoidea	Apidae	*Chelosoma*	*Chelostoma florisomne*	3
A010	Hymenoptera	Apocrita	Apoidea	Apidae	*Osmia*	*Osmia rufa*	4
A011	Hymenoptera	Apocrita	Apoidea	Apidae	*Andrena*	*Andrena nitida*	1
A012	Hymenoptera	Apocrita	Apoidea	Apidae	*Andrena*	*Andrena bicolor*	1
A013	Hymenoptera	Apocrita	Apoidea	Apidae	*Andrena*	*Andrena haemorrhoa*	8
A014	Hymenoptera	Apocrita	Apoidea	Apidae	*Andrena*	*Andrena chrysoceles*	1
A015	Hymenoptera	Apocrita	Apoidea	Apidae	*Andrena*	*Andrena dorsata*	1
A016	Hymenoptera	Apocrita	Apoidea	Apidae	*Andrena*	*Andrena cineraria*	1
A017	Hymenoptera	Apocrita	Apoidea	Apidae	*Andrena*	*Andrena fulva*	1
A018	Hymenoptera	Apocrita	Apoidea	Apidae	*Andrena*	*Andrena nigroaenea*	4
A019	Hymenoptera	Apocrita	Apoidea	Apidae	*Andrena*	*Andrena flavipes*	3
A020	Hymenoptera	Apocrita	Apoidea	Apidae	*Andrena*	*Andrena minutula*	4
A021	Hymenoptera	Apocrita	Apoidea	Apidae	*Andrena*	*Andrena subopaca*	2
A022	Hymenoptera	Apocrita	Apoidea	Apidae	*Lasioglossum*	*Lasioglossum leucopus*	2
A023	Hymenoptera	Apocrita	Apoidea	Apidae	*Lasioglossum*	*Lasioglossum calceatum*	3
A024	Hymenoptera	Apocrita	Apoidea	Apidae	*Lasioglossum*	*Lasioglossum leucozonium*	1
A025	Hymenoptera	Apocrita	Apoidea	Apidae	*Lasioglossum*	*Lasioglossum pauxillum*	7
A026	Hymenoptera	Apocrita	Apoidea	Apidae	*Hylaeus*	*Hylaeus cornutus*	3
A027	Hymenoptera	Apocrita	Apoidea	Apidae	*Hylaeus*	*Hylaeus nigritus*	1
A028	Hymenoptera	Apocrita	Apoidea	Apidae	*Hylaeus*	*Hylaeus gredleri*	4
A029	Hymenoptera	Apocrita	Apoidea	Apidae	*Hylaeus*	*Hylaeus communis*	6
A030	Hymenoptera	Apocrita	Apoidea	Apidae	*Heriades*	*Heriades truncorum*	1
A031	Hymenoptera	Apocrita	Apoidea	Apidae	*Colletes*	*Colletes daviesanus*	3
A032	Hymenoptera	Apocrita	Apoidea	Apidae	*Chelosoma*	*Chelostoma sp*	1
A033	Hymenoptera	Apocrita	Apoidea	Apidae	*Lasioglossum*	*Lasioglossum sp*	2
A034	Hymenoptera	Apocrita	Apoidea	Apidae	*NA*	*NA*	1
B001	Hymenoptera	Apocrita	Apoidea	Apidae	*Bombus*	*Bombus terrestris agg*	177
B002	Hymenoptera	Apocrita	Apoidea	Apidae	*Bombus*	*Bombus pratorum*	34
B003	Hymenoptera	Apocrita	Apoidea	Apidae	*Bombus*	*Bombus ruderarius*	15
B004	Hymenoptera	Apocrita	Apoidea	Apidae	*Bombus*	*Bombus lapidarius*	99
B005	Hymenoptera	Apocrita	Apoidea	Apidae	*Bombus*	*Bombus pascuorum*	13
B006	Hymenoptera	Apocrita	Apoidea	Apidae	*Bombus*	*Bombus hypnorum*	3
B007	Hymenoptera	Apocrita	Apoidea	Apidae	*Bombus*	*Bombus hortorum*	2
B008	Hymenoptera	Apocrita	Apoidea	Apidae	*Psithyrus*	*Psithyrus vestalis*	1
C001	Coleoptera	Polyphaga	Tenebrionoidea	Oedemeridae	*Oedemera*	*Oedemera nobilis*	71
C002	Coleoptera	Polyphaga	Tenebrionoidea	Oedemeridae	*Oedemera*	*Oedemera sp*	53
C003	Coleoptera	Polyphaga	Curculionoidea	Curculionidae	*Larinus*	*Larinus turbinatus*	24

C004	Coleoptera	Polyphaga	Chrysomeloidea	Chrysomelidae	*Bruchus*	*Bruchus rufipes*	1
C005	Coleoptera	Polyphaga	Cucujoidea	Nitidulidae	*Brassiogethes*	*Brassicogethes aeneus*	189
C006	Coleoptera	Polyphaga	Tenebrionoidea	Tenebrionidae	*Omphlus*	*Omophlus sp*	9
C007	Coleoptera	Polyphaga	Scarabaeoidea	Cetoniidae	*Cetonia*	*Cetonia aurata*	4
C008	Coleoptera	Polyphaga	Scarabaeoidea	Cetoniidae	*Trichius*	*Trichius fasciatus*	1
C009	Coleoptera	Polyphaga	Chrysomeloidea	Chrysomelidea	*Podagrica*	*Podagrica fuscicornis*	9
C010	Coleoptera	Polyphaga	Cleroidea	Malachiidae	*Malachius*	*Malachius bipustulatus*	2
C011	Coleoptera	Polyphaga	Scarabaeoidea	Rutelidae	*Phyllopertha*	*Phyllopertha horticola*	19
C012	Coleoptera	Polyphaga	Cucujoidea	Coccinellidae	*Harmonia*	*Harmonia axyridis*	6
C013	Coleoptera	Polyphaga	Cucujoidea	Coccinellidae	*Coccinella*	*Coccinella septempunctata*	2
C014	Coleoptera	Polyphaga	Cucujoidea	Coccinellidae	*Coccinula*	*Coccinula quatuordecimpustulata*	1
C015	Coleoptera	Polyphaga	Elateroidea	Elateridea	*Agrypnus*	*Agrypnus murinus*	3
C016	Coleoptera	Polyphaga	Elateroidea	Cantharidae	*Cantharis*	*Cantharis fusca*	10
C017	Coleoptera	Polyphaga	Buprestoidea	Buprestidea	*Anthaxia*	*Anthaxia nitidula*	1
C018	Coleoptera	Polyphaga	Buprestoidea	Buprestidae	*Agrilus*	*Agrilus pannonicus*	1
C019	Coleoptera	Polyphaga	Chrysomeloidea	Cerambycidea	*Stenopterus*	*Stenopterus rufus*	1
C020	Coleoptera	Polyphaga	Chrysomeloidea	Cerambycidea	*Stenurella*	*Stenurella melanura*	1
C021	Coleoptera	Polyphaga	Chrysomeloidea	Cerambycidea	*Agapanthia*	*Agapanthia villosoviridescens*	2
C022	Coleoptera	Polyphaga	Staphylinoidea	Staphylinidae	*Eusphalerum*	*Eusphalerum minutum*	1
C023	Coleoptera	Polyphaga	Curculionoidea	Curculionidae	*Ceutorhynchus*	*Ceutorhynchus sp*	1
C024	Coleoptera	Polyphaga	Curculionoidea	Rhynchitidae	*Deporaus*	*Deporaus betulae*	1
C025	Coleoptera	Polyphaga	Curculionoidea	Nemonychidae	*Cimberis*	*Cimberis sp*	1
C026	Coleoptera	Polyphaga	Tenebrionoidea	Oedemeridae	*Oedemera*	*Oedemera femorata*	8
C027	Coleoptera	Polyphaga	Tenebrionoidea	Tenebrionidae	*Tenebrio*	*Tenebrio sp*	2
C028	Coleoptera	Polyphaga	Elateroidea	Elateridea	*Ampedus*	*Ampedus sp*	1
C029	Coleoptera	Polyphaga	Scarabaeoidea	Cetoniidae	*Oxythyrea*	*Oxythyrea funesta*	10
C030	Coleoptera	Polyphaga	Elateroidea	Elateridea	*Ampedus*	*Ampedus sp*	1
C031	Coleoptera	Polyphaga	Elateroidea	Cantharidae	*Rhagonycha*	*Rhagonycha fulva*	113
C032	Coleoptera	Polyphaga	Cucujoidea	Coccinellidae	*NA*	*NA*	2
C033	Coleoptera	Polyphaga	Staphylinoidea	Staphylinidea	*NA*	*NA*	1
C034	Coleoptera	Polyphaga	Elateroidea	Elateridea	*Cardiophorus*	*Cardiophorus sp*	1
C035	Coleoptera	Polyphaga	Tenebrionoidea	Mordellidae	*NA*	*NA*	2
C036	Coleoptera	NA	NA	NA	*NA*	*NA*	1
C037	Coleoptera	NA	NA	NA	*NA*	*NA*	1
C038	Coleoptera	Polyphaga	Chrysomeloidea	Chrysomelidea	*NA*	*NA*	1
D001	Diptera	Brachycera	NA	Empidiae	*Empis*	*Empis opaca*	303
D002	Diptera	Brachycera	NA	Empididae	*Empis*	*Empis tesselata*	14
D003	Diptera	Brachycera	NA	Empididae	*Empis*	*Empis sp*	1
D004	Diptera	Brachycera	NA	Rhagionidae	*Rhagio*	*Rhagio sp*	6
D005	Diptera	Brachycera	NA	Rhagionidae	*Rhagio*	*Rhagio sp*	2
D006	Diptera	Brachycera	NA	Rhagionidae	*Rhagio*	*Rhagio sp*	1
D007	Diptera	Brachycera	NA	Rhagionidae	*Rhagio*	*Rhagio sp*	1
D008	Diptera	Brachycera	NA	Anthomyiidae	*NA*	*NA*	28
D009	Diptera	Brachycera	NA	Anthomyiidae	*NA*	*NA*	4
D010	Diptera	Brachycera	NA	Anthomyiidae	*NA*	*NA*	1
D011	Diptera	Brachycera	NA	Anthomyiidae	*NA*	*NA*	1
D012	Diptera	Brachycera	NA	Anthomyiidae	*NA*	*NA*	1
D013	Diptera	Brachycera	NA	Anthomyiidae	*NA*	*NA*	1

D014	Diptera	Brachycera	NA	Anthomyiidae	*NA*	*NA*	3
D015	Diptera	Brachycera	NA	Anthomyiidae	*NA*	*NA*	25
D016	Diptera	Brachycera	NA	Anthomyiidae	*NA*	*NA*	23
D017	Diptera	Brachycera	NA	Anthomyiidae	*NA*	*NA*	20
D018	Diptera	Brachycera	NA	Anthomyiidae	*NA*	*NA*	3
D019	Diptera	NA	NA	NA	*NA*	*NA*	11
D020	Diptera	Brachycera	NA	Calliphoridae	*Lucilia*	*Lucilia sp*	7
D021	Diptera	Brachycera	NA	Calliphoridae	*Lucilia*	*Lucilia sp*	14
D022	Diptera	Brachycera	NA	Sarcophagidae	*NA*	*NA*	5
D023	Diptera	Brachycera	NA	Sarcophagidae	*NA*	*NA*	5
D024	Diptera	Brachycera	NA	Sarcophagidae	*NA*	*NA*	1
D025	Diptera	Brachycera	NA	Sarcophagidae	*NA*	*NA*	5
D026	Diptera	Brachycera	NA	Sarcophagidae	*NA*	*NA*	8
D027	Diptera	Brachycera	NA	Sarcophagidae	*NA*	*NA*	9
D028	Diptera	NA	NA	NA	*NA*	*NA*	11
D029	Diptera	NA	NA	NA	*NA*	*NA*	1
D030	Diptera	NA	NA	NA	*NA*	*NA*	2
D033	Diptera	NA	NA	NA	*NA*	*NA*	1
D034	Diptera	NA	NA	NA	*NA*	*NA*	2
D035	Diptera	NA	NA	NA	*NA*	*NA*	1
D036	Diptera	NA	NA	NA	*NA*	*NA*	2
D037	Diptera	NA	NA	NA	*NA*	*NA*	3
D038	Diptera	NA	NA	NA	*NA*	*NA*	1
D039	Diptera	NA	NA	NA	*NA*	*NA*	20
D040	Diptera	Brachycera	NA	Platystomatidae	*NA*	*NA*	18
D041	Diptera	Brachycera	NA	Platystomatidae	*NA*	*NA*	1
D042	Diptera	Brachycera	NA	Tephritidae	*NA*	*NA*	1
D043	Diptera	Brachycera	NA	Tephritidae	*NA*	*NA*	1
D044	Diptera	Brachycera	NA	Tephritidae	*NA*	*NA*	2
D045	Diptera	Brachycera	NA	Tephritidae	*NA*	*NA*	2
D046	Diptera	Brachycera	NA	Tephritidae	*NA*	*NA*	3
D047	Diptera	Brachycera	NA	Tephritidae	*NA*	*NA*	3
D048	Diptera	Brachycera	NA	Tachinidae	*Nowickia*	*Nowickia ferox*	1
D049	Diptera	Brachycera	NA	Muscidae	*Mesembrina*	*Mesembrina sp*	3
D050	Diptera	Brachycera	NA	Calliphoridae	*Cynomya*	*Cynomya mortuorum*	3
D051	Diptera	Brachycera	NA	Tabanidae	*Haematopota*	*Haematopota sp*	2
D052	Diptera	Nematocera	Bibionoidae	Bibionidae	*Bibio*	*Bibio sp*	5
D053	Diptera	Brachycera	NA	Asilidae	*NA*	*NA*	3
D054	Diptera	Brachycera	NA	Stratiomyidae	*NA*	*NA*	2
D055	Diptera	Brachycera	NA	Conopidae	*Sicus*	*Sicus ferrugineus*	2
D056	Diptera	Brachycera	NA	Bombyliidae	*Bombylius*	*Bombylius major*	2
D057	Diptera	NA	NA	NA	*NA*	*NA*	1
D058	Diptera	Brachycera	NA	Muscidae	*NA*	*NA*	5
D059	Diptera	Brachycera	NA	Muscidae	*NA*	*NA*	4
D060	Diptera	Brachycera	NA	Muscidae	*NA*	*NA*	1
D061	Diptera	Brachycera	NA	Muscidae	*NA*	*NA*	1
D062	Diptera	Brachycera	NA	Muscidae	*NA*	*NA*	21
D063	Diptera	Brachycera	NA	Muscidae	*NA*	*NA*	2
D064	Diptera	Brachycera	NA	Muscidae	*NA*	*NA*	1

D065	Diptera	Brachycera	NA	Muscidae	*NA*	*NA*	1
D066	Diptera	Brachycera	NA	Muscidae	*NA*	*NA*	1
D067	Diptera	Brachycera	NA	Muscidae	*NA*	*NA*	2
D068	Diptera	Brachycera	NA	Muscidae	*NA*	*NA*	1
D069	Diptera	Brachycera	NA	Muscidae	*NA*	*NA*	2
D070	Diptera	Brachycera	NA	Muscidae	*NA*	*NA*	4
D071	Diptera	Brachycera	NA	Tachinidae	*Dexia*	*Dexia rustica*	2
D072	Diptera	Brachycera	NA	Anthomyiidae	*NA*	*NA*	1
D073	Diptera	Brachycera	NA	Tachinidae	*NA*	*NA*	1
D074	Diptera	Brachycera	NA	Tachinidae	*NA*	*NA*	2
D075	Diptera	Brachycera	NA	Tachinidae	*NA*	*NA*	2
D076	Diptera	Brachycera	NA	Tachinidae	*Gymnosoma*	*Gymnosoma rotundatum*	2
D077	Diptera	Brachycera	NA	Tachinidae	*NA*	*NA*	6
D078	Diptera	Brachycera	NA	Tachinidae	*NA*	*NA*	1
D079	Diptera	Brachycera	NA	Tachinidae	*NA*	*NA*	3
D080	Diptera	Brachycera	NA	Tachinidae	*NA*	*NA*	1
D081	Diptera	Brachycera	NA	Tachinidae	*NA*	*NA*	2
D082	Diptera	Nematocera	NA	Bibionidae	*NA*	*NA*	6
D083	Diptera	Nematocera	NA	Bibionidae	*NA*	*NA*	1
D084	Diptera	Nematocera	NA	Bibionidae	*NA*	*NA*	4
D085	Diptera	Brachycera	NA	Lauxaniidae	*NA*	*NA*	1
D087	Diptera	Brachycera	NA	Rhinophoridae	*NA*	*NA*	1
D088	Diptera	Brachycera	NA	Sepsidae	*NA*	*NA*	1
D089	Diptera	Nematocera	Sciaroidea	Mycetophilidae	*NA*	*NA*	1
D090	Diptera	Brachycera	NA	Platypezidae	*NA*	*NA*	1
D091	Diptera	Brachycera	NA	Calliphoridae	*NA*	*NA*	1
D092	Diptera	Brachycera	NA	Calliphoridae	*NA*	*NA*	1
D093	Diptera	Brachycera	NA	Calliphoridae	*NA*	*NA*	1
D094	Diptera	Brachycera	NA	Calliphoridae	*NA*	*NA*	1
D095	Diptera	Brachycera	NA	Calliphoridae	*NA*	*NA*	1
D096	Diptera	Brachycera	NA	Scathophagidae	*NA*	*NA*	1
D097	Diptera	Brachycera	NA	Scathophagidae	*NA*	*NA*	1
D099	Diptera	Brachycera	NA	Fanniidae	*NA*	*NA*	1
D100	Diptera	Brachycera	NA	Fanniidae	*NA*	*NA*	1
D101	Diptera	Brachycera	NA	Fanniidae	*NA*	*NA*	1
D102	Diptera	Nematocera	Pachyneuroidea	Pachyneuridae	*NA*	*NA*	1
D103	Diptera	Nematocera	Tipuloidea	Cylindrotomidae	*NA*	*NA*	1
D104	Diptera	Nematocera	Tipuloidea	Tipulidae	*Tipula*	*Tipula sp*	3
D105	Diptera	Nematocera	Tipuloidea	Tipulidae	*Nephrotoma*	*Nephrotoma terminalis*	9
D106	Diptera	Nematocera	Tipuloidea	Tipulidae	*Tipula*	*Tipula sp*	3
D107	Diptera	Nematocera	Tipuloidea	Tipulidae	*Tipula*	*Tipula sp*	2
H001	Hymenoptera	Symphyta	Tenthredinoidea	Tenthredinidae	*NA*	*NA*	1
H002	Hymenoptera	Symphyta	Tenthredinoidea	Tenthredinidae	*NA*	*NA*	4
H003	Hymenoptera	Symphyta	Tenthredinoidea	Tenthredinidae	*NA*	*NA*	1
H004	Hymenoptera	Symphyta	Tenthredinoidea	Tenthredinidae	*NA*	*NA*	1
H005	Hymenoptera	Symphyta	Cephoidea	Cephidae	*NA*	*NA*	3
H006	Hymenoptera	Symphyta	Cephoidea	Cephidae	*NA*	*NA*	1
H007	Hymenoptera	Apocrita	Vespoidea	Vespidae	*Polistes*	*Polistes dominulus*	1
H008	Hymenoptera	Apocrita	Vespoidea	Vespidae	*Polistes*	*Polistes nimpha*	2

H009	Hymenoptera	Apocrita	Apoidea	Crabronidae	*Ectemnius*	*Ectemnius sp*	1
H010	Hymenoptera	Apocrita	Apoidea	Crabronidae	*Ectemnius*	*Ectemnius sp*	1
H011	Hymenoptera	Apocrita	Apoidea	Crabronidae	*Lindenius*	*Lindenius sp*	2
H012	Hymenoptera	Apocrita	Ichneumonoidea	Braconidae	*NA*	*NA*	1
H013	Hymenoptera	Apocrita	Ichneumonoidea	Braconidae	*NA*	*NA*	1
H014	Hymenoptera	Apocrita	Ichneumonoidea	Braconidae	*NA*	*NA*	1
H015	Hymenoptera	Apocrita	Ichneumonoidea	Ichneumonidae	*NA*	*NA*	2
H016	Hymenoptera	Apocrita	Ichneumonoidea	Ichneumonidae	*NA*	*NA*	1
H017	Hymenoptera	Apocrita	Ichneumonoidea	Ichneumonidae	*NA*	*NA*	2
H018	Hymenoptera	Apocrita	Ichneumonoidea	Ichneumonidae	*NA*	*NA*	1
H019	Hymenoptera	Apocrita	Ichneumonoidea	Ichneumonidae	*NA*	*NA*	1
H020	Hymenoptera	Apocrita	Ichneumonoidea	Ichneumonidae	*NA*	*NA*	1
H021	Hymenoptera	Apocrita	Ichneumonoidea	Ichneumonidae	*NA*	*NA*	1
H022	Hymenoptera	Apocrita	Ichneumonoidea	Ichneumonidae	*NA*	*NA*	1
H023	Hymenoptera	Apocrita	Ichneumonoidea	Ichneumonidae	*NA*	*NA*	1
H024	Hymenoptera	Apocrita	Ichneumonoidea	Ichneumonidae	*NA*	*NA*	1
H025	Hymenoptera	Apocrita	Ichneumonoidea	Ichneumonidae	*NA*	*NA*	1
H026	Hymenoptera	Apocrita	Ichneumonoidea	Ichneumonidae	*NA*	*NA*	1
H027	Hymenoptera	Apocrita	Ichneumonoidea	Ichneumonidae	*NA*	*NA*	1
H028	Hymenoptera	Apocrita	Ichneumonoidea	Ichneumonidae	*NA*	*NA*	1
H029	Hymenoptera	Apocrita	Ichneumonoidea	Ichneumonidae	*NA*	*NA*	2
H030	Hymenoptera	Apocrita	Ichneumonoidea	Ichneumonidae	*NA*	*NA*	1
H031	Hymenoptera	Apocrita	Ichneumonoidea	Ichneumonidae	*NA*	*NA*	1
H032	Hymenoptera	Apocrita	Platygastroidea	Platygastridea	*NA*	*NA*	1
H033	Hymenoptera	Apocrita	Vespoidea	Formicidae	*Stenamma*	*Stenamma sp*	1
H034	Hymenoptera	Apocrita	Vespoidea	Formicidae	*NA*	*NA*	13
H035	Hymenoptera	Apocrita	Vespoidea	Formicidae	*NA*	*NA*	1
H036	Hymenoptera	Apocrita	Vespoidea	Formicidae	*NA*	*NA*	2
H037	Hymenoptera	Apocrita	Vespoidea	Formicidae	*NA*	*NA*	1
H038	Hymenoptera	Apocrita	Cnypoidea	Eucoilidae	*NA*	*NA*	1
H039	Hymenoptera	Apocrita	Ichneumonoidea	Braconidae	*NA*	*NA*	2
L001	Lepidoptera	NA	Papilionoidea	Nymphalidae	*Melanargia*	*Melanargia galatea*	1
L002	Lepidoptera	NA	Papilionoidea	Nymphalidae	*Aphantopus*	*Aphantopus hyperanthus*	5
L003	Lepidoptera	NA	Papilionoidea	Pieridae	*Pieris*	*Pieris rapae*	16
L004	Lepidoptera	NA	Papilionoidea	Pieridae	*Pieris*	*Pieris brassicae*	4
L005	Lepidoptera	NA	Papilionoidea	Pieridae	*Gonopteryx*	*Gonopteryx rhamni*	1
L006	Lepidoptera	NA	Papilionoidea	Pieridae	*Pieris*	*Pieris napi*	3
L007	Lepidoptera	NA	Papilionoidea	Nymphalidae	*Araschnia*	*Araschnia levana*	1
L008	Lepidoptera	NA	Papilionoidea	Nymphalidae	*Aglais*	*Aglais urticae*	38
L009	Lepidoptera	NA	Papilionoidea	Nymphalidae	*Maniola*	*Maniola jurtina*	26
L010	Lepidoptera	NA	Papilionoidea	Hesperidae	*Thymelicus*	*Thymelicus sylvestris*	4
L011	Lepidoptera	NA	Papilionoidea	Hesperidae	*Ochlodes*	*Ochlodes sylvanus*	1
L012	Lepidoptera	NA	Papilionoidea	Hesperidae	*Carcharodus*	*Carcharodus alcae*	1
L013	Lepidoptera	NA	Papilionoidea	Hesperidae	*Thymelicus*	*Thymelicus lineola*	47
L014	Lepidoptera	NA	Bombycoidea	Sphingidae	*Macroglossum*	*Macroglossum stellatarum*	1
L015	Lepidoptera	NA	Pterophoroidea	Pterophoridae	*Emmelina*	*Emmelina monodactyla*	1
L016	Lepidoptera	NA	NA	NA	*NA*	*NA*	1
L017	Lepidoptera	NA	Adeloidea	Adelidae	*Nemophora*	*Nemophora metallica*	1
L018	Lepidoptera	NA	NA	NA	*NA*	*NA*	2

L020	Lepidoptera	NA	NA	NA	*NA*	*NA*	1
L021	Lepidoptera	NA	NA	NA	*NA*	*NA*	1
L022	Lepidoptera	NA	NA	NA	*NA*	*NA*	1
L023	Lepidoptera	NA	NA	NA	*NA*	*NA*	5
L024	Lepidoptera	NA	NA	NA	*NA*	*NA*	2
M001	Mecoptera	NA	NA	Panorpidae	*Panorpa*	*Panorpa communis*	14
N001	Neuroptera	Hemerobiiformia	NA	Chrysopidae	*Chrysopa*	*Chrysopa sp*	2
N002	Neuroptera	Hemerobiiformia	NA	Chrysopidae	*Nineta*	*Nineta flava*	2
S001	Diptera	Brachycera	Syrphoidea	Syrphidae	*Syritta*	*Syritta pipiens*	38
S002	Diptera	Brachycera	Syrphoidea	Syrphidae	*Eumerus*	*Eumerus strigatus*	22
S003	Diptera	Brachycera	Syrphoidea	Syrphidae	*Cheilosia*	*Cheilosia impressa group sp*	16
S004	Diptera	Brachycera	Syrphoidea	Syrphidae	*Lejogaster*	*Lejogaster tarsata*	1
S005	Diptera	Brachycera	Syrphoidea	Syrphidae	*Lejogaster*	*Lejogaster metallina*	6
S006	Diptera	Brachycera	Syrphoidea	Syrphidae	*Melanostoma*	*Melanostoma mellinum*	3
S007	Diptera	Brachycera	Syrphoidea	Syrphidae	*Melanostoma*	*Melanostoma scalare*	2
S008	Diptera	Brachycera	Syrphoidea	Syrphidae	*Cheilosia*	*Cheilosia bergenstammi group sp*	1
S009	Diptera	Brachycera	Syrphoidea	Syrphidae	*Pipizella*	*Pipizella sp*	3
S010	Diptera	Brachycera	Syrphoidea	Syrphidae	*Parhelophilus*	*Parhelophilus frutetorum*	1
S011	Diptera	Brachycera	Syrphoidea	Syrphidae	*Sphaerophoria*	*Sphaerophoria sp*	110
S012	Diptera	Brachycera	Syrphoidea	Syrphidae	*Platycheirus*	*Platycheirus sp*	14
S013	Diptera	Brachycera	Syrphoidea	Syrphidae	*Syrphus_Parasyrphus*	*Syrphus Parasyrphus sp*	8
S014	Diptera	Brachycera	Syrphoidea	Syrphidae	*Cheilosia*	*Cheilosia illustrata*	1
S015	Diptera	Brachycera	Syrphoidea	Syrphidae	*Cheilosia*	*Cheilosia grossa*	1
S016	Diptera	Brachycera	Syrphoidea	Syrphidae	*Myathropa*	*Myathropa florea*	1
S017	Diptera	Brachycera	Syrphoidea	Syrphidae	*Parasyrphus*	*Parasyrphus sp*	2
S018	Diptera	Brachycera	Syrphoidea	Syrphidae	*Ersitalis*	*Eristalis sp*	31
S019	Diptera	Brachycera	Syrphoidea	Syrphidae	*Episyrphus*	*Episyrphus balteatus*	60
S020	Diptera	Brachycera	Syrphoidea	Syrphidae	*Eupeodes*	*Eupeodes lapponicus*	8
S021	Diptera	Brachycera	Syrphoidea	Syrphidae	*Eristalis*	*Eristalis interrupta*	6
S022	Diptera	Brachycera	Syrphoidea	Syrphidae	*Helophilus*	*Helophilus pendulus*	8
S023	Diptera	Brachycera	Syrphoidea	Syrphidae	*Helophilus*	*Helophilus trivitattus*	4
S024	Diptera	Brachycera	Syrphoidea	Syrphidae	*Eristalis*	*Eristalis similis*	1
S025	Diptera	Brachycera	Syrphoidea	Syrphidae	*Eristalis*	*Eristalis arbustorum*	2
S026	Diptera	Brachycera	Syrphoidea	Syrphidae	*Eristalis*	*Eristalis pertinax*	3
S027	Diptera	Brachycera	Syrphoidea	Syrphidae	*Epistrophe*	*Epistrophe nitidicollis*	1
S028	Diptera	Brachycera	Syrphoidea	Syrphidae	*Helophilus*	*Helophilus hybridus*	2
S029	Diptera	Brachycera	Syrphoidea	Syrphidae	*Sphiximorpha*	*Sphiximorpha subsessilis*	1
S030	Diptera	Brachycera	Syrphoidea	Syrphidae	*Chrysotoxum*	*Chrysotoxum cautum*	2
S031	Diptera	Brachycera	Syrphoidea	Syrphidae	*Chrysotoxum*	*Chrysotoxum bicinctum*	1
S032	Diptera	Brachycera	Syrphoidea	Syrphidae	*Eupeodes*	*Eupeodes luniger*	5
S033	Diptera	Brachycera	Syrphoidea	Syrphidae	*Chrysotoxum*	*Chrysotoxum festivum*	1
S034	Diptera	Brachycera	Syrphoidea	Syrphidae	*Volucella*	*Volucella pellucens*	2
S035	Diptera	Brachycera	Syrphoidea	Syrphidae	*Volucella*	*Volucella bombylans*	1
S036	Diptera	Brachycera	Syrphoidea	Syrphidae	*Eupeodes*	*Eupeodes corollae*	2
S037	Diptera	Brachycera	Syrphoidea	Syrphidae	*Eristalis*	*Eristalis tenax*	90
S038	Diptera	Brachycera	Syrphoidea	Syrphidae	*Brachypalpoides*	*Brachypalpoides lentus*	1
S039	Diptera	Brachycera	Syrphoidea	Syrphidae	*NA*	*NA*	8
W001	Hemiptera	Heteroptera	Miroidae	Miridae	*Closterotomus*	*Closterotomus norvegicus*	34

W002	Hemiptera	Heteroptera	Pentatomoidae	Pentatomidae	*Dolycoris*	*Dolycoris baccarum*	12
W003	Hemiptera	Heteroptera	Coreoidae	Coreidae	*Coreus*	*Coreus marginatus*	4
W004	Hemiptera	Heteroptera	Pentatomoidae	Pentatomidae	*Peribalus*	*Peribalus strictus*	2
W005	Hemiptera	Heteroptera	Pentatomoidae	Pentatomidae	*Carpocoris*	*Carpocoris fuscispinus*	2
W006	Hemiptera	Heteroptera	Pentatomoidae	Pentatomidae	*Carpocoris*	*Carpocoris purpureipennis*	1
W007	Hemiptera	Heteroptera	Pentatomoidae	Pentatomidae	*Palomena*	*Palomena prasina*	1
W008	Hemiptera	Heteroptera	Lygaeoidae	Lygaeidae	*Rhyparochromus*	*Rhyparochromus vulgaris*	1
W009	Hemiptera	Heteroptera	Coreoidae	Rhopalidae	*Stictopleurus*	*Stictopleurus punctatonervosus*	1
W010	Hemiptera	Heteroptera	Miroidae	Miridae	*Stenodema*	*Stenodema laevigata*	2
W011	Hemiptera	Heteroptera	Miroidae	Miridae	*Capsodes*	*Capsodes gothicus*	2
W012	Hemiptera	Heteroptera	Miroidae	Miridae	*Leptopterna*	*Leptopterna dolabrata*	14
W013	Hemiptera	Heteroptera	Miroidae	Miridae	*Lygus*	*Lygus pratensis*	3
W014	Hemiptera	Heteroptera	Miroidae	Miridae	*Lygus*	*Lygus sp*	2
W015	Hemiptera	Heteroptera	NA	NA	*NA*	*NA*	13
W016	Hemiptera	Heteroptera	NA	NA	*NA*	*NA*	5
W017	Hemiptera	Heteroptera	NA	NA	*NA*	*NA*	1
W018	Hemiptera	Heteroptera	NA	NA	*NA*	*NA*	6
W019	Hemiptera	Heteroptera	NA	NA	*NA*	*NA*	1
W020	Hemiptera	Heteroptera	NA	NA	*NA*	*NA*	1
W021	Hemiptera	Heteroptera	Miroidae	Miridae	*NA*	*NA*	1
W022	Hemiptera	Heteroptera	Miroidae	Miridae	*NA*	*NA*	1
W023	Hemiptera	Heteroptera	Miroidae	Miridae	*NA*	*NA*	1
W024	Hemiptera	Heteroptera	Miroidae	Miridae	*NA*	*NA*	5
W025	Hemiptera	Heteroptera	Miroidae	Miridae	*NA*	*NA*	23
X001	Dermaptera	NA	NA	NA	*NA*	*NA*	1
X002	Ensifera	NA	NA	NA	*NA*	*NA*	1
X003	Ensifera	NA	NA	NA	*NA*	*NA*	1
Z001	Hemiptera	Cicadomorpha	Cercopoidae	Cercopidae	*Ceropis*	*Cercopis vulnerata*	5
Z002	Hemiptera	Cicadomorpha	Cercopoidae	Aphrophoridae	*Philaenus*	*Philaenus spumarius*	8
Z003	Hemiptera	Cicadomorpha	Cercopoidae	Aphrophoridae	*Aphrophora*	*Aphrophora alni*	2
Z004	Hemiptera	Cicadomorpha	Membracoidae	Cicadelidae	*Diplocolenus*	*Diplocolenus bohemani*	1
Z005	Hemiptera	Cicadomorpha	NA	NA	*NA*	*NA*	1
Z006	Hemiptera	Cicadomorpha	NA	NA	*NA*	*NA*	1
Z007	Hemiptera	Cicadomorpha	NA	NA	*NA*	*NA*	1

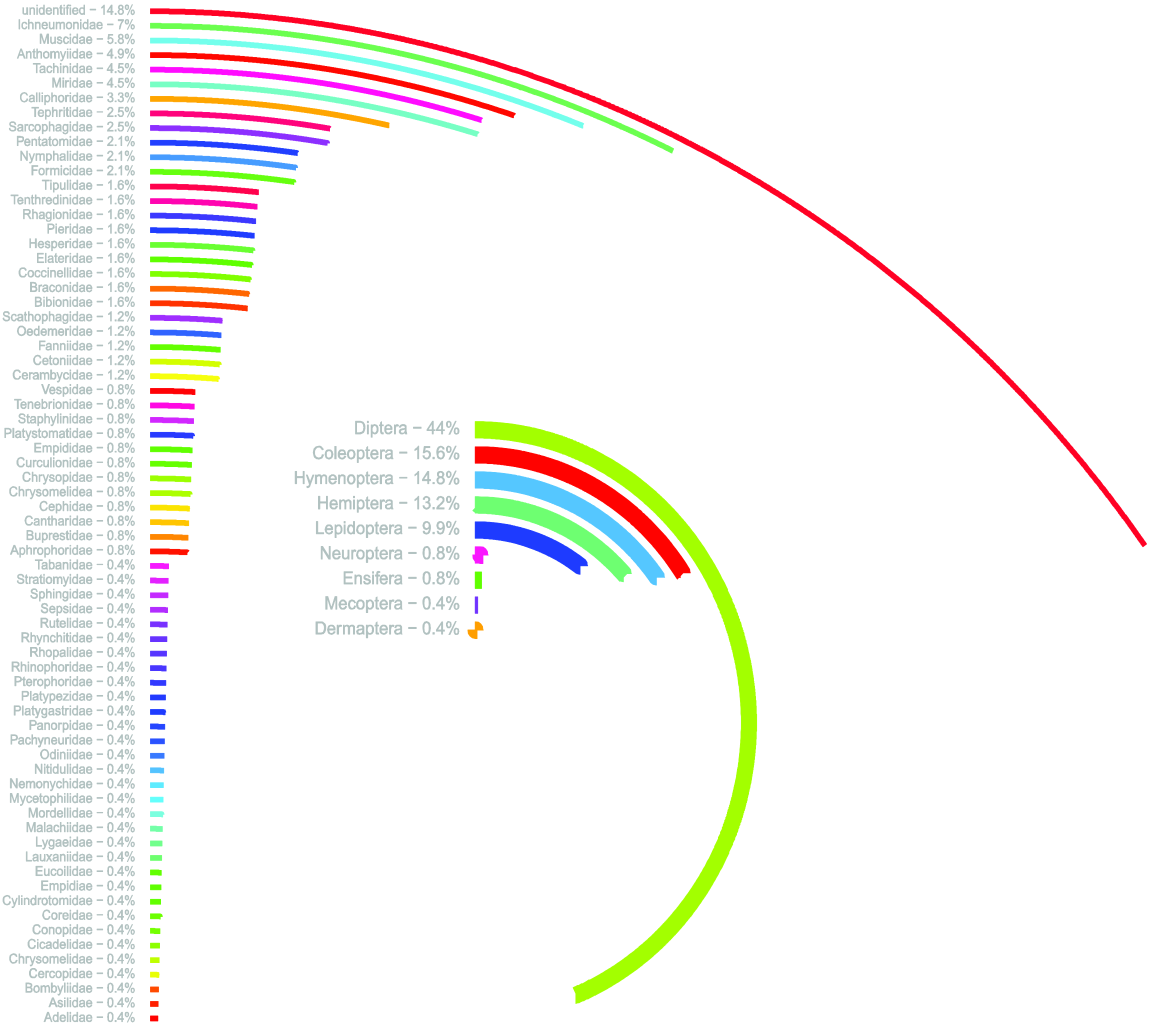


Figure A.1. Composition of those flower visitors that were not part of the three groups *A. mellifera*, wild bees or hoverflies. Shown are percentages of the number of species at the family and order level. Overall, 241 (74.8 %) out of the 322 sampled species were not bees or hoverflies.

KAPITEL III – BLÜHFLÄCHEN IM LANDSCHAFTSKONTEXT

SPATIAL CONFIGURATION AND LANDSCAPE CONTEXT OF FLOWERING FIELDS DETERMINE THEIR BENEFITS TO POLLINATOR α- AND β-DIVERSITY

Warzecha D, Diekötter T, Wolters V, Jauker F

Erschienen 2021 in *Basic and Applied Ecology* 56: 335–344

ELSEVIER

GfÖ
GfÖ Ecological Society of Germany,
Austria and Switzerland

Basic and Applied Ecology 56 (2021) 335−344

Basic and
Applied Ecology

www.elsevier.com/locate/baae

Spatial configuration and landscape context of wildflower areas determine their benefits to pollinator α- and β-diversity

Daniela Warzecha[a,b,*], Tim Diekötter[a,c], Volkmar Wolters[a], Frank Jauker[a]

[a]*Department of Animal Ecology, Justus Liebig University Giessen, Heinrich-Buff-Ring 26-32, Giessen D-35392, Germany*
[b]*Department of Terrestrial Zoology, Entomology III, Senckenberg Research Institute and Natural History Museum Frankfurt, Senckenberganlage 25, Frankfurt D-60325, Germany*
[c]*Department of Landscape Ecology, Institute for Natural Resource Conservation, Kiel University, Olshausenstrasse 75, Kiel D-24118, Germany*

Abstract

Wildflower areas have become a staple tool within agro-environmental schemes (AES) to counteract pollinator declines. While their role in providing food resources to resident flower-visiting insects is unambiguous, the conservation effectiveness in a landscape context is less clear. Particularly, how multiple vs. single wildflower area utilization differs between simple and complex landscapes is understudied. We examined colonisation and community dynamics of wild bees and hoverflies in 33 newly established wildflower areas across a gradient of landscape complexity (amount of semi-natural habitat) and connectivity (presence of additional wildflower areas) for seven weeks during three consecutive years (one year during and two after establishment). We recorded more than 25% of the wild bee and hoverfly species of Hesse in an area of approx. 10 ha, substantiating the general benefit of wildflower areas to pollinators. While alpha-diversity increased with landscape complexity in isolated wildflower areas, the opposite pattern was observed for connected areas. The low alpha-diversity in complex landscapes indicated a dilution effect between connected sites. The inverse relationship between alpha and beta diversity among wildflower areas within landscapes suggests interspecific trade-offs between local resource conditions and landscape context. Accordingly, the establishment of multiple wildflower areas within AES is advisable to increase connectivity of suitable habitats in simple landscapes. Moreover, adjusting local conditions (plant diversity) to landscape context likely optimizes conservation effectiveness in modern agroecosystems.

Keywords: Agri-environment scheme (AES); community structure; flower strips; flower visitors; landscape structure; syrphidae; wildflower plantings

---

Introduction

Agro-biodiversity decline is driven by multiple and interacting stressors (Brook et al., 2008), but loss, isolation, and degradation of resource-rich semi-natural habitats are considered major drivers (Potts et al. 2010; Foley et al. 2011). Wildflower areas initiated by financial compensation to farmers for lost income within agri-environmental schemes (AES) have become a staple measure to counteract loss of resources and to promote biological diversity, including that of flower-visiting insects, in agricultural areas (Haaland et al., 2011). While increased pollen and nectar availability in wildflower areas results in higher pollinator abundance and richness compared to conventionally

---

*Corresponding author at: Department of Terrestrial Zoology, Entomology III, Senckenberg Research Institute and Natural History Museum Frankfurt, Senckenberganlage 25, Frankfurt D-60325, Germany.
E-mail address: daniela.warzecha@senckenberg.de (D. Warzecha).

https://doi.org/10.1016/j.baae.2021.08.001
1439-1791/© 2021 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

managed crop fields (e.g. Carvell et al. 2007; Korpela et al. 2013), diversity effects vary substantially among AES sites (Scheper et al., 2013; Batáry et al., 2015). We argue that wildflower areas, in order to effectively counteract biodiversity declines, need to be optimized beyond the habitat scale by adjusting the configuration of implemented measures to the surrounding landscape structure. Thus, we studied the effects of isolated versus multiple connected wildflower areas in dependence of their landscape context on the diversity of wild bees and hoverflies.

A likely explanation for the variation in conservation effectiveness of wildflower areas, even within regions, is that most species are not confined to a specific locality but are dynamically using multiple, spatially dispersed partial habitats. As central-place foragers, wild bees are dependent on habitat elements for nesting and foraging within their activity ranges (Westrich, 2019). Although other pollinating taxa, like hoverflies, lack the necessity to return to nests and thus this spatial restriction, they too utilize different partial habitats for e.g. flower visitation and oviposition. Accordingly, small-scale contrast in flower resource availability is but one driver for pollinator diversity in wildflower areas (Scheper et al., 2015). Hence, it has been hypothesized that landscape context moderates the effectiveness of flowering AES (Tscharntke et al., 2012), even though multi-year landscape-ecological studies on the colonization of and species composition in wildflower areas are scarce (but see Scheper et al. 2015).

While it is assumed that flowering AES reveal the best response of pollinators in simple landscapes (Batáry et al., 2011; Scheper et al., 2013), these postulations are based on species numbers for restricted sites (alpha diversity) on small scales. Composition of pollinator communities, however, varies substantially over time (Kremen et al., 2002) and across regions (Winfree et al., 2018). A feedback between local and regional processes, moderating local community assemblage from regional species pools (Mittelbach & Schemske, 2015), may similarly be expected for wildflower areas. Accordingly, the spatio-temporal variation in pollinator communities is important for the development of spatially explicit best management practices adjusted to differently structured landscapes (Burkle et al., 2020). Consideration of species turnover (beta diversity) between sites and years is thus required to understand diversity effects apparent only at larger scales (Scherber et al., 2019) and to reveal how landscape context structures pollinator communities utilizing newly created wildflower areas as partial foraging habitats (Landis, 2017).

Here, we study how landscape context and the spatial arrangement of newly established wildflower areas shape community structures of wild bees and hoverflies to infer conservation effectiveness. We examine colonisation and community dynamics of wild bees and hoverflies in wildflower areas during three consecutive years (one year during and two years after establishment) across a gradient of landscape complexity (amount of semi-natural habitat) and connectivity (presence of additional wildflower areas in the landscape). First, we establish the general effect of landscape context on local communities in wildflower areas during establishment, i.e. in the absence of a distinct flowering aspect. We hypothesise a positive effect of landscape complexity on local communities (alpha diversity). Second, we assess the effect of landscape context on community structures after establishment of wildflower areas, including effects of wildflower area connectivity, in the subsequent years. We hypothesise a positive effect of wildflower area connectivity on local communities in simple landscapes resulting in a higher alpha diversity. Third, we address how communities differ among sites within the same landscapes during and after establishment of wildflower areas in relation to landscape context. We hypothesise that larger differences among local communities resulting in a higher beta diversity within complex landscapes and after establishment.

Materials and methods

Study area

The study was carried out in the county of Marburg-Biedenkopf (Hesse, Germany), covering an area of approximately 1260 km^2 (44% under agricultural use, 41% forest, 14% settlement and traffic, and 1% covered by water) (Maps are given in Appendix A: Fig. S1). Starting in 2010, subsidized wildflower areas were established within the regional AES ‘HIAP’ (Hessian Integrated Agri-environmental Program). Local farmers were contracted for the establishment of wildflower areas on previously cultivated arable land. After establishment, these wildflower areas were left undisturbed for five years without mowing and application of pesticides or fertilizer.

Study sites

Out of 194 subsidized wildflower areas established within the county in 2011, we selected a total of 33 as study sites. Main study sites ($N = 22$) were equally assigned to one of two isolation classes: “isolated” (no additional wildflower areas present within a radius of 500 m) and “connected” (at least one additional wildflower area present within a radius of 500 m). No additional wildflower areas were established within the radius of 500 m for the duration of the examination to ensure independence of isolation classes as the majority of wild bees forage at distances between 100−300 m (Zurbuchen et al., 2010b). Around each site, we assessed the main land-use types at four radii (125, 250, 375 and 500 m) for each study year using current InVeKoS data provided by the local nature conservation authority in ArcGIS 10 (ESRI, Ca., USA). We did not consider radii above 500 m to avoid spatial autocorrelation due to overlapping radii. As the proportion of land-use types barely differed between years, we averaged across years for each type. Sites represented a distinct gradient in landscape structure represented by the percentage of area covered by semi-natural habitats (hedges, gardens, alluvial meadows, clear cuttings, tree rows, quarries, orchards, and the respective study site; 4.2−14.0%; mean 8.9 ± 2.2% standard deviation STD), permanent grasslands (6.2−35.5%; 19.8 ± 8.2% STD) and arable land (17.4−81.9%; 46.5 ± 21.0% STD) and covered a broad geographic range (distance between sites 911−9,856 m; 2,520 ± 1919 m STD). Because landscape variables were highly intercorrelated, we ran a correlation matrix between all subsequent dependent variables with landscape variables at different spatial scales prior to analyses to identify the best predictor of landscape structure based on the highest correlation coefficient. Highest correlation coefficients for most dependent variables were achieved with cover of semi-natural habitat at a spatial scale of 500 m. We refer to this spatial scale as 'landscape' hereafter and this predictor was used for all subsequent analyses. Additional "satellite" sites ($N = 11$) were selected, representing the closest additional wildflower area to each "connected" site, resulting in eleven landscapes with an isolated wildflower area and eleven landscapes with a wildflower area connected to its satellite site. All study sites were similar in size (0.3 ± 0.04 ha STD; detailed information is given in Appendix B: Table S1).

Plant communities in wildflower areas

Because farmers could choose from different seed mixtures, sown seed mixtures differed randomly among sites. Field observations established that plant community composition varied substantially within seed mixture types. Accordingly, plant species composition was recorded on all study sites during peak flowering for the years 2012 and 2013. A 1 × 1 m frame was placed randomly at three sample points per site and all flowering plants present were recorded. Plant community data was unrelated to sown seed mixture and landscape parameters and was used in subsequent analyses to reflect flowering resource availability. Detailed information about sown seed mixtures and established plants within wildflower areas are given in Appendix B and Appendix C.

Pollinator sampling

To investigate benefits of wildflower areas for flower-visiting insects we chose bees (Hymenoptera: Apoidea: Apiformes) and hoverflies (Diptera: Syrphidae) as model organisms as they share a strong dependency on flower resources. Both are considered important pollinators (Rader et al., 2016) and we use the term 'pollinator' here although we did not quantify pollination efficiency in this study. Both taxa were sampled with yellow pan traps. Although pollinators, and especially wild bees, show colour preferences (Moreira et al., 2016), using pan traps of a single colour is an appropriate method to estimate relative wild bee species richness (Toler et al., 2005). As wildflower areas should fill gaps with reduced floral resources in agricultural landscapes later in the season (Scheper et al., 2014), sampling took place in midsummer for seven weeks from the beginning of June to the end of July in 2011, 2012 and 2013. Two traps were installed with an inter-trap distance of 20 m and placed in the middle of each wildflower area to avoid edge effects. They were emptied weekly and specimens were identified to species level in the lab. Due to late sowing of wildflower areas end of May 2011, a distinct flowering aspect was absent in the year of establishment and pan traps were placed on bare soil or sparsely covered arable fields when the sampling started in June (see Appendix A for vegetation and flowering aspects across years).

Because pan traps without co-flowering plants achieve best attraction of pollinators (Mayer, 2005), we used the first year as a baseline dataset representing the landscape-scale species pool. Similarly, analyses covering flower resources within wildflower areas are restricted to the following two years.

Statistical analysis

Pollinator communities during establishment of wildflower areas

We used separate linear models (lm-function in R) with the dependent variables alpha diversity (species richness) and abundance of all pollinators and wild bees (all bees except *Apis mellifera*) and hoverflies separately (collected in 2011). The predictor variable in these six models was the cover of semi-natural habitat within a 500 m radius around focal wildflower areas. Although we did not expect significant results in 2011, we added the isolation class (connected vs. isolated) and its interaction with cover of semi-natural habitat as co-variable to check for bias associated with isolation classes. Because seven out of the 22 wildflower areas did not feature bare soil but were instead covered by green herb vegetation (flower cover < 1% by visual estimation), we added a co-variable plant cover to account for co-variation.

All dependent variables were checked for normal distribution prior to analyses and all statistical models for homoscedasticity of residuals after analyses. Abundance of all pollinators and wild bees were log-transformed to meet assumptions.

Pollinator communities after establishment of wildflower areas

We used linear mixed-effect models (lme-function in *R*) with the dependent variables species richness and abundance of all pollinators and wild bees and hoverflies separately (collected in 2012 and 2013). The predictor variables in these six models were cover of semi-natural habitat within a 500 m radius around focal wildflower areas, isolation class (connected vs. isolated) and its interaction with cover of semi-natural habitat, the two-level factor year (to account for successional changes) and local taxonomic plant diversity in the wildflower areas for both years. We tested the highly correlated plant species number and plant family number separately in the models to account for local flower resources. No differences were detected and we used plant species number throughout for consistency. We added a random factor “site” to account for two annually subsequent samplings per site.

All dependent variables were checked for normal distribution prior to analyses and all statistical models for homoscedasticity of residuals after analyses. All dependent variables except species richness of all pollinators were log-transformed to meet assumptions.

Beta diversity of pollinator communities

Similar to community data, beta diversity in pollinator communities between connected study sites and their satellites within landscapes was analysed in a two-step approach. First, we were interested in differences within landscapes across years in general and in response to landscape structure to cover the effect of wildflower area establishment. We used linear mixed-effect models (lme-function in *R*) with the dependent variables beta diversity (Sørensen dissimilarity calculated with the functions betadiver and vegdist within the package vegan in *R*) of all pollinators and wild bees and hoverflies separately (across all years) and the predictor cover of semi-natural habitat within a 500 m radius around focal wildflower areas. We added the three-level factor year to account for successional changes and the interaction with cover of semi-natural habitat. We added the random factor “site” to account for three annually subsequent samplings per site.

Then, we were interested whether local flower resource diversity modulates responses in beta diversity between pollinator communities within landscapes. Because flower resources are only available in wildflower areas and not in baseline plots during establishment, we used only the years after establishment (2012, 2013). We used linear mixed-effect models (lme-function in *R*) with the dependent variables beta diversity of all pollinators and wild bees and hoverflies separately and the predictor cover of semi-natural habitat within a 500 m radius around focal wildflower areas. We added the two-level factor year to account for successional changes and the interaction with cover of semi-natural habitat within 500 m radius. We either used the highly correlated plant species number (for all pollinators and wild bees) or plant family number (for hoverflies) depending on model results. We added a random factor “site” to account for two annually subsequent samplings per site.

All dependent variables were checked for normal distribution prior to analyses and all statistical models for homoscedasticity of residuals after analyses. No transformation was necessary. All analyses were done in *R* version 3.6.2 (R Development Core Team, 2019).

Results

During three years of sampling, 16,305 specimens were collected belonging to the superfamily Apoidea and the family Syrphidae. Although wild bee and hoverfly abundance was considerably higher in 2011, number of species remained almost constant over the years (Table. 1). Given an overall number of 117 wild bee and 80 hoverfly species, species turnover between years was considerable. The predominant wild bee species were *Andrena flavipes* (20%) followed by *Bombus terrestris* agg. (15%) and *Bombus lapidarius* (12%). Overall, ground nesting species (mainly from the genera *Andrena* and *Lasioglossum*) were present in all consecutive years, cavity nesting species (mainly from the genera *Osmia, Megachile* and *Hylaeus*) were more common after establishment from the second year on (see Appendix E). *Episyrphus balteatus* and *Syrphus vitripennis* were the predominant syrphid species with 52 and 12% of all hoverflies (see Appendix D for a complete species list).

Pollinator communities during establishment

In the baseline year 2011, pollinator species richness increased significantly ($F_{1,17}$ = 4.97, *p* = 0.040) and abundance marginally ($F_{1,17}$ = 3.41, p = 0.082) with cover of semi-natural habitat (Fig. 1A, B). Separation of the pollinator groups showed that this pattern was based on wild bees, not hoverflies. Both species number ($F_{1,17}$ = 5.124, p = 0.035) and abundance (*F* = 8.10, *p*= 0.011) of wild bees were higher in more heterogeneous landscapes while hoverflies did not show a response to landscape complexity ($F_{1,17}$ < 1.21, *p*> 0.288) (Fig. 1A, B).

Plant cover had a significant effect on bee species richness ($F_{1,17}$ = 5.29, *p* = 0.034) and bee abundance ($F_{1,17}$ = 13.40, *p* = 0.002). The effect was marginally significant for pollinator species richness ($F_{1,17}$ = 3.95, *p* = 0.063) and hoverfly abundance ($F_{1,17}$ = 3.15, *p* = 0.094). Effects of isolation

Table 1. Numbers of species and individuals in each year for wild bees, hoverflies and combined recorded in the 33 study sites.

	Wild bees		Hoverflies		Combined	
	species	individuals	species	individuals	species	individuals
2011	79	4256	44	4702	123	8958
2012	80	1341	46	2006	126	3347
2013	78	1246	46	2754	124	4000

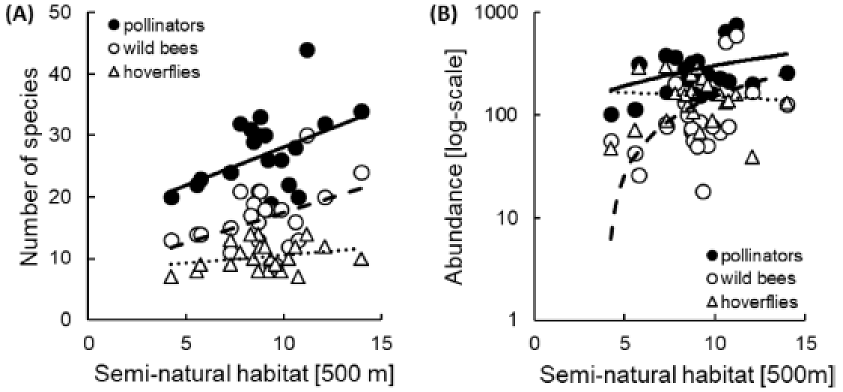


Fig. 1. Relation between the percentage of area covered by semi-natural habitat elements in a surrounding of 500 m around the 22 examined focal wildflower areas and the species number (A) and abundance (B) of all pollinators (black circles), wild bees (white circles) and hoverflies (white triangle) in the baseline year 2011 during establishment of wildflower areas.

class or the interaction between semi-natural habitat and isolation class were always non-significant ($F_{1,17} < 1.13$, $p > 0.302$).

Pollinator communities after establishment

After establishment of wildflower areas in the years 2012 and 2013, pollinator species richness showed a significant interaction between semi-natural habitat and isolation class ($F_{1,18} = 11.95$, $p = 0.003$). In isolated sites, species number increased with landscape complexity, while it decreased in connected sites (Fig. 2A). This trend remained when connected and satellite sites were pooled (although species numbers then exceeded isolated sites in most cases; Fig. 2A). Again, this pattern was based on wild bees which showed similar patterns in species richness ($F_{1,18} = 13.70$, $p = 0.002$; Fig. 2B). No further significances could be established for any explanatory or dependent variables.

Beta diversity of pollinator communities

Pollinator communities in established wildflower areas were less similar compared to those during establishment in the first year. This positive main effect was consistent for all pollinators ($F_{2,18} = 8.08$, $p = 0.003$; Fig. 3A), hoverflies ($F_{2,18} = 5.15$, $p = 0.017$; Fig. 3B) and wild bees ($F_{2,18} = 4.21$, $p = 0.031$). For bees, however, the effect increased with landscape complexity especially directly after establishment (interaction term year x semi-natural habitat; $F_{2,18} = 3.86$, $p = 0.040$; Fig. 3C).

After establishment, local plant resource diversity in wildflower areas marginally interacted with landscape

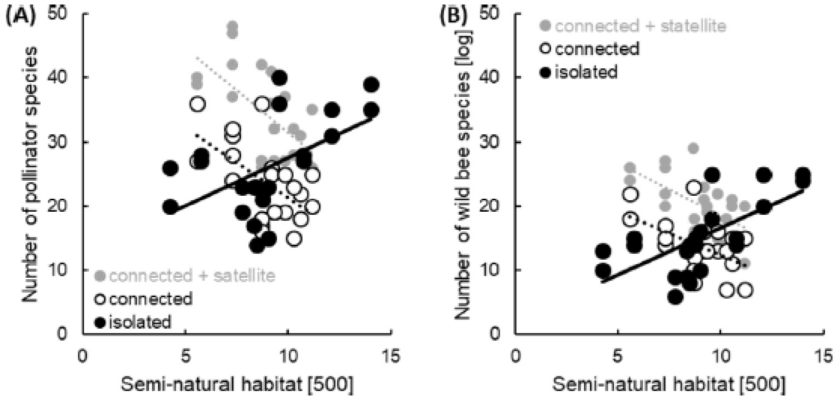


Fig. 2. Interactive relation between the percentage of area covered by semi-natural habitat elements in a surrounding of 500 m around connected (black circles) and isolated (white circles) focal wildflower areas on the species number of all pollinators (A) and wild bees (B) in the years 2012 and 2013. Plotted with grey circles and line are pooled data for connected sites and their satellite sites.

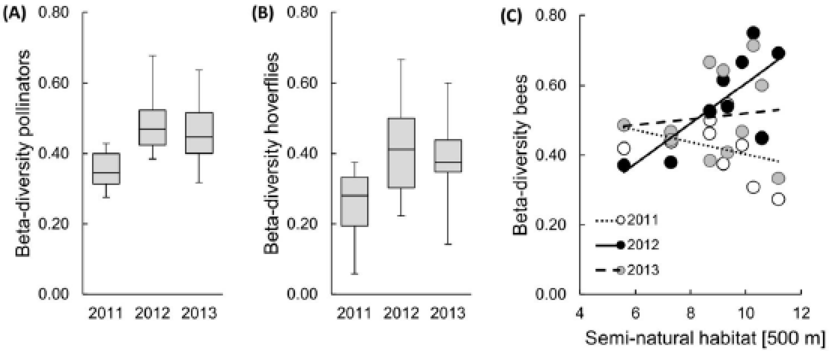


Fig. 3. Beta diversity between wildflower areas during establishment (2011) and between 11 connected wildflower areas and their satellites (2012, 2013) within landscapes for all pollinator (A), hoverfly (B) and wild bee (C) communities. For wild bees (C), the effect is more pronounced in landscapes with a high cover of semi-natural habitat in the first year of establishment.

complexity in affecting beta diversity for bees ($F_{1,8} = 3.51$, $p = 0.098$) and hoverflies ($F_{1,8} = 4.14$, $p = 0.076$). Because the effect of landscape complexity on beta diversity among wild bee communities increased with local flowering plant diversity (Fig. 4A), but decreased for hoverflies (Fig. 4B), no overall pollinator effect could be established.

Discussion

In an area of approximately 10 ha (0.0005% of the state area), we recorded 28% of the wild bee (Tischendorf, Frommer, Flügel, Schmalz, & Dorow, 2009) and 26% of the hoverfly fauna (Malec et al., 1999) of the federal state of Hesse. This number is especially remarkable, as sampling only covered the activity period of a part of the wild bee fauna (Westrich, 2019). Thus, our findings indicate that wildflower areas are a key AES for supporting pollinator communities, particularly in late summer when plant resources are scarce (Scheper et al., 2014). Benefits, however, are not general across landscapes or equal among pollinator groups, as dependence on landscape context was mostly evident for wild bees rather than for hoverflies. The observed species turnover over time and space was high and landscape-context dependent, suggesting that the utilization of flower resources within newly established AES is the result of trade-offs between local and landscape drivers. Our study is among the first to show that these trade-offs are moderated by the spatial arrangement of the newly established wildflower areas.

Before sown plants of wildflower areas were fully established (baseline year 2011), pollinator community structure in study sites was in line with most reports on landscape effects: Species richness and abundance increased with availability of neighbouring semi-natural habitat (Steffan-Dewenter et al., 2002; Ricketts et al., 2008). This pattern was mainly based on the response of wild bees, central-place foragers, which need to commute between different areas

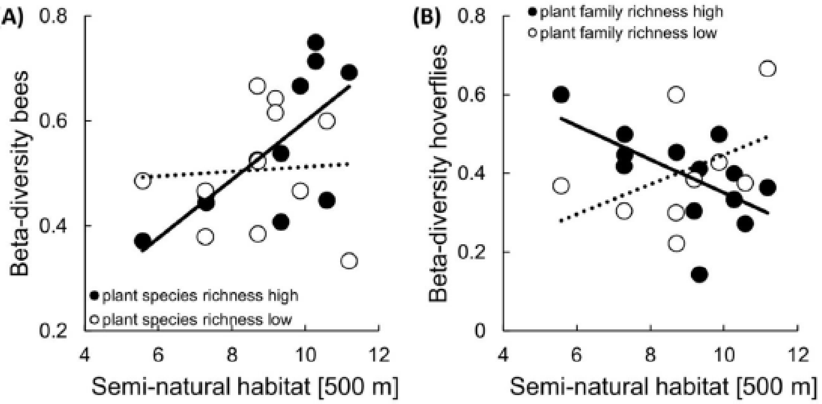


Fig. 4. Relationship of beta diversity between wild bee (A) and hoverfly (B) communities in wildflower areas interacting with high (black circles) and low (white circles) local plant family richness in the years 2012 and 2013.

they use for nesting sites, building material, and food plants (Westrich, 2019, Kleijn & van Langevelde, 2006). Because hoverflies do not have to return to their offspring after selecting suitable larval microhabitats for oviposition (Branquart & Hemptinne, 2000), they are less susceptible to habitat isolation at the landscape scale (Jauker et al., 2009; Aguirre-Gutiérrez et al., 2015), but equally affected by local habitat loss (Jauker et al., 2019). Although there was no distinct flowering aspect during the first year, plant cover had a (marginal) positive effect on species richness and abundance, confirming that most pollinators move easier across vegetated, non−tilled habitat patches than bare-soil fields (Clough et al., 2014). Still, the late sowing likely provided excellent nesting conditions on site to the first generation of the most frequent bivoltine bee species *Andrena flavipes, Andrena dorsata, Andrena bicolor* and *Andrena minutula*. This is emphasized by the fact that their respective cuckoos of the genus *Nomada* almost exclusively occurred in the first year (Appendix E).

After the establishment of wildflower areas (years 2012 and 2013), pollinator community structure in isolated wildflower areas mirrored landscape effects identified during establishment and the increase in species numbers along the gradient in neighbouring semi-natural habitat was remarkably similar (approx. 50% increase from under 20 species at 5% to over 30 species at 15% cover of semi-natural habitat). Abundances were considerably higher on sites during establishment, probably due to the prominent contrast of yellow pan traps (Saunders & Luck, 2013). Thus, the similar species numbers in wildflower areas were recorded at lower abundances than in the year during the establishment indicating a high attractiveness of the flower resources to a wide range of pollinator species within the local community.

Establishment of connected wildflower areas reversed the landscape effect on pollinator community structure. In simple landscapes, connected wildflower areas attracted up to 50% more species than isolated areas. This value approximately doubled when pooling pollinator communities of focal and their satellite sites, suggesting a combination of area (Blaauw & Isaacs, 2014) and connectivity effects (Haaland et al., 2011). In complex landscapes, by contrast, connected wildflower areas attracted fewer species than isolated areas, suggesting a dilution effect when resource availability increases with the cover of semi-natural habitats in the surrounding (Kleijn & van Langevelde, 2006, Wenninger et al., 2016). Additionally, establishment of multiple wildflower areas within landscapes almost inevitably leads to distinct plant communities, even when identical flower mixtures are applied (Warzecha et al., 2018). The resulting spatial heterogeneity in resource availability among habitat patches likely partitions pollinator communities into separate wildflower areas, increasing beta rather than alpha diversity within landscapes (Rösch et al., 2015).

Pollinator communities were generally more similar among wildflower areas during establishment than among wildflower areas after establishment. This is most likely due to increased local structural heterogeneity and flower diversity (Hewitt et al., 2005), as both bees and, to a lesser extent, hoverflies show preferences for plant genera or at least flower types. Beta diversity among wildflower areas within landscapes, however, was interactively dependent on local resource conditions and landscape context. Within complex landscapes, wildflower areas hosted specific subsets of the regional community, either because traits matched the local flower resources or the nesting resources in varying nearby (partial) habitats. Accordingly, turnover especially in small and rare species (mostly of the bee genera *Lasioglossum* and *Halictus* in our case) seems to be a major driver of beta diversity. In contrast, within structurally simple landscapes, wildflower areas host similar communities, because local factors prevail when neighbouring (partial) habitat diversity is low. This contrasting relationship between alpha and beta diversity suggests an additional role of biotic interactions in community structuring invoked by interspecific trade-offs (Kneitel & Chase, 2004): performing well in one partial habitat (e.g. wildflower area) comes at the cost of performance in another partial habitat (e.g. neighbouring partial habitats). When trade-offs promoting coexistence in wildflower areas are relevant at the local scale (e.g. flower resource partitioning), alpha diversity is relatively high, but beta diversity is relatively low. Alternatively, when trade-offs promoting coexistence in wildflower areas are relevant at the landscape scale (e.g. partial habitat partitioning), alpha diversity is low (restricted to good competitors / dispersers), and beta diversity is high because of species-specific responses to spatially dynamic and variable landscape conditions. Successional changes in floral composition of wildflower areas and the declining effect strength of landscape context on beta diversity over time suggest a continuum in trade-offs at both local and landscape scales for the co-utilization of flowering AES by regional pollinator communities, which is yet not fully understood.

Conclusion

Put into practice regarding wild bees, multiple wildflower areas are clearly beneficial in simple landscapes as they harboured more species (higher alpha diversity) compared to isolated wildflower areas. The fact that wild bee and hoverfly communities are more similar among closely connected sites (relatively low beta diversity) indicates that trade-offs at the landscape scale play a minor role, as the homogeneous landscape is likely limiting the regional species pool. In more complex landscapes, the relatively high beta diversity suggests considerable species turnover linked to relevant trade-offs at the landscape scale. A broad range of varying partial habitats provide niches for a diverse species pool. Here, the establishment of multiple wildflower areas within AES might shorten flight distances to suitable foraging patches, minimize energetic costs and facilitate bee survival (Zurbuchen et al., 2010a). However, the associated benefits relate to landscape scale diversity (see Kleijn et al. 2018) and conservation effectiveness may be apparent only at larger scales (Scherber et al., 2019).

The role of local plant species richness is similarly linked to landscape complexity. In simple landscapes, functional richness at a higher plant taxonomic level is more important than plant species richness per se (few species, but from different families; see also Warzecha et al. 2018). These local conditions are most effectively achieved by permanent or multi-year AES, because successional declines in plant species numbers are less important than permanency of resources (Albrecht et al., 2020). In complex landscapes, a high local plant species diversity relaxes interspecific competition among flower visitors, which is most effectively achieved in the first year of wildflower areas before successional declines (Albrecht et al., 2020) or partial mowing. Management practices like mowing not only reduce successional plant species decline but also preserve nesting sites for ground-nesting bees. Still, sections with overgrown vegetation benefit cavity-nesting bees that increasingly colonize wildflower areas from the second year on. Although it is still a major challenge, a framework incorporating effective amounts and duration of wildflower areas opens opportunities for managing AES in landscape contexts to increase conservation effectiveness in modern agroecosystems.

Declaration of Competing Interest

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

Acknowledgment

D. Warzecha was financially supported by the German Federal Environmental Foundation (DBU) with a PhD. scholarship. We thank M. Zerbe and K. Weiss of Amt für Ländlichen Raum Landkreis Marburg Biedenkopf for cooperation in site selection and farmers for access to their land. The Hessisches Ministerium für Energie, Landwirtschaft und Verbraucherschutz (HMUELV) and the Hessisches Landesamt für Umwelt, Naturschutz und Geologie (HLNUG) kindly provided digital land-use maps. We thank M. Gorski, A. Boufarra, A. G. Müller, U. S. Hoffmann, P. Schmidt, A. Wieske, A. Mattivi, M. Brohm and I. Hampel for assistance in the field, S. Ettling and V. L. Mader for providing the plant data and three anonymous reviewers for helpful comments.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2021.08.001.

References

Albrecht, M., Kleijn, D., Williams, N., Tschumi, M., Blaauw, B., Bommarco, R., et al. (2020). The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: a quantitative synthesis. *Ecology Letters*, *24*(8), 1738. doi:10.1111/ele.13576.

Aguirre-Gutiérrez, J., Biesmeijer, J. C., van Loon, E. E., Reemer, M., WallisDeVries, M. F., & Carvalheiro, L. G. (2015). Susceptibility of pollinators to ongoing landscape changes depends on landscape history. *Diversity and Distributions*, *21*, 1129–1140. doi:10.1111/ddi.12350.

Blaauw, B. R., & Isaacs, R. (2014). Larger patches of diverse floral resources increase insect pollinator density, diversity, and their pollination of native wildflowers. *Basic and Applied Ecology*, *15*, 701–711. doi:10.1016/j.baae.2014.10.001.

Batáry, P., Báldi, A., Kleijn, D., & Tscharntke, T. (2011). Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proceedings of the Royal Society B Biological Sciences*, *278*, 1894–1902. doi:10.1098/rspb.2010.1923.

Batáry, P., Dicks, L. V., Kleijn, D., & Sutherland, W. J. (2015). The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, *29*, 1006–1016. doi:10.1111/cobi.12536.

Branquart, E., & Hemptinne, J. L. (2000). Selectivity in the exploitation of floral resources by hoverflies (Diptera: Syrphinae). *Ecography*, *23*, 732–742. doi:10.1111/j.1600-0587.2000.tb00316.x.

Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. A. (2008). Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, *23*, 453–460. doi:10.1016/j.tree.2008.03.011.

Burkle, L. A., Delphia, C. M., & O`Neill, K. M (2020). Redundancy in wildflower strip species helps support spatiotemporal variation in wild bee communities on diversified farms. *Basic and Applied Ecology*, *44*, 1–13. doi:10.1016/j.baae.2020.02.005.

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

Clough, Y., Ekroos, J., Báldi, A., Batáry, P., Bommarco, R., Gross, N., et al. (2014). Density of insect-pollinated grassland plants decreases with increasing surrounding land-use intensity. *Ecology Letters*, *17*, 1168–1177. doi:10.1111/ele.12325.

Foley, J. A., Ramankutty, N., Brauman, K. A., Cassidy, E. S., Gerber, J. S., Johnston, M., et al. (2011). Solutions for a cultivated planet. *Nature*, *478*, 337–342. doi:10.1038/nature10452.

Haaland, C., Naisbit, R. E., & Bersier, L. F. (2011). Sown wildflower strips for insect conservation: A review. *Insect Conservation and Diversity*, *4*, 60–80. doi:10.1111/j.1752-4598.2010.00098.x.

Hewitt, J. E., Thrush, S. F., Halliday, J., & Duffy, C. (2005). The importance of small-scale habitat structure for maintaining beta diversity. *Ecology*, *86*, 1619–1626. doi:10.1890/04-1099.

Jauker, F., Diekötter, T., Schwarzbach, F., & Wolters, V. (2009). Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecology*, *24*, 547–555. doi:10.1007/s10980-009-9331-2.

Jauker, F., Jauker, B., Grass, I., Steffan-Dewenter, I., & Wolters, V. (2019). Partitioning wild bee and hoverfly contributions to plant-pollinator network structure in fragmented habitats. *Ecology*, *100*, 1–3. doi:10.1002/ecy.2569 https://doi.org/.

Kleijn, D., & van Langevelde, F. (2006). Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. *Basic and Applied Ecology*, *7*, 201–214. doi:10.1016/j.baae.2005.07.011.

Kleijn, D., Linders, T. E. W., Stip, A., Biesmeijer, J. C., Wäckers, F. L., & Bukovinszky, T. (2018). Scaling up effects of measures mitigating pollinator loss from local-to landscape-level population responses. *Methods in Ecology and Evolution*, *9*, 1727–1738. doi:10.1111/2041-210X.13017.

Kneitel, J. M., & Chase, J. M. (2004). Trade-offs in community ecology: Linking spatial scales and species coexistence. *Ecology Letters*, *7*, 69–80. doi:10.1046/j.1461-0248.2003.00551.x.

Korpela, E. L., Hyvönen, T., Lindgren, S., & Kuussaari, M. (2013). Can pollination services, species diversity and conservation be simultaneously promoted by sown wildflower strips on farmland? *Agriculture Ecosystems and Environment*, *179*, 18–24. doi:10.1016/j.agee.2013.07.001.

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

Landis, D. A. (2017). Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic and Applied Ecology*, *18*, 1–12.

Malec, F., Löhr, P. W., Geller-Grimm, F., Hauser, M., Mansfeld, P., & Stuke, J. H. (1999). Vorläufige Artenliste der Schwebfliegen Hessens (Diptera: Syrphidae). *Philippia*, *9*, 145–149.

Mayer, C. (2005). Does grazing influence bee diversity? In B. A. Huber, B. J. Sinclair, K. H. Lampe (Eds.), *African biodiversity: molecules, organisms, ecosystems* (pp. 173−179). New York: Springer.

Mittelbach, G. G., & Schemske, D. W. (2015). Ecological and evolutionary perspectives on community assembly. *Trends in Ecology & Evolution*, *30*, 241–247. doi:10.1016/j.tree.2015.02.008.

Moreira, E. F., Santos, R. L.d. S., Penna, U. L., Angel-Coca, C., de Oliveira, F. F., & Viana, B. F. (2016). Are pan traps colors complementary to sample community of potential pollinator insects? *Journal of Insect Conservation*, *20*, 583–596. doi:10.1007/s10841-016-9890-x.

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*, 345–353. doi:10.1016/j.tree.2010.01.007.

R Core Team. (2019). *R: A language and environment for statistical computing*Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/.

Rader, R., Bartomeus, I., Garibaldi, L. A., Garratt, M. P. D., Howlett, B. G., Winfree, R., et al. (2016). Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences*, *113*, 146–151. doi:10.1073/pnas.1517092112.

Ricketts, T. H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdanski, A., et al. (2008). Landscape effects on crop pollination services: Are there general patterns? *Ecology Letters*, *11*, 499–515. doi:10.1111/j.1461-0248.2008.01157.x.

Rösch, V., Tscharntke, T., Scherber, C., & Batáry, P. (2015). Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments. *Oecologia*, *179*, 209–222. doi:10.1007/s00442-015-3315-5.

Saunders, M. E., & Luck, G. W. (2013). Pan trap catches of pollinator insects vary with habitat. *Australian Journal of Entomology*, *52*, 106–113. doi:10.1111/aen.12008.

Scheper, J., Bommarco, R., Holzschuh, A., Potts, S. G., Riedinger, V., Roberts, S. P. M., et al. (2015). Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. *Journal of Applied Ecology*, *52*, 1165–1175. doi:10.1111/1365-2664.12479.

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

Scheper, J., Reemer, M., van Kats, R., Ozinga, W. A., van der Linden, G. T. J., Schaminée, J. H. J., et al. (2014). Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in the Netherlands. *PNAS*, *111*, 17552–17557. doi:10.1073/pnas.1412973111.

Scherber, C., Beduschi, T., & Tscharntke, T. (2019). Novel approaches to sampling pollinators in whole landscapes: A lesson for landscape-wide biodiversity monitoring. *Landscape Ecology*, *34*, 1057–1067. doi:10.1007/s10980-018-0757-2.

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., & Tscharntke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, *83*, 1421–1432. doi:10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2.

Tischendorf, S., Frommer, U., Flügel, H. J., Schmalz, K. H., & Dorow, W. H. O. (2009). *Kommentierte Rote Liste der Bienen Hessens - Artenliste, Verbreitung, Gefährdung*. Wiesbaden: Hessisches Ministerium für Umwelt, Energie, Landwirtschaft und Verbraucherschutz.

Toler, T. R., Evans, E. W., & Tepedino, V. J. (2005). Pan-trapping for bees (Hymenoptera: Apiformes) in Utah's west desert: The importance of color diversity. *Pan Pacific Entomology*, *81*, 103–113.

Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., et al. (2012). Landscape moderation of biodiversity patterns and processes-eight hypotheses. *Biological Reviews*, *87*, 661–685. doi:10.1111/j.1469-185X.2011.00216.x.

Warzecha, D., Diekötter, T., Wolters, V., & Jauker, F. (2018). Attractiveness of wildflower mixtures for wild bees and hoverflies depends on some key plant species. *Insect Conservation and Diversity*, *11*, 32–41. doi:10.1111/icad.12264.

Wenninger, A., Kim, T., Spiesman, B., & Gratton, C. (2016). Contrasting foraging patterns: Testing resource-concentration and dilution effects with pollinators and seed predators. *Insects*, *7*, e23. doi:10.3390/insects7020023.

Westrich, P. (2019). *Die Wildbienen Deutschlands* (2nd ed.). Stuttgart: Ulmer.

Winfree, R., Reilly, J. R., Bartomeus, I., Cariveau, D. P., Williams, N. M., & Gibbs, J. (2018). Species turnover promotes the importance of bee diversity for crop pollination at regional scales. *Science*, *359*, 791–793. doi:10.1126/science.aao2117.

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

Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., & Dorn, S. (2010b). Maximum foraging ranges in solitary bees: Only few individuals have the capability to cover long foraging distances. *Biological Conservation*, *143*, 669–676. doi:10.1016/j.biocon.2009.12.003.

ANHANG KAPITEL III

Appendix A. Supporting information.

Fig. S1. Study region. (A) The county Marburg-Biedenkopf is located in the center of Hesse, Germany and (B) is covering an area of approximately 1,260 km² (44 % under agricultural use, 41 % forest, 14 % settlement and traffic, and 1 % covered by water). Out of 194 subsidized wildflower areas established within the county in 2011 (marked in red), a total of 33 were selected as study sites. (C) Study sites were equally assigned to isolation classes: "isolated" (no additional wildflower areas present within a radius of 500 m; black spot), "connected" (at least one additional wildflower area present within a radius of 500 m; white spot) and "satellite" (the closest additional wildflower area to each "connected" site; gray spot).

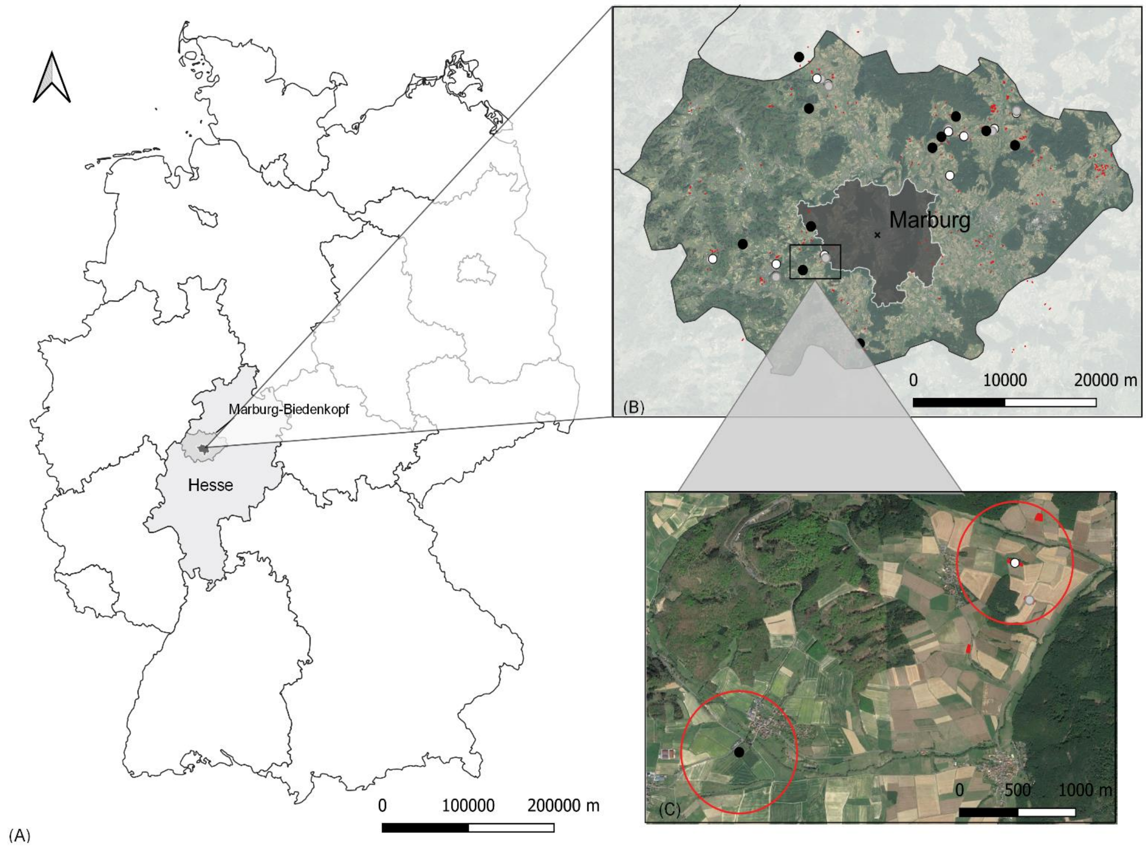


Fig. S2. Flowering aspect of selected study sites during and after establishment of wildflower areas. Out of 33 selected study sites, seven are shown here as examples to highlight differences in vegetation between the years. While the vegetation was sparse with few flowers in the first year, in the following years the vegetation grew taller and with more flowers avialable. In the third year the amount of flowers decreased due to the advancing succession**.**

Appendix B. Supporting information.

Table S1. Detailed information for the 33 study sites. 22 wildflower areas were equally assigned to one of two isolation classes: “isolated” (no additional wildflower areas present within a radius of 500 m) and “connected” (at least one additional wildflower area present within a radius of 500 m). Additional 11 “satellite” sites were selected, representing the closest additional wildflower area to each “connected” site. Beta-diversity between connected sites and their satellites are shown for wild bees (d(bees)), hoverflies (d(syr)) and the community (d(poll)) for the year 2012.

						Biodiversity 2012		
Isolation class	Site	Sowing	Seed mixture	Town	Size [m²]	d(bees)	d(syr)	d(poll)
connected	36	2011	Odin-Blühfläche	Halsdorf	2980.95	0.62	0.30	0.47
satellite	209	2011	Wildsaatenmischung	Halsdorf	4902.16			
connected	42	2011	Odin-Blühfläche	Halsdorf	3045.27	0.54	0.41	0.49
satellite	43	2011	Odin-Blühfläche	Halsdorf	3030.40			
satellite	79	2011	Lebensraum1	Schwarzenborn	5027.06	0.52	0.22	0.38
connected	81	2011	Kranichsteiner Mischung	Schwarzenborn	3066.30			
satelitte	84	2011	Odin-Blühfläche	Schwabendorf	3007.22	0.67	0.50	0.59
connected	204	2011	Odin-Blühfläche	Schwabendorf	2998.72			
satellite	89	2011	Odin-Blühfläche	Betziesdorf	2277.77	0.38	0.42	0.40
connected	90	2011	Odin-Blühfläche	Betziesdorf	3017.04			
connected	120	2011	Odin-Blühfläche	Niederasphe	2077.74	0.45	0.27	0.40
satellite	121	2011	Lebensraum1	Niederapshe	5028.12			
satellite	123	2011	Wildsaatenmischung	Niederasphe	2891.17	0.46	0.50	0.48
connected	124	2011	Wildsaatenmischung	Niederasphe	4078.11			
connected	125	2011	Odin-Blühfläche	Weihershausen	3034.37	0.53	0.30	0.45
satellite	127	2011	Odin-Blühfläche	Weihershausen	2754.76			
satellite	173	2011	Odin-Blühfläche	Dernbach	2180.70	0.69	0.67	0.68
connected	174	2011	Odin-Blühfläche	Dernbach	2953.61			
satellite	195	2011	Lebensraum 1	Gladenbach	2925.45	0.75	0.40	0.56
connected	196	2011	Lebensraum 1	Gladenbach	3067.11			
connected	192	2011	Odin-Blühfläche	Gladenbach	3013.68	0.37	0.60	0.45
satellite	208	2011	Lebensraum 1	Gladenbach	3007.56			
isolated	45	2011	Odin-Blühfläche	Halsdorf	3092.93			
isolated	76	2011	Kranichsteiner Mischung	Bracht	3168.19			
isolated	86	2011	Wildsaatenmischung	Schwarzenborn	3253.89			
isolated	92	2011	HIAP-Saatgutmischung	Schönstadt	3161.58			
isolated	129	2011	Lebensraum 1	Dilschhausen	3502.20			
isolated	130	2011	Odin-Blühfläche	Friebertshausen	2892.40			
isolated	137	2011	Wildsaatenmischung	Treisbach	2371.42			
isolated	138	2011	Wildsaatenmischung	Frohnhausen	3025.08			
isolated	144	2011	Odin-Blühfläche	Runzhausen	2967.25			
isolated	212	2011	Kranichsteiner Mischung	Ernsthausen	2962.02			
isolated	226	2011	Wildsaatenmischung	Bellnhausen	3056.04			

Appendix C. Supporting information.

Table S2. Plant species list. On the 33 selected study sites the five mixtures Kranichsteiner-Mixture (O2), Lebensraum 1 (L1), Odin 1 (O1), Wildsaaten (WS) and HIAP-Saatgut (no information available) were applied. Shown is the share of seeds [%] per wildflower mixture. Composition and proportion of the plant species is based on the producer formula from 2011. Recent mixtures may be subtly different to the used ones.

		Seed mixture German commercial brand name			
Species	Family	L1	O1	O2	WS
Achillea millefolium	Asteraceae	1		0.25	1
Anthemis tinctoria	Asteraceae	1		1.2	1.5
Anthoxanthum odoratum	Poaceae			2.25	
Artemisia vulgaris	Asteraceae	0.1			
Barbarea vulgaris	Brassicaceae	1			
Borago officinalis	Boraginaceae	0.2	2		4
Calendula officinalis	Asteraceae		2		7
Carum carvi	Apiaceae	2.5	2	2.25	4
Centaurea cyanus	Asteraceae			9	2
Centaurea jacea	Asteraceae	1.8		0.6	
Centaurea scabiosa	Asteraceae	0.1			
Cerastium holosteoides	Caryophyllaceae	0.1			
Chrysanthemum segetum	Asteraceae	0.2			4
Cichorium intybus	Asteraceae	2.5		4.5	1
Clinopodium vulgare	Lamiaceae	0.1			
Coriandrum sativum	Apiaceae		2		
Crepis biennis	Asteraceae	1			1
Cynosurus cristatus	Poaceae			2.25	
Daucus carota	Apiaceae	1	2	1.2	3.5
Dipsacus fullonum	Caprifoliaceae	1			0.5
Echium vulgare	Boraginaceae	0.8			
Fagopyrum esculentum	Polygonaceae	7.5	8	10	10
Foeniculum vulgare	Apiaceae	5			6
Galium album	Rubiaceae	0.5			
Galium mollugo	Rubiaceae			0.35	
Galium verum	Rubiaceae	0.5		0.6	0.5
Helianthus annuus	Asteraceae	5	8	9	15
Heracleum sphondylium	Apiaceae	0.4		0.6	
Hypericum perforatum	Hypericaceae	0.1		1.2	1
Isatis tinctoria	Brassicaceae				1
Lathyrus pratensis	Fabaceae			0.1	
Leucanthemum ircutianum	Asteraceae	0.5			3
Leucanthemum vulgare	Asteraceae			1.2	
Linum usitatissimum	Linaceae	8	6	2.8	5
Lotus corniculatus	Fabaceae	2			2
Malva alcea	Malvaceae			0.6	
Malva moschata	Malvaceae	0.5		0.6	1
Malva sylvestris	Malvaceae	1	4	4.75	

Malva verticiliata	Malvaceae	0.5			
Medicago lupulina	Fabaceae	2			1
Medicago sativa	Fabaceae	7.5	6	5	4
Melilotus alba	Fabaceae				2
Melilotus officinalis	Fabaceae			0.25	
Oenothera biennis	Onagraceae	0.5			1
Onobrychis viciifolia	Fabaceae	15	8	6.5	
Origanum vulgare	Lamiaceae	0.2			
Ornithopus sativus	Fabaceae		8		
Papaver rhoeas	Papaveraceae				1
Pastinaca sativa	Apiaceae			4.5	
Petroselinum sativum	Apiaceae	1			
Phacelia tanacetifolia	Boraginaceae		2		
Phleum pratense	Poaceae			5	
Plantago lanceolata	Plantaginaceae	0.5			1
Poa pratensis	Poaceae			5	
Prunella vulgaris	Lamiaceae	0.1			
Reseda luteola	Resedaceae	0.1			0.5
Salvia pratensis	Lamiaceae	0.5		3.7	1
Sanguisorba minor	Rosaceae	5.8	2		3
Secale multicaule	Poaceae			4.7	4
Setaria italica	Poaceae	1			
Silene alba	Caryophyllaceae	1.5			1
Silene dioica	Caryophyllaceae	0.5			
Silene vulgaris	Caryophyllaceae	1.8			0.5
Silene-flos-cuculi	Caryophyllaceae	0.2			
Silybum marianum	Asteraceae	1			
Sinapis alba	Brassicaceae		3		
Sinapis arvensis	Brassicaceae				2.8
Tanacetum corymbosum	Asteraceae	0.2			
Tanacetum vulgare	Asteraceae	0.1			
Trifolium hybridum	Fabaceae	0.5			
Trifolium incarnatum	Fabaceae		6	2.2	
Trifolium pratense	Fabaceae	5	6	5	1
Trifolium resupinatum	Fabaceae		6		
Trigonella caerulea	Fabaceae		5		
Trigonella foenum-graecum	Fabaceae		6		
Verbascum lychnitis	Scrophulariaceae	0.3			0.2
Verbascum nigrum	Scrophulariaceae	0.3		0.25	
Verbascum phoeniceum	Scrophulariaceae			0.6	
Verbascum thapsus	Scrophulariaceae	0.3			
Vicia sativa	Fabaceae	2.8	8	2	2
Vicia villosa	Fabaceae	5			

Table S3. Origin of recorded plants. On the 33 selected study sites the five mixtures Kranichsteiner-Mixture (O2), Lebensraum 1 (L1), Odin 1 (O1), Wildsaaten (WS) and HIAP-Saatgut (HS) were applied in May 2011 and flowering plants were recorded in 2012 and 2013. For each recorded plant species per study site the origin is given as mixture (M), seedbank (SB) or not available (NA) (only site i92 with the mixture HIAP-Saatgut).

	HS	O2			L1						O1																WS						
Species	i92	c81	i212	i76	c196	i129	sc120	sc192	sc196	sc81	c120	c125	c174	c192	c204	c36	c42	c90	i130	i144	i45	sc125	sc174	sc204	sc42	sc90	c124	i137	i138	i226	i86	sc124	sc36
Achillea millefolium	NA		M		M	M	M	M	M		SB		SB	SB			SB		SB	SB		SB					M	M	M	M	M	M	M
Aegopodium podagraria																					SB												
Agrimonia eupatoria							SB																										
Althaea officinalis																			SB														
Anthemis arvensis												SB																					
Anthemis tinctoria	NA		M		M	M	M	M	M					SB					SB								M	M	M	M	M	M	M
Anthriscus sylvestris											SB		SB				SB				SB			SB									
Artemisia vulgaris																							SB		SB						SB		
Barbarea vulgaris																										SB							
Betula pendula																								SB									
Borago officinalis		SB		SB						M	M	M				M	M	M			M	M				M	M	M	M	M		M	
Brassica napus																SB	SB	SB			SB												
Calendula officinalis	NA										M	M					M					M					M			M		M	
Campanula patula										SB	SB				SB			SB														SB	
Capsella bursa-pastoris																				SB													
Carum carvi																													M				
Centaurea cyanus	NA	M		M	SB			SB					SB		SB	SB			SB	SB		SB		SB	SB	SB	M	M	M	M	M	M	M
Centaurea jacea					M	M		M						SB																	SB		
Centaurea scabiosa	NA		SB		M		M	M	M										SB			SB											
Cerastium holosteoides				SB			M																					SB			SB		
Chenopodium album				SB																SB													
Cichorium intybus	NA				M	M	M	M	M					SB													M	M	M	M	M		M
Cirsium arvense	NA	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB		SB	SB	SB	SB	SB	SB	SB	SB		SB	SB	SB	SB	SB	SB	SB	SB	
Cirsium vulgare		SB		SB						SB	SB			SB	SB	SB	SB	SB		SB						SB		SB	SB	SB	SB		
Clinopodium vulgare		SB	SB		M			M	M				SB	SB	SB	SB	SB	SB			SB		SB	SB	SB							SB	SB

Convolvulus arvensis							SB								SB		SB		SB														
Conyza canadensis	NA							SB							SB			SB								SB				SB			
Crepis biennis	NA	SB		SB	M	M		M	M	M			SB				SB			SB		SB	SB				M	M	M	M	M	M	
Crepis capillaris																				SB													
Daucus carota	NA	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
Dipsacus fullonum	NA				M	M	M	M	M					SB													M	M	M	M	M	M	M
Echium vulgare						M	M							SB																			
Epilobium angustifolium																															SB		SB
Epilobium parviflorum		SB							SB	SB	SB	SB	SB	SB	SB		SB	SB	SB			SB		SB	SB	SB						SB	SB
Epilobium tetragonum agg.				SB																									SB		SB		
Erigeron annuus												SB																					
Erodium cicutarium																				SB													
Fagopyrum esculentum		M								M														M									
Fallopia convolvulus				SB											SB	SB				SB			SB						SB				
Foeniculum vulgare																														M			
Galeopsis bifida																															SB		
Galinsoga ciliata															SB								SB										SB
Galium aparine		SB	SB	SB	SB	SB	SB		SB	SB			SB	SB			SB		SB	SB	SB		SB		SB		SB	SB	SB	SB		SB	
Galium mollugo agg.	NA		M		M	M	M	M	M										SB								SB	SB	SB				
Galium verum	NA				M	M	M	M	M					SB					SB									M		M	M	M	M
Geranium dissectum																				SB													
Geranium pusillum																				SB													
Geranium pyrenaicum																				SB													
Geum urbanum				SB						SB	SB																SB				SB		
Helianthus annuus						M	M	M	M			M					M		M		M	M		M		M	M			M	M		
Helianthus tuberosus				SB																													
Heracleum sphondylium											SB																						
Hypericum perforatum	NA						M		M							SB	SB	SB		SB				SB				M		M	M	M	M
Impatiens glandulifera										SB																							
Lactuca serriola				SB													SB												SB				
Lactuca virosa													SB			SB		SB							SB	SB				SB			
Lamium purpureum									SB											SB									SB				

Lapsana communis														SB																			
Leontodon sp.																									SB		SB						
Leucanthemum vulgare agg.	NA				M			M	M										SB								M	M	M	M	M	M	M
Lotus corniculatus	NA				M	M		M	M		SB			SB													M	M	M	M	M	M	
Lupinus angustifolius			SB																														
Lychnis flos-cuculi					SB																												
Malva moschata	NA		M		M	M	M	M	M					SB					SB								M	M	M	M	M	M	M
Malva spec.																						SB											
Malva sylvestris							M			M															M							SB	SB
Malva verticiliata		SB		SB		M	M			M	SB	SB	SB		SB	SB	SB	SB	SB		SB	SB	SB		SB	SB							
Matricaria chamomilla	NA	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB
Medicago lupulina	NA				M	M	M		M																		M		M		M	M	M
Medicago sativa	NA	M	M	M	M	M	M	M	M	M	M	M	M	M		M	M	M	M	M	M	M		M	M	M	M	M	M	M	M		
Medicago x varia	NA	SB	SB		SB		SB		SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB		SB	SB	SB	SB	SB	SB	SB			SB		SB	
Melampyrum sylvaticum																				SB													
Melilotus albus	NA		SB																								M	M	M	M		M	
Melilotus officinalis													SB							SB			SB										
Myosotis arvensis		SB		SB	SB	SB	SB	SB	SB			SB	SB		SB	SB	SB			SB	SB	SB	SB	SB	SB	SB	SB				SB		SB
Oenothera parviflora	NA				M		M	M	M	M				SB													M		M	M	M	M	M
Onobrychis viciifolia				M	M	M	M		M	M	M	M	M	M				M	M	M					M	M							
Origanum vulgare					M				M																								
Oxalis sp.																				SB													
Papaver rhoeas	NA			SB	SB	SB		SB	SB	SB				SB			SB						SB		SB		M		M	M	M	M	M
Pastinaca sativa	NA		M			SB	SB								SB				SB								SB	SB	SB	SB	SB	SB	
Persicaria	NA	SB					SB								SB						SB			SB		SB							SB
Persicaria maculosa								SB	SB				SB	SB																			
Phacelia tanacetifolia		SB	SB	SB	SB			SB	SB	SB	M	M	M	M	M	M	M	M		M	M	M	M	M	M	M							
Plantago lanceolata	NA				M	M	M	M	M		SB			SB			SB										M	M	M	M	M	M	M
Plantago major				SB		SB					SB				SB						SB	SB	SB	SB			SB					SB	
Prunella vulgaris					M	M	M	M	M					SB					SB									SB			SB		SB
Ranunculus acris							SB	SB				SB			SB		SB				SB	SB											
Ranunculus repens						SB																						SB			SB		

Reseda luteola																															M	
Rubus fruticosus agg.											SB																					
Rubus idaeus				SB																												
Rumex acetosa	NA		SB	SB	SB	SB	SB	SB		SB	SB	SB		SB	SB	SB	SB	SB	SB	SB	SB	SB		SB	SB		SB				SB	SB	SB
Rumex acetosella																	SB			SB												
Rumex crispus				SB				SB		SB	SB	SB		SB	SB	SB			SB	SB	SB	SB			SB	SB	SB	SB					
Rumex obtusifolius						SB														SB								SB	SB		SB		
Rumex sp.																	SB															
Salvia pratensis			M	M																												
Sanguisorba minor			SB	SB		M	M	M	M			M		M		M		M	M	M		M	M			M		M	M	M	M	M	
Senecio jacobaea																						SB								SB			
Silene spec.						SB																										
Silene dioica					M	M	M	M	M					SB													SB					SB	
Silene latifolia	NA		SB		M	M	M		M										SB	SB							M	M	M	M	M	M	M
Silene vulgaris	NA				M	M		M	M					SB														M	M	M		M	M
Sinapis arvensis		SB								SB	M		M				M				M		M		M			M		M		M	M
Sisymbrium officinale				SB																												
Sonchus arvensis	NA	SB															SB									SB						SB	
Sonchus asper				SB		SB		SB									SB																
Sonchus oleraceus	NA																																
Stachys recta		SB											SB										SB	SB	SB					SB			SB
Stellaria graminea			SB				SB													SB				SB		SB							SB
Stellaria media																				SB									SB				
Tanacetum vulgare	NA				M			M	M								SB							SB	SB			SB		SB	SB		
Taraxacum officinale	NA	SB		SB	SB	SB				SB	SB	SB		SB	SB	SB	SB	SB		SB		SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	SB	
Tragopogon pratensis	NA																																
Trifolium arvense																				SB													
Trifolium hybridum		SB	SB		M	M	M	M	M				SB	SB			SB			SB	SB		SB					SB					
Trifolium incarnatum										SB			M									M		M									
Trifolium pratense	NA	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M		M	M	M	M		
Trifolium repens	NA					SB														SB	SB			SB				SB			SB		
Tripleurospermum perforatum				SB									SB							SB									SB				
Urtica dioica		SB				SB	SB			SB	SB		SB			SB	SB		SB		SB		SB		SB	SB			SB	SB	SB		

Verbascum lychnitis																																	M
Veronica arvensis																				SB													
Veronica persica																				SB													
Vicia cracca																				SB			SB										
Vicia hirsuta																				SB	SB												
Vicia sativa													M								M												
Vicia villosa	NA	SB	SB							M		SB			SB	SB	SB	SB			SB	SB			SB	SB	SB	SB	SB		SB	SB	SB
Viola arvensis				SB										SB						SB			SB						SB				
Viola tricolor																																	SB

Appendix D. Supporting information.

Table S4. Species List. For nomenclature of wild bees (Hymenoptera: Apoidea: Apiformes) we followed Westrich (2019) and for hoverflies (Diptera: Syrphidae) van Veen (2010). Wild bees were determined by using the keys of Schmid-Egger and Scheuchl (1997); Amiet (1996) and Amiet et al. (2001, 2004, 2007, 2010, 2014), for hoverflies we used the key from van Veen (2010).

			Specimens per sampling year			
Order	Family	Species/Taxonomic group	2011	2012	2013	Total
Hymenoptera	Andrenidae	*Andrena agilissima*		3		3
Hymenoptera	Andrenidae	*Andrena alfkenella*	2			2
Hymenoptera	Andrenidae	*Andrena angustior*	1	6	2	9
Hymenoptera	Andrenidae	*Andrena anthrisci*		1		1
Hymenoptera	Andrenidae	*Andrena barbilabris*		2	1	3
Hymenoptera	Andrenidae	*Andrena bicolor*	91	1	2	94
Hymenoptera	Andrenidae	*Andrena chrysosceles*		8	2	10
Hymenoptera	Andrenidae	*Andrena cineraria*		45	12	57
Hymenoptera	Andrenidae	*Andrena dorsata*	466	6	4	476
Hymenoptera	Andrenidae	*Andrena flavipes*	1284	75	12	1371
Hymenoptera	Andrenidae	*Andrena fulva*			12	12
Hymenoptera	Andrenidae	*Andrena gelriae*	3			3
Hymenoptera	Andrenidae	*Andrena gravida*		9		9
Hymenoptera	Andrenidae	*Andrena haemorrhoa*	1	250	23	274
Hymenoptera	Andrenidae	*Andrena hattorfiana*	1	1		2
Hymenoptera	Andrenidae	*Andrena helvola*			12	12
Hymenoptera	Andrenidae	*Andrena labialis*		1	1	2
Hymenoptera	Andrenidae	*Andrena lapponica*			2	2
Hymenoptera	Andrenidae	*Andrena minutula*	116	6	2	124
Hymenoptera	Andrenidae	*Andrena minutuloides*	14	18	5	37
Hymenoptera	Andrenidae	*Andrena nigroaenea*	4	205	59	268
Hymenoptera	Andrenidae	*Andrena nigrospina*	1			1
Hymenoptera	Andrenidae	*Andrena nitida*		101	11	112
Hymenoptera	Andrenidae	*Andrena ovatula*		1		1
Hymenoptera	Andrenidae	*Andrena pilipes*	1			1
Hymenoptera	Andrenidae	*Andrena proxima*		5	2	7
Hymenoptera	Andrenidae	*Andrena semilaevis*	4	4		8
Hymenoptera	Andrenidae	*Andrena similis*	1			1
Hymenoptera	Andrenidae	*Andrena subopaca*		3	1	4
Hymenoptera	Andrenidae	*Andrena wilkella*	1			1
Hymenoptera	Andrenidae	*Panurgus banksianus*	1	3	2	6
Hymenoptera	Andrenidae	*Panurgus calcaratus*	132	8	18	158
Hymenoptera	Apidae	*Anthophora aestivalis*	1			1
Hymenoptera	Apidae	*Anthophora furcata*	1		1	2
Hymenoptera	Apidae	*Bombus barbutellus*	1			1
Hymenoptera	Apidae	*Bombus bohemicus*	62	11	1	74
Hymenoptera	Apidae	*Bombus campestris*	1			1
Hymenoptera	Apidae	*Bombus hortorum*	11	8	66	85

Order	Family	Species/Taxonomic group	Specimens per sampling year			Total
			2011	2012	2013	
Hymenoptera	Apidae	*Bombus lapidarius*	632	45	160	837
Hymenoptera	Apidae	*Bombus pascuorum*	21	4	47	72
Hymenoptera	Apidae	*Bombus pratorum*	1	1	2	4
Hymenoptera	Apidae	*Bombus rupestris*	39	6		45
Hymenoptera	Apidae	*Bombus soroeensis*	1		1	2
Hymenoptera	Apidae	*Bombus sylvarum*	17		42	59
Hymenoptera	Apidae	*Bombus sylvestris*	3			3
Hymenoptera	Apidae	*Bombus terrestris* agg.	674	71	296	1041
Hymenoptera	Apidae	*Bombus vestalis*	3			3
Hymenoptera	Apidae	*Eucera longicornis*			1	1
Hymenoptera	Apidae	*Nomada fabriciana*	3		1	4
Hymenoptera	Apidae	*Nomada flavoguttata*	1			1
Hymenoptera	Apidae	*Nomada fucata*	2			2
Hymenoptera	Apidae	*Nomada lathburiana*		1	1	2
Hymenoptera	Apidae	*Nomada marshamella*		1		1
Hymenoptera	Apidae	*Nomada melathoracica*	1			1
Hymenoptera	Apidae	*Nomada panzeri*		1		1
Hymenoptera	Apidae	*Nomada succinata*		1		1
Hymenoptera	Apidae	*Nomada zonata*	3			3
Hymenoptera	Colletidae	*Colletes daviesanus*	8	1	3	12
Hymenoptera	Colletidae	*Hylaeus annularis*	16	1	16	33
Hymenoptera	Colletidae	*Hylaeus brevicornis*			11	11
Hymenoptera	Colletidae	*Hylaeus communis*	25	18	61	104
Hymenoptera	Colletidae	*Hylaeus confusus*	1	2	12	15
Hymenoptera	Colletidae	*Hylaeus cornutus*		1		1
Hymenoptera	Colletidae	*Hylaeus difformis*	2	3	10	15
Hymenoptera	Colletidae	*Hylaeus gredleri*	1	8	14	23
Hymenoptera	Colletidae	*Hylaeus hyalinatus*	1	3	9	13
Hymenoptera	Colletidae	*Hylaeus nigritus*	5	7	9	21
Hymenoptera	Colletidae	*Hylaeus paulus*			5	5
Hymenoptera	Colletidae	*Hylaeus signatus*	2		5	7
Hymenoptera	Colletidae	*Hylaeus styriacus*		1	4	5
Hymenoptera	Colletidae	*Hylaeus variegatus*			1	1
Hymenoptera	Halictidae	*Halictus maculatus*	15	6	3	24
Hymenoptera	Halictidae	*Halictus rubicundus*	8	4	8	20
Hymenoptera	Halictidae	*Halictus scabiosae*	32	13	7	52
Hymenoptera	Halictidae	*Halictus simplex*	1	1		2
Hymenoptera	Halictidae	*Halictus tumulorum*	33	11		44
Hymenoptera	Halictidae	*Lasioglossum albipes/calceatum*	109	3	4	116
Hymenoptera	Halictidae	*Lasioglossum costulatum*	2		1	3
Hymenoptera	Halictidae	*Lasioglossum fulvicorne*	1	1		2
Hymenoptera	Halictidae	*Lasioglossum laevigatum*		1		1
Hymenoptera	Halictidae	*Lasioglossum laticeps*	86	10	4	100
Hymenoptera	Halictidae	*Lasioglossum lativentre*	39	34	4	77
Hymenoptera	Halictidae	*Lasioglossum leucopus*	14	11	23	48
Hymenoptera	Halictidae	*Lasioglossum leucozonium*	32	10	1	43

Order	Family	Species/Taxonomic group	Specimens per sampling year 2011	2012	2013	Total
Hymenoptera	Halictidae	*Lasioglossum malachurum*	29	4	1	34
Hymenoptera	Halictidae	*Lasioglossum minutissimum*	1		1	2
Hymenoptera	Halictidae	*Lasioglossum morio*	22	9	47	78
Hymenoptera	Halictidae	*Lasioglossum nitidiusculum*	3	16	7	26
Hymenoptera	Halictidae	*Lasioglossum nitidulum*		1		1
Hymenoptera	Halictidae	*Lasioglossum parvulum*	1	9	6	16
Hymenoptera	Halictidae	*Lasioglossum pauperatum*	41	114	21	176
Hymenoptera	Halictidae	*Lasioglossum pauxillum*	84	21	19	124
Hymenoptera	Halictidae	*Lasioglossum punctatissimum*	1			1
Hymenoptera	Halictidae	*Lasioglossum pygmaeum*		3	2	5
Hymenoptera	Halictidae	*Lasioglossum quadrinotatum*	4	13	2	19
Hymenoptera	Halictidae	*Lasioglossum villosulum*	17	10	8	35
Hymenoptera	Halictidae	*Lasioglossum xanthopus*		7		7
Hymenoptera	Halictidae	*Lasioglossum zonulum*	1			1
Hymenoptera	Halictidae	*Sphecodes crassus*		1		1
Hymenoptera	Halictidae	*Sphecodes ephippius*	1	23	4	28
Hymenoptera	Halictidae	*Sphecodes puncticeps*	2	1	1	4
Hymenoptera	Halictidae	*Sphecodes rubicundus*	3	1		4
Hymenoptera	Halictidae	*Sphecodes spec.*			1	1
Hymenoptera	Megachilidae	*Anthidium manicatum*			1	1
Hymenoptera	Megachilidae	*Chelostoma campanularum*	2	1	9	12
Hymenoptera	Megachilidae	*Chelostoma florisomne*	2	8	54	64
Hymenoptera	Megachilidae	*Chelostoma rapunculi*		1		1
Hymenoptera	Megachilidae	*Coelioxys inermis*	1			1
Hymenoptera	Megachilidae	*Coelioxys mandibularis*			1	1
Hymenoptera	Megachilidae	*Heriades truncorum*	4	29	7	40
Hymenoptera	Megachilidae	*Megachile alpicola*			3	3
Hymenoptera	Megachilidae	*Megachile centuncularis*		3		3
Hymenoptera	Megachilidae	*Megachile circumcincta*	1		1	2
Hymenoptera	Megachilidae	*Megachile nigriventris*			1	1
Hymenoptera	Megachilidae	*Megachile versicolor*		1	4	5
Hymenoptera	Megachilidae	*Osmia bicornis*		1	24	25
Hymenoptera	Megachilidae	*Stelis breviuscula*	1	1	2	4
Hymenoptera	Megachilidae	*Stelis punctulatissima*		1		1
Diptera	Syrphidae	*Brachyopa maculipennis*		1		1
Diptera	Syrphidae	*Chalcosyrphus nemorum*	1			1
Diptera	Syrphidae	*Cheilosia albitarsis*	1			1
Diptera	Syrphidae	*Cheilosia Antiqua Gr.*		3	13	16
Diptera	Syrphidae	*Cheilosia barbata*	1			1
Diptera	Syrphidae	*Cheilosia Bergenstammi Gr.*		18	3	21
Diptera	Syrphidae	*Cheilosia Canicularis-Gr.*		1	1	2
Diptera	Syrphidae	*Cheilosia Illustrata Gr.*			3	3
Diptera	Syrphidae	*Cheilosia Impressa Gr.*			3	3
Diptera	Syrphidae	*Cheilosia Pagana Gr.*		2	3	5
Diptera	Syrphidae	*Cheilosia Proxima-Gr.*		6		6
Diptera	Syrphidae	*Cheilosia spec.*		1		1

Order	Family	Species/Taxonomic group	Specimens per sampling year			
			2011	2012	2013	Total
Diptera	Syrphidae	*Chrysotoxum arcuatum*		2		2
Diptera	Syrphidae	*Chrysotoxum bicinctum*	1	16	4	21
Diptera	Syrphidae	*Chrysotoxum cautum*		3		3
Diptera	Syrphidae	*Chrysotoxum fasciatum*	1			1
Diptera	Syrphidae	*Chrysotoxum fasciolatum*	1			1
Diptera	Syrphidae	*Chrysotoxum festivum*			1	1
Diptera	Syrphidae	*Chrysotoxum octomaculatum*	8			8
Diptera	Syrphidae	*Chrysotoxum verralli*	2	12	8	22
Diptera	Syrphidae	*Dasysyrphus albostriatus*		1		1
Diptera	Syrphidae	*Dasysyrphus venustus*		1		1
Diptera	Syrphidae	*Epistrophe melanostomoides*			1	1
Diptera	Syrphidae	*Episyrphus balteatus*	2386	669	1819	4874
Diptera	Syrphidae	*Eristalinus sepulchralis*		1	24	25
Diptera	Syrphidae	*Eristalis abusivus*			6	6
Diptera	Syrphidae	*Eristalis arbustorum*	1		9	10
Diptera	Syrphidae	*Eristalis horticola*	1			1
Diptera	Syrphidae	*Eristalis interrupta*	5	15	25	45
Diptera	Syrphidae	*Eristalis lineata*	1			1
Diptera	Syrphidae	*Eristalis pertinax*			6	6
Diptera	Syrphidae	*Eristalis picea*	3	4		7
Diptera	Syrphidae	*Eristalis similis*	2	1	1	4
Diptera	Syrphidae	*Eristalis tenax*	119	30	78	226
Diptera	Syrphidae	*Eumerus ruficornis*	4			4
Diptera	Syrphidae	*Eumerus spec.*	1			1
Diptera	Syrphidae	*Eumerus strigatus/sogdianus*			1	1
Diptera	Syrphidae	*Eupeodes corollae*	529	96	25	650
Diptera	Syrphidae	*Eupeodes latifasciatus*		1	1	2
Diptera	Syrphidae	*Helophilus pendulus*		1	1	2
Diptera	Syrphidae	*Helophilus trivittatus*	3		5	8
Diptera	Syrphidae	*Melangyna cincta*	1			1
Diptera	Syrphidae	*Melanogaster hirtella*			2	2
Diptera	Syrphidae	*Melanostoma mellinum/scalare*	80	529	65	674
Diptera	Syrphidae	*Merodon equestris*		1		1
Diptera	Syrphidae	*Myathropa florea*	3	5	13	21
Diptera	Syrphidae	*Neoascia podagrica*			1	1
Diptera	Syrphidae	*Parhelophilus frutetorum*	1	1	3	5
Diptera	Syrphidae	*Parhelophilus versicolor*			7	7
Diptera	Syrphidae	*Pipiza bimaculata*	1	1		2
Diptera	Syrphidae	*Pipiza noctiluca*			1	1
Diptera	Syrphidae	*Pipizella spec.*		30	25	55
Diptera	Syrphidae	*Platycheirus albimanus*	1	18		19
Diptera	Syrphidae	*Platycheirus clypeatus*		5	4	9
Diptera	Syrphidae	*Platycheirus complicatus*	1			1
Diptera	Syrphidae	*Platycheirus scutatus*	2			2
Diptera	Syrphidae	*Platycheirus spec.*		1		1
Diptera	Syrphidae	*Scaeva pyrastri*	93	28	8	129

			Specimens per sampling year			
Order	Family	Species/Taxonomic group	2011	2012	2013	Total
Diptera	Syrphidae	*Scaeva selenitica*	22	1		23
Diptera	Syrphidae	*Sphaerophoria rueppellii*	1			1
Diptera	Syrphidae	*Sphaerophoria scripta* agg.	223	55	153	431
Diptera	Syrphidae	*Syritta pipiens*	3	4	3	10
Diptera	Syrphidae	*Syrphus ribesii*	163	33	5	201
Diptera	Syrphidae	*Syrphus spec.*	1			1
Diptera	Syrphidae	*Syrphus torvus*	153	8	10	171
Diptera	Syrphidae	*Syrphus vitripennis*	710	275	135	1120
Diptera	Syrphidae	*Temnostoma bombylans*		1	1	2
Diptera	Syrphidae	*Trichopsomyia flavitarsis*	1			1
Diptera	Syrphidae	*Volucella bombylans*		2	1	3
Diptera	Syrphidae	*Xanthandrus comtus*		1		1
Diptera	Syrphidae	*Xanthogramma pedissequum*		6	5	11
Diptera	Syrphidae	*Xylota abiens*			1	1
Diptera	Syrphidae	*Xylota caeruleiventris*		2		2
Diptera	Syrphidae	*Xylota florum*			2	2
Diptera	Syrphidae	*Xylota meigeniana*	1			1
Diptera	Syrphidae	*Xylota segnis*	155	79	200	434
Diptera	Syrphidae	*Xylota spec.*	5			5
Diptera	Syrphidae	*Xylota sylvarum*	5	34	67	106
Diptera	Syrphidae	*Xylota tarda*	1			1
Diptera	Syrphidae	*Xylota xanthocnema*	4	1	1	6
Sum	Apiformes		4256	1341	1246	6843
	Syrphidae		4702	2006	2754	9462
	total		8958	3347	4000	16305

Amiet, F. (1996). Insecta Helvetica – Fauna 12. HYMENOPTERA, Apidae, 1. Neuchatel: Schweizerische Entomologische Gesellschaft.

Amiet, F., Herrmann, M., Müller, A., & Neumeyer, R (1996). Fauna Helvetica 6, Apidae 3. Neuchatel: Schweizerische Entomologische Gesellschaft.

Amiet, F., Herrmann, M., Müller, A., & Neumeyer, R. (2004). Fauna Helvetica 9, Apidae 4. Neuchatel: Schweizerische Entomologische Gesellschaft.

Amiet, F., Herrmann, M., Müller, A., & Neumeyer, R. (2007). Fauna Helvetica 20, Apidae 5. Neuchatel: Schweizerische Entomologische Gesellschaft.

Amiet, F., Herrmann, M., Müller, A., & Neumeyer, R. (2010). Fauna Helvetica 26, Apidae 6. Neuchatel: Schweizerische Entomologische Gesellschaft.

Amiet, F., Müller, A., & Neumeyer, R. (2014). Fauna Helvetica 4, Apidae (2nd ed.). Neuchatel: Schweizerische Entomologische Gesellschaft.

Schmid-Egger, C., & Scheuchl, E. (1997). Illustrierte Bestimmungsschlüssel der Wildbienen Deutschlands und Österreichs. Band III: Andrenidae. Velden: Self-published.

Van Veen, M. P. (2010). Hoverflies of Northwest Europe: identification keys to the Syrphidae, (2nd ed.). Zeist: KNNV Publishing.

Westrich, P. (2019). Die Wildbienen Deutschlands. (2nd ed.). Stuttgart: Ulmer.

Appendix E. Supporting information

Table S5. Detailed information on solitary wild bees. Solitary bee species are listed with nesting-type and sampling date. Bivoltine species are highlighted in gray.

Species	Nesting	16.06.2011	25.06.2011	01.07.2011	08.07.2011	15.07.2011	22.07.2011	29.07.2011	12.06.2012	19.06.2012	26.06.2012	03.07.2012	09.07.2012	16.07.2012	24.07.2012	16.06.2013	24.06.2013	01.07.2013	08.07.2013	15.07.2013	23.07.2013	29.07.2013
		Sampling Date																				
Andrena agilissima	ground								2		1											
Andrena alfkenella	ground				1		1															
Andrena angustior	ground	1							2	3			1				2					
Andrena anthrisci	ground									1												
Andrena barbilabris	ground								1	1							1					
Andrena bicolor	ground	1	5	20	31	18	12				1					1	1					
Andrena chrysosceles	ground								4	2	2					2						
Andrena cineraria	ground								32	10	3					10	2					
Andrena dorsata	ground		1	43	176	149	38	9	2				1		3						2	2
Andrena flavipes	ground	10	38	114	259	373	238	52	20			3	12	11	29	5			2	1	3	1
Andrena fulva	ground															12						
Andrena gelriae	ground	1		1			1															
Andrena gravida	ground								9													
Andrena haemorrhoa	ground	1							195	53	2					21	1		1			
Andrena hattorfiana	ground						1		1													
Andrena helvola	ground															12						
Andrena labialis	ground										1								1			
Andrena lapponica	ground															2						
Andrena minutula	ground	1	6	10	36	46	12		2			1		1	2			1			1	
Andrena minutuloides	ground	1	1	1	1	4	5		11	6		1				2		2				1
Andrena nigroaenea	ground	4							155	47	2	1				43	11	2	3			
Andrena nigrospina	ground																					
Andrena nitida	ground								89	11	1					10		1				
Andrena ovatula	ground												1									
Andrena pilipes	ground																					
Andrena proxima	ground								4	1							1	1				
Andrena semilaevis	ground	2	1		1					1	1	1		1								
Andrena similis	ground	1																				
Andrena subopaca	ground								3								1					
Andrena wilkella	ground																					
Anthophora aestivalis	ground	1																				
Colletes daviesanus	ground		1		1		3							1						1		2
Eucera longicornis	ground																					1
Halictus maculatus	ground			1	7	4	1			4		1			1	1	2					
Halictus rubicundus	ground			3	1	2	1			1					3			1			4	3
Halictus scabiosae	ground	4	3	3	6	8	4		10	2				1		6					1	
Halictus simplex	ground	1							1													

Halictus tumulorum	ground	6	4	6	4	4	3		2				4		5							
Lasioglossum calceatum/albipes	ground	9	13	10	37	26	13					1	1	1		3	1					
Lasioglossum costulatum	ground	1				1											1					
Lasioglossum fulvicorne	ground		1										1									
Lasioglossum laevigatum	ground								1													
Lasioglossum laticeps	ground	18	3	13	26	20	6			1	1	3	2	1	2			1	1	1	1	
Lasioglossum lativentre	ground	5	6	6	8	3	3		11	8	5	5	3		2	1		1	1	1		
Lasioglossum leucopus	ground			1	5	8			1	3	1	4	2			8	4		3	2	3	3
Lasioglossum leucozonium	ground	14	5	4	6	3			3	2	3			2		1						
Lasioglossum malachurum	ground	7	5	3	6	3	2						1	1	2	1						
Lasioglossum minutissimum	ground			1													1					
Lasioglossum morio	ground	4		2	3	9					1	3	1	2	2	5	3	1	7	12	12	7
Lasioglossum nitidiusculum	ground			3					2	6	1	4	2		1	5	1	1				
Lasioglossum nitidulum	ground														1							
Lasioglossum parvulum	ground				1				3	3		3				5	1					
Lasioglossum pauperatum	ground	9	2	12	3	9	4		37	19	16	24	12	2	4	4	11		4	2		
Lasioglossum pauxillum	ground	31	10	11	8	18	2		3	3	2	3	3	3	4	6		1	4	3	5	
Lasioglossum punctatissimum	ground				1																	
Lasioglossum pygmaeum	ground								1	2							1		1			
Lasioglossum quadrinotatum	ground	1	2		1				6	2	1	3			1	1		1				
Lasioglossum villosulum	ground	2	3	3	4		4		5	3	1			1		3	3	2				
Lasioglossum xanthopus	ground								5	1	1											
Lasioglossum zonulum	ground			1																		
Panurgus banksianus	ground			1									1		2					1	1	
Panurgus calcaratus	ground	5	1	14	41	37	23	1				1			7					2	9	7
Anthidium manicatum	cavity																			1		
Anthophora furcata	cavity																					1
Chelostoma campanularum	cavity					1	1					1						1	1		6	1
Chelostoma florisomne	cavity	2							3	3	2					42	9	2	1			
Chelostoma rapunculi	cavity												1									
Heriades truncorum	cavity		1	1	2						2	4	5	4	14					1	3	3
Hylaeus annularis	cavity	1		8	3	3	1					1					3	1	3		5	4
Hylaeus brevicornis	cavity																	2	4	1	1	3
Hylaeus communis	cavity			4	7	10	3					6	5	5	2			3	11	10	28	9

Hylaeus confusus	cavity									1		1					2	1	2	4	1	2
Hylaeus cornutus	cavity										1											
Hylaeus difformis	cavity			1			1					1			2			1	1	2	5	1
Hylaeus gredleri	cavity	1										2	2	1	3		1	1	1	1	3	7
Hylaeus hyalinatus	cavity					1							1	1	1				2	4	3	
Hylaeus nigritus	cavity	1	1		1	2				4	1	1		1		2	2	1	1	2	1	
Hylaeus paulus	cavity															1					2	2
Hylaeus signatus	cavity			1	1																2	3
Hylaeus styriacus	cavity													1				1	1		1	1
Hylaeus variegatus	cavity																			1		
Megachile alpicola	cavity																1				2	
Megachile centuncularis	cavity											1		1	1							
Megachile circumcincta	cavity	1															1					
Megachile nigriventris	cavity																1					
Megachile versicolor	cavity												1			1		1	1	1		
Osmia bicornis	cavity									1						16	5	2	1			
Coelioxys inermis	cuckoo				1																	
Coelioxys mandibularis	cuckoo																			1		
Nomada fabriciana	cuckoo				1	1	1											1				
Nomada flavoguttata	cuckoo																					
Nomada fucata	cuckoo				1																	
Nomada lathburiana	cuckoo								1							1						
Nomada marshamella	cuckoo									1												
Nomada melathoracica	cuckoo				1																	
Nomada panzeri	cuckoo								1													
Nomada succinata	cuckoo									1												
Nomada zonata	cuckoo			1	1	1																
Sphecodes crassus	cuckoo								1													
Sphecodes ephippius	cuckoo			1					13	6	2				2	2		1	1			
Sphecodes puncticeps	cuckoo					1	1		1							1						
Sphecodes rubicundus	cuckoo				1				1													
Stelis breviuscula	cuckoo														1			1			1	

KAPITEL IV – INTRASPEZIFISCHE KÖRPERGRÖßE

INTRASPECIFIC BODY SIZE INCREASES WITH HABITAT FRAGMENTATION IN WILD BEE POLLINATORS

Warzecha D, Diekötter T, Wolters V, Jauker F

Erschienen 2016 in *Landscape Ecology* 31: 1449–1455

Landscape Ecol (2016) 31:1449–1455
DOI 10.1007/s10980-016-0349-y

RESEARCH ARTICLE

Intraspecific body size increases with habitat fragmentation in wild bee pollinators

**Daniela Warzecha · Tim Diekötter ·
Volkmar Wolters · Frank Jauker**

Received: 12 August 2015 / Accepted: 9 February 2016 / Published online: 15 February 2016

Abstract
Context In modern agricultural landscapes, fragmentation of partial habitats is a significant filter for multi-habitat users, reducing local taxonomic and functional diversity. There is compelling evidence that small species are more susceptible than large species. The impact of habitat fragmentation on intraspecific body-size distribution, however, is yet unexplored.
Objectives We tested habitat fragmentation, a major driver of pollinator loss, for its impact on intraspecific body-size distributions of solitary wild-bee species. Subsequently, we tested individual body size for its impact on pollination services.
Methods We sampled 1272 individuals of the four most common Andrena wild bee species in 22 newly established flowering fields (0.21–0.41 ha) in Hessen, Central Germany, over two consecutive years. Study sites were located in a ca. 80 ha landscape context of increasing habitat fragmentation. We analysed the pollen loads of the most abundant species.
Results Body size within local populations of the two medium-sized bees increased with fragmentation, suggesting intraspecific selection for higher dispersal capacity. Pollen analysis carried out for the most common species revealed that larger individuals visited a significantly smaller plant spectrum. Habitat fragmentation may thus alter pollination services without necessarily affecting species richness or composition.
Conclusions Systematic body-size variation at the population level thus explains the considerable variability between simple community measures and ecosystem functioning. Filtering processes at the individual level require increased understanding for targeting pollination services under current and future land-use change.

Keywords Dispersal · Environmental filtering · Habitat isolation · Inter-tegular distance · Phenotypic plasticity · Pollination

Introduction

The relevance of intraspecific body-size variation for the biology of insects and their interactions with the environment is pervasive. Substantial feedbacks between body size and physiological, life history,

---

Electronic supplementary material The online version of this article (doi:10.1007/s10980-016-0349-y) contains supplementary material, which is available to authorized users.

D. Warzecha (✉) · T. Diekötter · V. Wolters · F. Jauker
Department of Animal Ecology, Justus Liebig University Giessen, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany
e-mail: daniela.warzecha@bio.uni-giessen.de

Present Address:
T. Diekötter
Department of Landscape Ecology, Institute for Natural Resource Conservation, Kiel University, Olshausenstrasse 75, 24118 Kiel, Germany

and ecological traits entail systematic alterations along size clines in e.g. mortality rates, individual fitness, reproductive success, and dispersal ability (Chown and Gaston 2010). Natural variation in intraspecific body size with latitude (Peat et al. 2005) or altitude (Levy and Nufio 2015) is generally acknowledged. While the effect of man-made alterations in land use on body-size distributions within species received considerable less attention, subsequent functional responses remain largely unexplored. In this study, we tested how habitat fragmentation affects body-size distributions and ecosystem functioning of wild-bee pollinators in modern agroecosystems.

Loss and isolation of semi-natural habitats are major threats to the diversity of wild bees (Winfree et al. 2009; Williams et al. 2010), the most important pollinators of native plants and agricultural crops (Kremen 2005; Klein et al. 2007). Increasing habitat fragmentation also shifts the composition of local bee communities towards a higher share of large as compared to smaller species (Jauker et al. 2013). This is because bees are central-place foragers frequently commuting between foraging and nesting habitats (Kleijn and van Langevelde 2006) that become functionally disconnected when the distance between habitat patches exceeds the species' activity radius (Zurbuchen et al. 2010). The latter is related to body size (Greenleaf et al. 2007) thus rendering small species more susceptible to land-use change than large ones (Steffan-Dewenter and Tscharntke 1999; Steffan-Dewenter et al. 2002). It is, however, unknown whether the interspecific shift in body size with increasing fragmentation among species is mirrored by intraspecific shifts within individual populations.

Intraspecific body-size distributions along environmental gradients are poorly documented. For bees, only longitudinal size clines in one bumblebee species have been reported so far (Peat et al. 2005). Other insect taxa, however, responded to habitat fragmentation with an intraspecific increase in size of dispersal-related body parts such as wings (butterflies, Hill et al. 1999), thorax (damselflies, Taylor and Merriam 1995) or hind femurs (bush-crickets, Berggren 2005). Such a selection towards increased dispersal ability in fragmented landscapes may be advantageous with regard to colonization of new habitats or gene flow (Taylor and Merriam 1995; Hanski et al. 2004). But at the same time, shifts in body-size distributions can alter ecosystem services provided by populations within fragmented habitats. While a reduced interspecific trait spectrum within pollinator communities has been shown to diminish the associated pollination service (Fründ et al. 2013), potential consequences of intraspecific shifts in body sizes are less clear (but see Willmer and Finlayson 2014).

Here, we hypothesized that (1) habitat fragmentation increases mean intraspecific body-size within pollinator populations, but that (2) this effect depends on the average body size of the individual species. In addition we hypothesized that (3) shifts in size-class distributions alter pollination services in modern agroecosystems.

Materials and methods

Study area and pollinator sampling

The study was carried out in the region of Marburg-Biedenkopf (Hesse, Germany). It covers an area of approximately 1260 km^2 (44 % under agricultural use, 41 % forest, 14 % settlement and traffic, and 1 % covered by water). A total of 22 subsidized flowering fields established in 2011 were selected as study sites. Sites were similar in size (0.3 ± 0.04 ha standard deviation STD), represented a distinct gradient in the area of permanent grassland and semi-natural habitats in a 500 m radius (combined 2011: 6–37 %; 2012: 9–49 %), and covered a broad geographic range (distance between sites 911 and 9856 m, mean 2520 ± 1919 m STD).

Around each site, we assessed the land use at four radii (125, 250, 375, 500 m) for 2011 and 2012. To adjust for inter-annual management changes, the digital land-use maps were updated with InVeKoS data each year in ArcGIS 10 (ESRI, Ca., USA). Permanent grasslands (pastures and grasslands) and semi-natural habitats (hedges, gardens, alluvial meadows, clear cuttings, tree rows, quarries, orchards, and the respective study site) were considered to reduce adverse fragmentation effects of the focal study sites, while arable land (without flowering crops) and forest were considered to increase fragmentation effects.

Bees were sampled with yellow pan traps for 7 weeks from the beginning of June to the end of July in 2011 and 2012. Traps were emptied weekly and specimens were identified to species level. We assessed body size by measuring the inter-tegular distance (ITD) for the two most abundant species of the genus Andrena in each year (2011: *Andrena dorsata*, *A. flavipes*; 2012: *A. haemorrhoa*, *A. nigroaenea*). ITD has been shown to sufficiently reflect the dispersal ability of bees (Greenleaf et al. 2007).

Study species

Andrena is the largest bee genus with about 1500 valid species worldwide (Michener 2007) and over 100 species in Germany (Westrich 1989). Andrena bees are solitary, nesting below-ground in a variety of substrates. The four Andrena species of this study represent one small (*A. dorsata*), two intermediate (*A. flavipes*, *A. haemorrhoa*), and one large species (*A. nigroaenea*; Table 1).

Pollen sampling

Additional females of *A. flavipes*, i.e. the most abundant medium-sized species, were sampled within 1 week in August 2013 at one study site for which a wide ITD range had been found. Bees were caught by sweep netting to preserve pollen loads. Pollen collected from the bees' head and thorax (avoiding pollen packets stored at the scopae) was fixated and stained using fuchsine gel (Beattie 1971). It was identified to the highest taxonomic resolution possible following Beug (2004) and the share of different plant species was determined based on a count of 100 pollen grains per sample.

Statistical analysis

Because of the strong sexual dimorphism, only females were used for statistical analyses. Sites with less than three individuals were excluded. For each species, mean ITD per site was correlated with the area percentage of each of the four landscape variables (grassland, semi-natural habitats, arable land, and forest) within the four radii (spatial scales) to determine the most relevant scale using the R function cor.test. In a few cases of intercorrelation between two or more landscape variables, only the variable with the highest correlation coefficient in the previous analysis entered the full model. Full models for each species included the mean ITD per site as dependent and all non-correlated landscape variables at the relevant scale as explanatory variables, using the lm function in R. Models were then reduced by manually removing the non-significant variable with the lowest *p* value until only significant variables remained. After each step of model reduction, model performance was statistically compared to the prior model.

Dependent variables were checked for normal distribution and homoscedasticity of residuals. Both the smallest (*A. dorsata*) and the largest (*A. nigroaenea*) species showed non-normal distribution, which could not by solved by transformation. Because degrees of freedom were not sufficient for non-parametric generalized additive models, and since Shapiro–Wilk tests indicated non-normality only for the most parsimonious models, the (non-significant) explanatory variables of the final model were

Table 1 Size (body length in mm), sociality, phenology, and food sources of the four examined study species *Andrena dorsata*, *A. haemorrhoa*, *A. flavipes*, and *A. nigroaenea*. Information is taken from Westrich (1989)

Species	Size (mm)	Sociality	Phenology	Food source
A. dorsata	9–10	Probably not aggregated	Bivoltine 1: April–May 2: July–August	Polylectic 8 plant families
A. haemorrhoa	10–12	Mostly solitary, sometimes in small aggregations	Univoltine April–June	Polylectic 15 plant families
A. flavipes	11–13	Often aggregated	Bivoltine 1: March–May 2: July–September	Polylectic 17 plant families
A. nigroaenea	13–15	Potentially communal	Univoltine April–July	Polylectic 12 plant families

additionally tested non-parametrically with a Spearman rank correlation for their effects on body size (ITD). Differences between models were low (p-values lm vs. Spearman: 0.058 vs. 0.052 for *A. dorsata* and 0.592 vs. 0.881 for *A. nigroaenea*). The procedure was repeated for the smallest species *A. dorsata* using presence-absence data from all sites with the glm-function and a binomial distribution in R. Because normal distribution of abundance data could not be achieved, Spearman rank correlation with untransformed data was used to assess the relation between mean ITD and abundance per site and species.

The correlation between the numbers of pollen types collected from *A. flavipes* females sampled in 2013 and the individual ITD was analysed using the lm function in R. The number of pollen types had to be log-transformed for achieving normal distribution. One outlier was removed based on the cut-off of $D = 4/n$ for the Cook's distance (Bollen and Jackman 1990).

Results

A total of 1272 Andrena individuals went into the analysis: 232 *A. dorsata* (eleven sites; mean 21.1 ± 39.5 STD), 748 *A. flavipes* (19 sites; mean 39.4 ± 84.7 STD), 169 *A. haemorrhoa* (15 sites; mean 11.3 ± 9.4 STD), and 123 *A. nigroaenea* (18 sites; mean 6.9 ± 8.9 STD). In accordance with body sizes derived from the literature (Table 1), the mean body size per site of the four species constituted three non-overlapping size classes with considerable intraspecific variation: small (*A. dorsata*: 2.19–2.24 mm), intermediate (*A. flavipes*: 2.53–2.64 mm and *A. haemorrhoa*: 2.41–2.56 mm), and large (*A. nigroaenea*: 3.07–3.27 mm; see supplementary material 1 for details).

The two intermediate species showed a significant positive relationship between ITD and measures of habitat fragmentation (Table 2). The ITD of *A. flavipes* was negatively related to the cover of semi-natural habitat at the 500 m scale and that of *A. haemorrhoa* to grassland at the 125 m scale (Fig. 1). In contrast, the ITDs of the smallest (*A. dorsata*) and of the largest species (*A. nigroaenea*) did not respond to any landscape variable at any scale. The same applies to the presence-absence data for *A. dorsata*. Abundance was not significantly related to ITD for any species.

Of the 15 pollen types collected from the thorax of 15 *A. flavipes* females (ITD: 2.16–2.67 mm, mean 2.44 mm), single individuals carried between two and ten types (mean 5.1 ± 2.36 STD). The log-transformed number of pollen types carried was significantly related to the ITD ($F = 5.47$, $p = 0.037$, adjusted $R^2 = 0.27$), with smaller individuals carrying more pollen types (Fig. 2). The most abundant pollen types belonged to the Achillea type (81 %) and to the Taraxacum type (11 %; see supplementary material 2 for all pollen types).

Discussion

We show that habitat fragmentation not only drives the body-size distribution within wild bee communities but also within individual species. More specifically, populations of medium-sized solitary wild bee species shifted towards larger individuals with decreasing area of permanent bee habitat in the landscape, while the largest and smallest species did not show any comparative response. Concerning the medium-sized bees, pollination services were critically affected by alterations in the body-size spectrum.

Similar to the landscape's filtering effect on the composition of wild bee communities, dispersal limitation seems to be the major mechanism explaining the intraspecific body-size shifts observed with habitat fragmentation in our study. While at the community level medium-sized species–in contrast to small ones–are often unaffected by habitat fragmentation (Schweiger et al. 2005), they showed the strongest response at the population level. Population dynamics seem thus to be unaffected by the selection for larger individuals in fragmented habitats. Instead, the missing relation between bee abundance and mean body size suggests density compensation to occur, i.e. larger individuals of medium-sized bee species compensate for the loss of smaller con-specifics in fragmented habitats. The implied intraspecific competition for limited resources (MacArthur et al. 1972) results in competitive release at flower resources shared between size classes once dispersal-limited intraspecific competitors are excluded in fragmented habitats. This process may explain why habitat fragmentation has comparably little effect on the

Table 2 Results of the most parsimonious linear regression models for each of the study species

Species	Landscape variable	Scale (m)	Estimate	df	F	P	Adj. R^2
A. dorsata	NS						
A. flavipes	Semi-natural habitat	500	−0.005	1.17	4.78	0.043	0.17
A. haemorrhoa	Grassland	125	−0.003	1.13	8.17	0.013	0.33
A. nigroaenea	NS						

Estimates are non-standardized coefficients

NS not significant

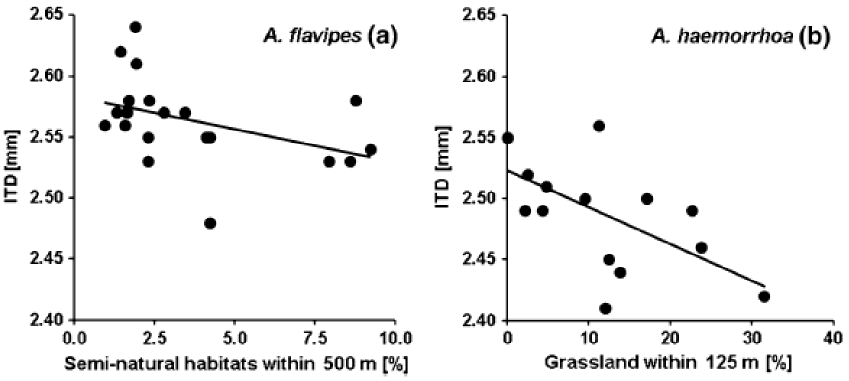


Fig. 1 Relation between mean inter-tegular distance (ITD) in mm and **a** percentage of semi-natural habitats in a 500 m radius around study sites for *Andrena flavipes* and **b** percentage of grassland in a 125 m radius around study sites for *A. haemorrhoa*. Individuals were collected using pan traps in 2011 and 2012

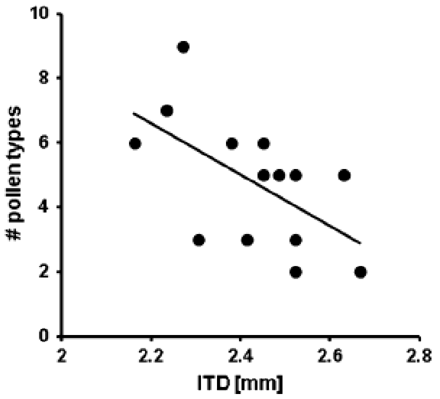


Fig. 2 Relation between the number of pollen types collected from *Andrena flavipes* females and inter-tegular distance in mm of the respective individual. Data shown are original values. Individuals were caught by sweep netting in 2013

extinction risk of medium-sized species (Bommarco et al. 2010).

The functional consequences for insect-pollinated plants, however, may be severe since pollinator size in relation to flower size critically affects several aspects of the pollination process, such as the amount and position of pollen on flower-visiting insects (Tepedino et al. 1999) and handling time or mode (Stout 2000; Vivarelli et al. 2011). Accordingly, a distortion of plant-pollinator interactions with the observed shifts towards larger individuals in medium-sized species with increasing habitat fragmentation may be assumed. This assumption was confirmed by the negative relation between individual body size and the number of pollen types collected by *A. flavipes* females.

The decrease in the diversity of pollen collected by larger females probably reflects their ability to adjust their foraging behaviour to resource availability and/or quality (Fontaine et al. 2008). There is evidence that such changes can increase the reproductive success of bees (Génissel et al. 2002; Radmacher and Strohm 2010). At the same time, a decrease in heterospecific pollen types carried by flower visitors increase pollination efficiency for those plants that are actually visited (Areco-Gómez and Ashman 2014). Other plants, in contrast, almost inevitably receive fewer visits and may thus suffer from reduced seed set in fragmented habitats (cf. Kunin 1993). As a consequence, alterations in pollination services may occur even if population sizes remain unaffected by habitat fragmentation. This convincingly explains that the reproductive success of bee-dependent plants in semi-natural European grasslands is more sensitive to land-use intensification than bee diversity (richness, abundance and evenness; Clough et al. 2014).

Habitat fragmentation did not affect body-size distributions of the smallest and the largest bee species. The largest species *A. nigroaenea* obviously is adapted for covering larger distances between foraging and nesting habitats. Yet, the smallest and most dispersal-limited species *A. dorsata* was only present in half of the studied sites. This indicates that the presence of small species in fragmented habitats depends on stochastically distributed founding individuals with high patch fidelity (cf. Franzen et al. 2009), while the absence from well-connected habitats rather is the consequence of local extinctions (Franzen and Nilsson 2013). In both cases, changes in body-size distribution with habitat fragmentation are not to be expected.

We conclude that if the here observed intraspecific body-size variation in relation to landscape structure and the potential functional consequences prove to be common in the pollinator guild, the ecological effects of changes in landscape structure need to be considered not only at the community but also the population level. Future studies will be required to investigate the long-term consequences of this filtering process for population dynamics and the evolution of wild bees and the associated plant species in highly variable human-dominated landscapes.

Acknowledgments DW was funded by Deutsche Bundesstiftung Umwelt (DBU). We thank M. Zerbe and K. Weiss of Amt für Ländlichen Raum Landkreis Marburg Biedenkopf for cooperation in site selection and farmers for access to their land. The Hessisches Ministerium für Energie, Landwirtschaft und Verbraucherschutz (HMUELV) and the Hessisches Landesamt für Umwelt und Geologie (HLUG) kindly provided digital land-use maps. We thank Stefanie Ettling for supporting pollen analysis and two anonymous reviewers for helpful comments.

References

Areco-Gómez G, Ashman T (2014) Heterospecific pollen receipt affects self pollen more than outcross pollen: implications for mixed-mating plants. Ecology 95:2946–2952

Berggren A (2005) Effect of propagule size and landscape structure on morphological differentiation and asymmetry in experimentally introduced Roesel's bush-crickets. Conserv Biol 19:1095–1102

Beattie AJ (1971) A technique for the study of insect-borne pollen. Pan-Pac Entomol 47:82

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

Bollen K, Jackman R (1990) Regression diagnostics: an expository treatment of outliers and influential cases. In: Fox J, Long J (eds) Modern methods of data analysis. Sage Publications, Beverly Hills, pp 257–291

Bommarco R, Biesmeijer JC, Meyer B, Potts SG, Pöyry J, Roberts SP, Steffan-Dewenter I, Öckinger E (2010) Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. Proc Roy Soc B-Biol Sci 277:2075–2082

Chown SL, Gaston KJ (2010) Body size variation in insects: a macroecological perspective. Biol Rev 85:139–169

Clough Y, Ekroos J, Báldi A, Batáry P, Bommarco R, Gross N, Holzschuh A, Hopfenmüller S, Knop E, Kuussaari M, Lindborg R (2014) Density of insect-pollinated grassland plants decreases with increasing surrounding land-use intensity. Ecol Lett 17:1168–1177

Fontaine C, Collin CL, Dajoz I (2008) Generalist foraging of pollinators: diet expansion at high density. J Ecol 96:1002–1010

Franzen M, Larsson M, Nilsson S (2009) Small local population sizes and high habitat patch fidelity in a specialised solitary bee. J Insect Conserv 13:89–95

Franzen M, Nilsson SG (2013) High population variability and source-sink dynamics in a solitary bee species. Ecology 94:1400–1408

Fründ J, Dormann CF, Holzschuh A, Tscharntke T (2013) Bee diversity effects on pollination depend on functional complementarity and niche shifts. Ecology 94:2042–2054

Génissel A, Aupinel P, Bressac C, Tasei JN, Chevrier C (2002) Influence of pollen origin on performance of *Bombus terrestris* micro-colonies. Entomol Exp Appl 104:329–336

Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. Oecologia 153:589–596

Hanski I, Erälahti C, Kankare M, Ovaskainen O, Sirén H (2004) Variation in migration propensity among individuals maintained by landscape structure. Ecol Lett 7:958–966

Hill JK, Thomas CD, Blakeley DS (1999) Evolution of flight morphology in a butterfly that has recently expanded its geographic range. Oecologia 121:165–170

Jauker B, Krauss J, Jauker F, Steffan-Dewenter I (2013) Linking life history traits to pollinator loss in fragmented calcareous grasslands. Landscape Ecol 28:107–120

Kremen C (2005) Managing ecosystem services: what do we need to know about their ecology? Ecol Lett 8:468–479

Kleijn D, van Langevelde F (2006) Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. Basic Appl Ecol 7:201–214

Klein AM, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proc Roy Soc B-Biol Sci 274(1608):303–313

Kunin WE (1993) Sex and the single mustard: population density and pollinator behavior effects on seed-set. Ecology 74:2145–2160

Levy RA, Nufio CR (2015) Dispersal potential impacts size clines of grasshoppers across an elevation gradient. Oikos 124:610–619

MacArthur RH, Diamond JM, Karr JR (1972) Density compensation in island faunas. Ecology 53:330–342

Michener CD (2007) The bees of the world, 2nd edn. Johns Hopkins University Press, Baltimore

Peat J, Darvill B, Ellis J, Goulson D (2005) Effects of climate on intra- and interspecific size variation in bumble-bees. Funct Ecol 19:145–151

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

Schweiger O, Maelfait JP, van Wingerden W, Hendrickx F, Billeter R, Speelmans M, Augenstein I, Aukema B, Aviron S, Bailey D, Bukacek R (2005) Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. J Appl Ecol 42:1129–1139

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

Steffan-Dewenter I, Tscharntke T (1999) Effects of habitat isolation on pollinator communities and seed set. Oecologia 121:432–440

Stout JC (2000) Does size matter? Bumblebee behaviour and the pollination of *Cytisus scoparius* L. (Fabaceae). Apidologie 31:129–139

Taylor PD, Merriam G (1995) Wing morphology of a forest damselfly is related to landscape structure. Oikos 73:43–48

Tepedino VJ, Sipes SD, Griswold TL (1999) The reproductive biology and effective pollinators of the endangered beardtongue *Penstemon penlandii* (Scrophulariaceae). Plant Syst Evol 219:39–54

Vivarelli D, Petanidou T, Nielsen A, Cristofolini G (2011) Small-size bees reduce male fitness of the flowers of *Ononis masquillierii* (Fabaceae), a rare endemic plant in the northern Apennines. Bot J Linn Soc 165:267–277

Westrich P (1989) Die Wildbienen Baden-Württembergs. Eugen Ulmer, Stuttgart

Williams NM, Crone EE, Roulston TH, Minckley RL, Packer L, Potts SG (2010) Ecological and life-history traits predict bee species responses to environmental disturbances. Biol Conserv 143:2280–2291

Willmer PG, Finlayson K (2014) Big bees do a better job: intraspecific size variation influences pollination effectiveness. J Poll Ecol 14:244–254

Winfree R, Aguilar R, Vázquez DP, LeBuhn G, Aizen MA (2009) A meta-analysis of bees' responses to anthropogenic disturbance. Ecology 90:2068–2076

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. J Anim Ecol 79:674–681

ANHANG KAPITEL IV

Supplementary material 1: Table of abundance, mean inter-tegular distance (ITD) and sample-based variance of ITD for four Andrena wild bee species analysed. An individual-based dataset can be obtained from the corresponding author upon request.

	Andrena dorsata			*Andrena flavipes*			*Andrena haemorrhoa*			*Andrena nigroaenea*		
site_ID	abundance	Ø ITD [mm]	variance (sample)	abundance	Ø ITD [mm]	variance (sample)	abundance	Ø ITD [mm]	variance (sample)	abundance	Ø ITD [mm]	variance (sample)
36				18	2.57	0.012	3	2.50	0.007	7	3.26	0.046
42				5	2.53	0.005	11	2.41	0.016	3	3.27	0.017
45							6	2.55	0.026			
76	3	2.23	0.028	18	2.56	0.025	27	2.56	0.009	3	3.19	0.017
81	16	2.21	0.010	5	2.64	0.004	5	2.46	0.009	4	3.25	0.017
86							4	2.50	0.038	4	3.25	0.001
90				15	2.55	0.017				5	3.19	0.022
92	3	2.23	0.012	21	2.53	0.014	9	2.49	0.011	5	3.09	0.075
120	34	2.24	0.010	382	2.57	0.013	21	2.55	0.013	12	3.20	0.017
124	7	2.21	0.005	20	2.58	0.013	6	2.42	0.016	3	3.24	0.058
125	8	2.23	0.020	27	2.61	0.016	18	2.45	0.024	40	3.22	0.012
129	4	2.20	0.003	7	2.58	0.008	34	2.51	0.017	7	3.21	0.007
130							6	2.49	0.011	7	3.16	0.006
137				33	2.57	0.016	5	2.52	0.023	4	3.21	0.006
138	4	2.19	0.019	22	2.55	0.033						
144				5	2.57	0.014						
174	137	2.22	0.011	76	2.58	0.017	5	2.44	0.016			
192				13	2.62	0.020	9	2.49	0.012	7	3.18	0.053
196				5	2.55	0.021				4	3.21	0.010
204	6	2.23	0.010	9	2.53	0.020						
212	10	2.23	0.009	23	2.56	0.028				5	3.07	0.011
226				44	2.54	0.015				3	3.23	0.001

Supplementary material 2: Pollen types collected from 15 *Andrena flavipes* females sampled in 2013. Total share is the percentage of the respective pollen type in relation to all pollen sampled. Frequency gives the percentage of female *A. flavipes* carrying the respective pollen type.

Pollen type	Total share [%]	Frequency [%]
Achillea type	81	100
Taraxacum type	11	50
Apiaceae	2	43
Quercus	2	79
Morphotype 1	2	43
Chenopodium	1	43
Ranunculus	<1	21
Rumex	<1	21
Brassicaceae	<1	14
Centaurea cyanus	<1	14
Pinus	<1	14
Salix	<1	14
Poaceae	<1	7
Helianthus	<1	7
Prunus	<1	7

KAPITEL V – BLÜHMISCHUNGEN DER HIAP FLÄCHEN

ATTRACTIVENESS OF WILD-FLOWER MIXTURES FOR WILD BEES AND HOVERFLIES DEPENDS ON SOME KEY PLANT SPECIES

Warzecha D, Diekötter T, Wolters V, Jauker F

Erschienen 2018 in *Insect Conservation and Diversity* 11: 32–41

Insect Conservation and Diversity

Insect Conservation and Diversity (2018) **11,** 32–41 doi: 10.1111/icad.12264

Attractiveness of wildflower mixtures for wild bees and hoverflies depends on some key plant species

DANIELA WARZECHA,[1,*] TIM DIEKÖTTER,[1,†] VOLKMAR WOLTERS [1] and FRANK JAUKER [1] [1]Department of Animal Ecology, Justus Liebig University Giessen, Giessen, Germany

Abstract. 1. Agricultural intensification is considered to be a major driver of terrestrial biodiversity decline. Resulting loss, isolation and degradation of flower-rich habitats are threatening pollinators. Agri-environmental schemes (AES) aim to counteract these negative effects, including measures to enhance floral resources in agricultural landscapes. The impact of plant species composition on their efficiency to mitigate pollinator loss, however, is largely unexplored.

2. We tested four recommended seed mixtures for their attractiveness to wild bees and hoverflies in a replicated plot design over two consecutive years against the background of the seedbank. Of the 94 available plant species, 14 key plant species were crucial for the whole flower-visiting bee and hoverfly community. Approximately one third of each originated from the seedbank. The four top plants already supported 80% of flower visitors. Although seed mixtures differed significantly in attracting flower visitors at the plot level, the presence of key plants was more important than plant species diversity *per se*.

3. Seed mixtures showed contrasting attractiveness for wild bees and hoverflies. Identification of plant species exclusively utilised by specific taxonomic groups opens opportunities for assorting plant mixtures for specific ecosystem functions or taxa of conservation concern. Plant species shared by common pollinators are valuable for overall pollinator diversity.

4. The fact that rare and specialised pollinator species were mostly absent, however, substantiates that within 2 years of establishment, flowering resources are not the sole limiting factor in modern agricultural landscapes. Considering additional resources seems indispensable to maximise the conservation of species-rich pollinator communities.

Key words. Apoidea, flowering fields, greening, habitat fragmentation, pollinator loss, supporting ecosystem services, Syrphidae, wildflower plantings, wildflower strips.

Introduction

The global decline of pollinators increasingly concerns scientists and policy makers because the species involved play a critical role in preserving wild plant diversity (Biesmeijer *et al*., 2006; Carvell *et al*., 2006) and have a paramount commercial relevance (Klein *et al*., 2007; Winfree, 2010). Agricultural intensification and expansion is generally considered to be the most important driver of global terrestrial biodiversity decline as it has led to loss, fragmentation and

Correspondence: Daniela Warzecha, Department of Animal Ecology, Justus Liebig University Giessen, Giessen, Germany. E-mail: daniela.warzecha@smnk.de

*Present address: State Museum of Natural History Karlsruhe, Karlsruhe, Germany

†Present address: Department of Landscape Ecology, Institute for Natural Resource Conservation, Kiel University, Kiel, Germany

degradation of relevant habitats (Foley *et al*., 2011). Landscape diversity was reduced when farms became more industrialised, leading to larger fields instead of mixed farming (Robinson & Sutherland, 2002). As a consequence, semi-natural habitats like hedgerows, extensive grasslands and field margins, which provide essential resources to many species (Marshall & Moonen, 2002; Öckinger & Smith, 2007; Hannon & Sisk, 2009; Dahms *et al*., 2010), have become increasingly scarce in modern agricultural landscapes (Potts *et al*., 2010). The remaining semi-natural habitat islands are small and isolated, often of poor quality and therefore predominantly utilised by generalists (Dramstad & Fry, 1995; Biesmeijer *et al*., 2006; Jauker *et al*., 2009).

To counteract these negative effects of modern agricultural practices, agri-environmental schemes (AES) are implemented in numerous European countries to maintain and restore biodiversity in agricultural landscapes (Batáry *et al*., 2015). Although AES may have different objectives depending on both regional conditions and target taxa, they generally include measures that potentially benefit a wide range of species occurring in agricultural land. A common practice is the establishment of flowering fields and field margins, initiated by financial compensation to farmers for income lost (Ovenden *et al*., 1998). In addition to providing refuges for endangered farmland birds and mammals, a major target is to enhance the supply of pollen and nectar sources for pollinators (Carvell *et al*., 2007). Within the regional AES 'HIAP' (Hessian Integrated Agri-environmental Program) of the federal state Hesse (Germany), local farmers were contracted for the establishment of flowering fields on previously cultivated arable land for 5 years. Once flowering fields have been established, mowing, weeding and fertilising are permitted to allow for colonisation and establishment of species from the regional species pool.

Recent studies have proven the importance of such AES-induced flowering fields for a variety of flower-visiting insect groups (Carvell *et al*., 2011; Korpela *et al*., 2013; Scheper *et al*., 2013, 2015; Grass *et al*., 2016). While most studies confirm that increased flower availability results in higher pollinator abundance and diversity in general (Carvell *et al*., 2007; Korpela *et al*., 2013), it remains unclear whether the attractiveness of commercial seed mixtures depends on the overall number of plant species or the presence of key plant species. Previous studies either focused on one single seed mixture (Korpela *et al*., 2013; Scheper *et al*., 2015) or on one single pollinator group such as bumblebees (Carvell *et al*., 2007). The development of modelling tools for identifying optimised plant mixtures is challenging (M'Gonigle *et al*., 2016). These first approaches, however, show the need for more information on the taxon-specific utilisation of flower resources.

Here we assessed the attractiveness of four different seed mixtures mandated by the authorities for AES in Hessen for a local flower-visitor community in two consecutive years to address the following research questions: (i) Do species-rich seed mixtures generally attract more pollinator species than species poor mixtures? (ii) Do wild bees and hoverflies respond differently to plant species richness in seed mixtures? (iii) Is the occurrence of important key plant species in commercially available seed mixtures a better determinant of their potential in attracting pollinators than plant species richness?

Materials and methods

Study design

The study was carried out at the experimental research station Oberer Hardthof of the Justus Liebig University of Giessen (Hesse, Germany) in 2013 and 2014. The experimental farm is located in the periphery of the city Giessen and cultivates 110 ha of arable land and 117 ha of grassland. In one of these previously cultivated fields, 28 experimental plots (4 × 4 m), covering an area of approximately 2000 m^2, were established. Four different seed mixtures were sown in a randomised block design (Fig. 1) and were separated by strips of sown grass (3.5 m). The suggested time frame for sowing is April–June depending on ground frost, but agreements between authorities and farmers through AES are usually not concluded before late spring. Thus, sowing date in our study was late May in 2013 corresponding to the earliest common practice. Site preparation included ploughing twice in April 2013 to reduce weeds. Seed mixtures were sown mechanically by experienced staff of the experimental farm (mixture names and seed rate: Lebensraum 1 = L1, 20 kg/ha; Veitshöchheimer Bienenweide = VH, 20 kg/ha; Odin 2 = O2, 40 kg/ha; Odin 1 = O1, 40 kg/ha). No further applications were conducted after sowing except mowing of the grass strips between plots. The four chosen seed mixtures were the three most frequently used mixtures within HIAP in the region of Marburg-Biedenkopf, Hesse, Germany (L1, O2, O1) and one mixture advertised specifically for bees (VH). This selection covers a distinct gradient of plant species richness in seed mixtures recommended for flowering fields within HIAP: L1 with 57 plant species, VH with 50 species, O2 with 34 species and O1 with 21 species. All mixtures comprise varying compositions of a broad range of both annual plants providing vegetation cover in the year of establishment and perennial plants persisting during the following years. For a detailed list of the plant species composition, see Appendix S1.

Pollinator sampling

Starting in June, established plots were checked weekly for the onset of the main blooming period. Sampling started accordingly in mid-July in 2013 and in early July in 2014 and ended in both years when the majority of flowers were faded in August. In each survey, plots were observed for flower-visiting insects for 15 minutes by slowly walking its sides in a random order. Surveys were conducted between 09:00 and 18:00 under warm, sunny

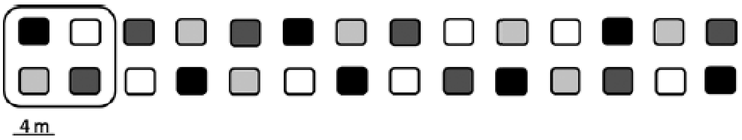


Fig. 1. Experimental design: four seed mixtures were established in a randomised block design; black: Odin 1; dark grey: Lebensraum1; light grey: Veitshöchheimer Bienenweide; white: Odin 2.

conditions with little or no wind. Flower-visiting insects (bees and hoverflies) were individually collected from plants with a sweep net and the visited plant species was recorded. Specimen were brought to the laboratory and identified to species level. While sites were surveyed seven times covering a period of 5 weeks in 2013, poor climatic conditions in the second year after the sowing limited the surveys to four times over a period of 3 weeks in 2014. One survey round covered two consecutive days with a 3- (minimum) to 10-day (maximum) interval between survey rounds. After each sampling survey, we recorded all plant species in each plot and estimated the flower cover [%] of each plant. Grasses were excluded from the data set for further analyses. Because plant data were missing for one block, statistical analyses for seed mixture potential were based on a set of six blocks (24 plots) out of the seven blocks (28 plots).

Statistical analysis

Total network. We compiled an interaction network with the sampled pollinators and their visited plant species across the total sampling area. To identify the plant species most important for the pollinator community, we calculated their species strength. Species strength is defined as the sum of dependencies (proportion of visits) of flower visitors relying on a specific plant species (Bascompte *et al.*, 2006). For the network analysis, we used the package bipartite (Dormann, 2011). To identify the minimum plant species composition needed to cover all observed pollinator species (hereafter 'key plant species'), we first took the plant species attracting the highest number of pollinator species and subsequently added plant species attracting most of the remaining pollinator species until all pollinator species were covered.

Seed mixture analyses. To confirm that seed mixtures differed in plant species composition despite expected variability in plant species composition among plots of the same mixture, pairwise dissimilarities of all plots were calculated with the function 'betadiver' within the package vegan (Oksanen *et al.*, 2015). For analysing differences in beta diversity within and among seed mixtures, we used the Kruskal–Wallis rank sum test because dissimilarity values did not follow a normal distribution.

Seed mixture potential. We examined whether seed mixtures differed in the presence of key plant species (hereafter 'seed mixture potential'). Seed mixture potential was defined as the proportion of key plant species within mixtures in general and within plots. Differences between seed mixtures at the plot level were examined with R's 'aov' (analysis of variance) function.

Seed mixture attractiveness. We examined whether seed mixtures differed in attracting pollinator species and individuals (hereafter 'seed mixture attractiveness'). The relation between pollinators and seed mixture was analysed using R's 'aov' function. Dependent variables were species richness and abundance of all pollinators and of wild bees and hoverflies separately. Residuals were checked for normal distribution with the Shapiro–Wilk normality test.

All analyses were done in R version 3.0.3 (R Core Team, 2014).

Results

A total of 1835 flower-visiting specimen were collected belonging to the superfamily Apoidea (1134 individuals out of 46 species) and the family Syrphidae (701 individuals out of 28 species). The wild bees comprised predominantly bumblebees (67%) of three species (*Bombus lapidarius*, *Bombus terrestris agg.*, *Bombus sylvarum*) followed by *Andrena flavipes* (10%). *Episyrphus balteatus* and *Sphaerophoria scripta agg.* were the predominant hoverfly species with 40% and 27% of all hoverflies (Appendix S2). We recorded a total number of 94 plant species, including both sown (58) and unsown (36) species from the seedbank. For 41 of these plant species we recorded visits by pollinators (Table 1). Sampling time covered the blooming period of all plant species from seed mixtures which could not be recorded in the field. Two of the plant species that were recorded, however, had a mismatch between the blooming period given in the literature and sampling time (*Trifolium resupinatum* and *Taraxacum sect. Ruderalia*; Appendix S3).

Total network

The network analysis for all visited plants identified four species (*Achillea millefolium*, *Anthemis tinctoria*, *Chenopodium album* and *Phacelia tanacetifolia*) with the highest species strength values (hereafter 'top 4 species'). While *Chenopodium album* was found in all plots,

Table 1. Plants visited by the sampled pollinators within the two study years.

		Plant species	Species strength	Visitation frequency	Origin	Frequency mixtures	Frequency plots [%]
Covers the total flower visitor community	Top 4 plant species	*Anthemis tinctoria*	11.72	194	SM	3	88
		Chenopodium album	9.59	221	SB	–	100
		Achillea millefolium	9.22	102	SM	3	75
		Phacelia tanacetifolia	8.09	261	SM	1	63
		Fagopyrum esculentum	5.81	121	SM	4	92
		Malva sylvestris	5.29	309	SM	4	100
		Daucus carota	3.74	30	SM	4	71
		Echium vulgare	3.29	69	SM	2	46
		Calendula officinalis	2.22	30	SM	2	71
		Linum usitatissimum	2.19	18	SM	3	71
		Centaurea cyanus	2.18	133	SM	2	79
		Lactuca spec.	1.29	3	SB	–	4
		Persicaria hydropiper	1.05	4	SB	–	50
		Lactuca serriola	1.03	2	SB	–	46
		Sinapis alba	2.87	116	SM	1	63
		Centaurea jacea	0.58	3	SM	2	50
		Sonchus oleraceus	0.56	8	SB	–	54
		Borago officinalis	0.45	45	SM	3	63
		Onobrychis viciifolia	0.41	10	SM	4	75
		Erigeron annuus	0.32	4	SB	–	4
		Lamium purpureum	0.26	15	SB	–	79
		Matricaria chamomilla	0.23	12	SB	–	50
		Medicago sativa	0.23	12	SM	4	75
		Tripleurospermum perforatum	0.18	9	SB	–	71
		Trifolium pratense	0.16	17	SM	4	96
		Pastinaca sativa	0.16	8	SM	2	13
		Plantago lanceolata	0.15	12	SM	1	42
		Malva moschata	0.13	18	SM	3	75
		Helianthus annuus	0.13	6	SM	4	42
		Anethum graveolens	0.12	2	SM	1	46
		Cichorium intybus	0.11	14	SM	2	54
		Leucanthemum ircutianum	0.06	5	SM	2	29
		Malva verticillata	0.05	3	SM	1	58
		Trifolium resupinatum	0.04	4	SM	1	25
		Silene latifolia	0.03	1	SB	–	63
		Melilotus officinalis	0.02	3	SM	1	25
		Trifolium incarnatum	0.02	2	SM	2	42
		Sonchus asper	0.02	3	SB	–	71
		Lotus corniculatus	0.01	3	SM	2	13
		Solanum nigrum	0.01	2	SB	–	50
		Ornithopus sativus	11.72	1	SM	1	33

The top four plant species are based on the species strength network index. Visitation frequency refers to number of pollinators recorded. Origin defines whether the plant species originated from a seed mixture (SM) or the seedbank (SB). Frequency mixtures give the number of seed mixtures containing the respective plant species. Frequency plots gives the proportion of occurrence in the 24 plots (note that plants may not occur on all plots per mixture or may spread in plots with other seed mixtures, see Table 2 for detailed information).

Anthemis tinctoria and *Achillea millefolium* were missing in the species-poorest mixture (O1) and *Ph. tanacetifolia* was only present in this mixture. At these top four plant species, we found 778 (42%) specimens of the 1835 sampled pollinators and 60 (81%) of 74 species. Both *A. millefolium* (5%/39% of bee individuals/species; 6%/46% of hoverfly individuals/species) and *A. tinctoria* (10%/44% of bee individuals/species; 11%/43% of hoverfly individuals/species) were similarly attractive for both flower visitor groups. *Chenopodium album* was dominated by hoverflies (30%/50% hoverfly individuals/species; 1%/9% bee individuals/species) and *Ph. tanacetifolia* dominated by bees (19%/44% bee individuals/species; 7%/18% hoverfly individuals/species). Of the other 37 visited plant species, 10 were necessary to cover the remaining 22 pollinator species of the local species pool (Table 1). While flower cover was positively related to the absolute number of pollinator species recorded (Spearman's rank correlation: $R = 0.66$, $t_{(97)} = 8.59$, $P < 0.001$), the rank of key plant species in cumulatively attracting the whole pollinator community was unrelated to flower cover ($R = -0.52$, $t_{(12)} = -2.11$, $P > 0.05$).

One of the top four (*Chenopodium album*) and three of the remaining 10 key plant species (*Persicaria hydropiper*, *Lactuca spec.* and *Lactuca serriola*) were not sown and originated from the seedbank. Similarly of all recorded plant species one-third originated from the seedbank (see Table 2). The 14 key plant species covering the total flower visitor species pool belonged to the families Apiaceae, Asteraceae, Boraginaceae, Linaceae, Malvaceae and Polygonaceae.

Seed mixture potential

Although the plots varied considerably in their plant species number (Table 2), analysis of the beta diversity confirmed that plant communities were significantly more similar within than between mixtures ($P < 0.001$; Appendix S4). The number of key plant species in the producers' lists of mixtures was similar, but their relation to the total number of plant species within mixtures differed substantially (O1 = 6 key plant species, 0.27 of total plant species number; O2 = 7, 0.21; L1 = 7, 0.13; VH = 8, 0.16). For established plant communities observed at the plot level, seed mixture potential, that is, the proportion of key plant species per plot, differed significantly among seed mixtures ($F_{3,24} = 23.21$, $P < 0.001$). The proportion of the 14 key plant species per plot successively decreased from the species-poorest to the species-richest seed mixture (Fig. 2). Higher relative occurrence per plot than within mixture is due to key plants originating from either the seedbank or invading from other seed mixtures (see Table 2). Excluding key plants from the seedbank did not change the statistical results ($F_{3,24} = 16.86$, $P < 0.001$) or the ranking of seed mixtures according to their potential.

Seed mixture attractiveness

The attractiveness of the four seed mixtures differed significantly for all tested pollinator variables except overall pollinator species richness (marginally significant) and hoverfly species richness (Table 3). While no significant differences could be established for overall pollinator species richness (Fig. 3a), overall pollinator abundance was the highest in VH (Fig. 3b). Bee species richness was highest in the least plant species-rich mixture and lowest in the most plant species-rich mixture (Fig. 3c), while the non-significant responses of hoverfly species richness were the likely driver for the marginally significant effect on overall species richness (Fig. 3e). Similarly, the lower overall abundance of the species-poorest mixture (O1) was mainly due to the lowest hoverfly abundance of all mixtures (Fig. 3f), while it was preferred by wild bee individuals (Fig. 3d). The contribution of plant species originating from the seedbank to the attractiveness was similar across mixtures, except for a high contribution in the most plant species-rich mixture (percentage of pollinator species only recorded on seedbank plant species: L1 = 21.4, VH = 8.7, O2 = 7.9, O1 = 8.2; percentage of abundance of those species: L1 = 2.5, VH = 1.0, O2 = 0.7, O1 = 1.3). This effect was mostly due to hoverflies (15 out of 20 occurrences) and the seedbank plant species *Ch. album*.

Pollinator species unique to only one seed mixture (O1 = 2 hoverfly/7 bee species, VH = 4 hoverfly/4 bee species, L1 = 4 hoverfly/3 bee species, O2 = 3 hoverfly/1 bee species) were all recorded on plant species also present in other mixtures except for *Platycheirus clypeatus*, which

Table 2. Plant species number of the examined seed mixtures.

	Plant sp. mix	Plant sp. total	Plant sp. per plot	Origin, per plot [%]		
				Mix	SB	Inv.
L1	57	62	36 ± 4.5	58.6	28.8	12.6
VH	50	67	40 ± 4.2	59.3	25.4	15.3
O2	34	53	29 ± 3.7	54.0	32.8	13.2
O1	21	48	26 ± 4.1	48.4	28.4	23.2

Presented are species numbers given by the producer (Plant sp. mix) and the total (Plant sp. total) and mean (Plant. sp. per plot) recorded species numbers. Origin per plot gives the mean percentage of plant species originating from the seed mixture (Mix) and the seedbank (SB) or invaded from other seed mixtures (Inv.). L1, Lebensraum 1; VH, Veitshöchheimer Bienenweide; O2, Odin 2; O1, Odin 1.

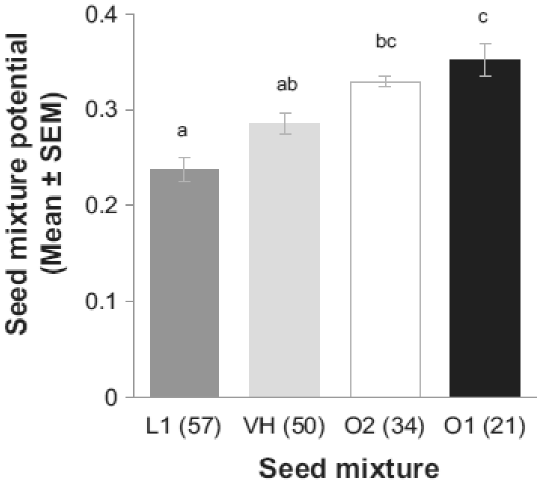


Fig. 2. Mean seed mixture potential (±SEM) of the four tested seed mixtures. Seed mixture potential is calculated as the number of present 14 key plants per plot divided by the number of all observed plant species of the same plot. L1, Lebensraum 1; VH, Veitshöchheimer Bienenweide; O2, Odin 2; O1, Odin 1. Species numbers per mixture given by the producer are added in parentheses. Lower case letters give significant differences based on R's Tukey honest significant differences.

was solely recorded on *Lactuca spec*. This nested structure (i.e. specialist pollinators being interaction partners of generalist plants) was also evident at the total network level with only two cases of pollinators visiting only one plant species that in turn was visited by less than three more pollinator species (the aforementioned *Pl. clypeatus* and *Lasioglossum villosulum* on *Lactuca serriola*; see also Appendix S5).

Discussion

Pollinator diversity is generally related to flowering plant diversity in natural systems (Potts *et al*., 2003; Hegland & Boeke, 2006). Accordingly, highly diverse commercial seed mixtures are thought to be necessary in order to promote the diversity of flower visitors in the homogenous agricultural landscapes of our time. Indeed, 14 key plant species constituted the necessary minimum to cover the whole pollinator community. Of these, four top plant species proved especially important, providing resources to 81% of the recorded pollinator species. Flower visitors were, however, recorded on only half of the plant species present over 2 years. Additionally, the plant species from the seedbank played a crucial role for the local pollinator community (Marshall *et al*., 2003; Gibson *et al*., 2006), with four of the 14 key plant species not originating from the commercial mixtures. One top four plant species attracting large shares of visitations by hoverfly species, *Chenopodium album*, is often considered an agricultural weed. Beside the highly attractive cultivated plant species *Ph. tanacetifolia*, attracting large shares of visitations by wild bee species, the observed pollinators visited mainly typical field flora like *Achillea millefolium*, *Anthemis tinctoria* and *Centaurea cyanus*. The importance of relatively few key plant species in combination with partially contrasting attractiveness to different flower visitor groups shows the potential to improve seed mixtures for usually temporal AES.

Commercial seed mixtures differed in their attractiveness for local pollinator communities independently from plant species richness. The floral background from the local seedbank had little influence on this pattern. Both mixtures with the highest and the lowest number of plant species established in the plots showed the highest attractiveness. The species poor mixture showed a high share of key plant species that holds responsible for its attractiveness and substantiates the need for a careful selection of plant species for AES (M'Gonigle *et al*., 2016). The mixture with the highest number of plant species in the original mixture and second highest established on site performed poorest in our experiment showing a considerable amount of uncertainty for solely relying on a positive plant diversity – pollinator diversity relationship. Accordingly, poor plant species selection may offset additive positive effects of co-flowering heterospecific neighbours observed in natural systems (Lázaro *et al*., 2009; Bruckman & Campbell, 2014) and significantly reduce the attractiveness of diverse flower mixtures.

Table 3. Pollination visitation rate ANOVA.

Property	Variable	d. f.	*F*	*P*
Pollinator species richness	Seed mix	3, 24	2.78	0.063
Pollinator abundance	Seed mix	3, 24	3.72	0.025*
Bee species richness	Seed mix	3, 24	4.95	0.008**
Bee abundance	Seed mix	3, 24	9.50	<0.001***
Hoverfly species richness	Seed mix	3, 24	1.76	0.182
Hoverfly abundance	Seed mix	3, 24	6.53	0.002**

Correlation of total visitors per 15-min observation session for each of the four seed mixtures.
Significance codes: * = 0.01; ** = 0.001; *** = 0.

Tailored flower mixtures until now are targeting specific functional groups of the flower-visiting community, such as bees (Scheper *et al*., 2015; Ramseier *et al*., 2016) and predators of pest species (Tschumi *et al*., 2016). A great challenge in optimising seed mixtures, however, is to simultaneously provide resources for flower visitors representing providers of different services and functions. In our experiment, attractiveness of flower mixtures differed substantially between bees and hoverflies. In fact, species richness of hoverflies did not respond to the examined seed mixtures, probably due to their rather generalist flower selection and relative insensitivity to anthropogenic land use (Jauker *et al*., 2009). Their abundances responded contrary to the availability of key plant species in the mixtures, suggesting that plant species selection is still not optimal for flower visitors other than bees, although up to 75% of the flower-visiting species in flowering fields are neither bees nor hoverflies (Grass *et al*., 2016). The role of flower-independent traits such as suitability for phytophagous hoverfly larvae or prey support for aphidophagous larvae remain yet unsolved. In contrast to hoverflies, wild bees favoured the mixture with the most key plant species and the – specifically designed – diverse mixture, substantiating that they respond fairly well to tailored flowering areas within AES (Scheper *et al*., 2015). In conclusion, the mixtures in our experiment target specific flower visitors (O1 – wild bees; L1 – hoverflies) or – with different success – the whole flower visitor community (VH – more suitable; O2 – less suitable).

The identification of specific top plant species equally suitable for both taxa (e.g. *A. millefolium* and *A. tinctoria*) and specifically for bees (e.g. *Ph. tanacetifolia*) or hoverflies (e.g. *Ch. album*) opens opportunities for seed mixture optimisation. Both *Ch. album* and *Ph. tanacetifolia*, and probably *S. alba* and *F. esculentum*, are long-established and common arable flora in cultivated landscapes (Westrich, 1989) and have likely developed strong associations with pollinator species equally common in agricultural landscapes (Scheper *et al*., 2014). It thus seems ecologically worthwhile to prioritise precisely those plant species for seed mixtures that are abundant in agroecosystems and support a broad range of flower visitors. In general,

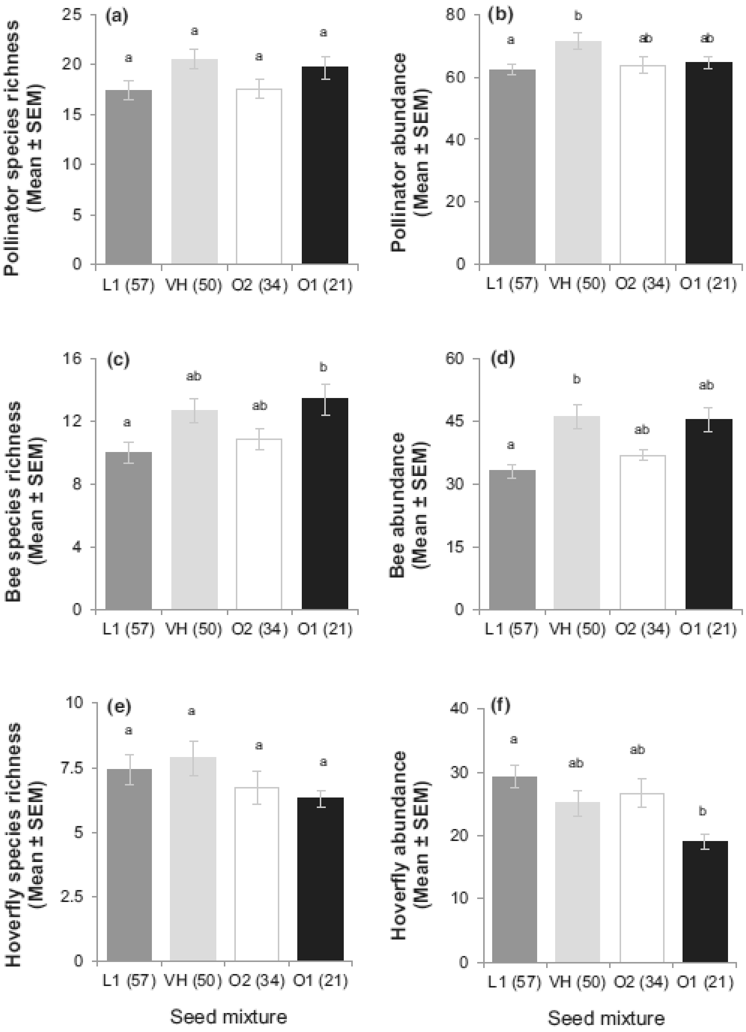


Fig. 3. Attractiveness (mean ± SEM) of four different seed mixtures (L1, Lebensraum 1; O1, Odin 1; O2, Odin 2 and VH, Veitshöchheimer Bienenweide) for pollinators based on (a) all pollinator species; (b) abundance of all pollinators; (c) bee species richness; (d) bee abundance; (e) hoverfly species richness and (f) hoverfly abundance. Plant species numbers per mixture given by the producer are added in parentheses. Lower case letters give significant differences based on R's Tukey honest significant differences.

we observed that easily accessible flowers like those of the families Apiaceae, Asteraceae and Malvaceae were preferred by hoverflies and bees equally. Surprisingly, this was also the case for bumblebees, although Fabaceae and red clover in particular have been identified as key pollen and nectar sources (Goulson *et al*., 2005). This was true for both short-tongued (adapted to open flowers) and long-tongued (more adapted to deep corollas) species. In contrast, herbs like *Salvia pratensis*, *Anethum graveolens*, *Foeniculum vulgare* and *Origanum vulgare*, considered important resources for a wide range of wild bee genera (Westrich, 1989), received only single or no visitations by the suggested target genera. The pollinator fauna of such rare plants, however, can vary considerably across their geographical range (Gibson *et al*., 2006).

With 74 pollinator species, the species pool of pollinators at the study site was relatively high for agricultural landscapes. Most species, however, were common generalists with good dispersal capacities which can readily utilise the newly established resources (Kleijn *et al*., 2006; Bommarco *et al*., 2010). Connectivity of AES to potential source habitats is a key driver for population and community structure (Warzecha *et al.*, 2016) and is perceived differently among taxa (Jauker *et al.*, 2009). Thus, flowering fields are suitable for generally promoting pollination services mainly delivered by dominant species (Kleijn *et al.*, 2015). Conservation of rare pollinator species, however, needs species-specific consideration of local conditions and landscape context, both regarding movement among partial habitats (Schmid-Egger & Witt, 2014) and temporal resource availability (Diekötter *et al.*, 2014).

Time lags in the administrative processes to arrange subsidies often result in comparably late sowing and flowering of commercial seed mixtures, which is unfortunate especially for annual mixtures. In our case, the relatively short sampling period limits the detection of changes in the role of plant species during the flowering season (Carvell *et al.*, 2007; M'Gonigle *et al.*, 2016). Providing flower resources over the whole season is necessary as potential gaps might prevent pollinators from completing their life cycles (Memmott *et al.*, 2010; Burkle *et al.*, 2013). The role of seed mixture composition for specific functions of flowering fields, for example, providing flowering resources in the early season after mass-flowering crops disappear (Diekötter *et al.*, 2010) and in mid and late flowering season after mowing of managed grasslands (Di Giulio *et al.*, 2001), thus need further evaluation in the landscape context.

Conclusion

Flower mixtures for sown flowering fields within AES may not need to be highly diverse to support pollinators in agricultural landscapes. Especially the influence of the seedbank, reflecting local land preparation, management and history, lowers the predictability for final plant community compositions in species-rich mixtures. The common arable flora represented by the seedbank, accordingly, still plays an important role for flower visitors that may have adapted to this resource in agroecosystems. Still, a selection of efficient key plant species, targeted at different pollinator groups throughout the flowering season, seems a promising tool for future development.

Acknowledgement

D.W. was financially supported by the German Federal Environmental Foundation (DBU) with a Ph.D. scholarship. We thank M. Beisel from ODIN Wildäsung for seed provision, Dipl.-Ing. agr. A. Bodenbender and the staff at experimental farm Oberer Hardthof Giessen for management of the plots and A. Gorenflo, V. S. Grob, J. Schwarz and L.-M. Weil for assistance in the field and two anonymous reviewers for helpful comments. Sampling of animals was conformed to the legal requirements of the state of Hessen and Germany.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12264:

Appendix S1. Wildflower mixtures used to for the random block design in this study. Shown is the share of seeds [%] per wildflower mixture. Composition of the plant species is based on the producer formula from 2012. Recent mixtures may be subtly different to the used ones. Plant species are arranged by their occurrence across seed mixtures visualised by grey filling.

Appendix S2. Specimen sampled by slowly walking the sides of the 28 wildflower plots during flower visitor surveys. A detailed data set including visited plant species is available from the authors upon request.

Appendix S3. Blooming periods of relevant plant species. Listed are all recorded plant species from the experimental site as well as plants from the mixtures that have not grown up. Information is taken from Jäger and Werner (2005). Longevity is given as: a = annual, b = biennial and *p* = perennial.

Appendix S4. Beta diversity of four different seed mixtures. Beta diversity was pairwise calculated for 24 sites as a dissimilarity matrix with the function betadiver in R. Each boxplot represents the comparison of dissimilarity data for one mixture (A) L1; (B) O1; (C) O2 and (D) VH. The first three boxes per boxplot show the dissimilarity of the beta diversity values of the given mixture compared to any other mixtures and the last box compared within itself. The box represents the lower and upper quartiles, the solid line, the median and the circle, the minimum or maximum observation. L1 = Lebensraum 1; VH = Veitshöchheimer Bienenweide; O2 = Odin 2; O1 = Odin 1.

Appendix S5. Graph of the total plant–pollinator network. Black rectangles represent plant (below) and flower-visiting insect (above) species. Rectangle width is proportional to the number of interactions recorded per species. Lines represent links between species; line width is proportional to the frequency of interactions (number of visits recorded by a visitor species to a plant species).

References

Bascompte, J., Jordano, P. & Olesen, J.M. (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, **312**, 431–433.

Batáry, P., Dicks, L.V., Kleijn, D. & Sutherland, W.J. (2015) The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, **29**, 1006–1016.

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

Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Pöyry, J., Roberts, S.P.M., Steffan-Dewenter, I. & Öckinger, E. (2010)

Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 2075–2082.

Bruckman, D. & Campbell, D.R. (2014) Floral neighborhood influences pollinator assemblages and effective pollination in a native plant. *Oecologia*, **176**, 465–476.

Burkle, L.A., Marlin, J.C. & Knight, T.M. (2013) Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science*, **339**, 1611–1615.

Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D. & Nowakowski, M. (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology*, **44**, 29–40.

Carvell, C., Osborne, J.L., Bourke, A.F.G., Freeman, N., Pywell, R.F. & Heard, M.S. (2011) Bumble bee species' responses to a targeted conservation measure depend on landscape context and habitat quality. *Ecological Applications*, **21**, 1760–1771.

Carvell, C., Roy, D.B., Smart, S.M., Pywell, R.F., Preston, C.D. & Goulson, D. (2006) Declines in forage availability for bumblebees at a national scale. *Biological Conservation*, **132**, 481–489.

Dahms, H., Mayr, S., Birkhofer, K., Chauvat, M., Melnichnova, E., Wolters, V. & Dauber, J. (2010) Contrasting diversity patterns of epigeic arthropods between grasslands of high and low agronomic potential. *Basic and Applied Ecology*, **11**, 6–14.

Di Giulio, M., Edwards, P.J. & Meister, E. (2001) Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. *Journal of Applied Ecology*, **38**, 310–319.

Diekötter, T., Kadoya, T., Peter, F., Wolters, V. & Jauker, F. (2010) Oilseed rape crops distort plant–pollinator interactions. *Journal of Applied Ecology*, **47**, 209–214.

Diekötter, T., Peter, F., Jauker, B., Wolters, V. & Jauker, F. (2014) Mass-flowering crops increase richness of cavity-nesting bees and wasps in modern agro-ecosystems. *Global Change Biology Bioenergy*, **6**, 219–226.

Dormann, C.F. (2011) How to be a specialist? Quantifying specialisation in pollination networks. *Network Biology*, **1**, 1–20.

Dramstad, W. & Fry, G. (1995) Foraging activity of bumblebees (Bombus) in relation to flower resources on arable land. *Agriculture, Ecosystems & Environment*, **53**, 123–135.

Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., Mueller, N.D., O'Connell, C., Ray, D.K., West, P.C., Balzer, C., Bennett, E.M., Carpenter, S.R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., Tilman, D. & Zaks, D.P.M. (2011) Solutions for a cultivated planet. *Nature*, **478**, 337–342.

Gibson, R.H., Nelson, I.L., Hopkins, G.W., Hamlett, B.J. & Memmott, J. (2006) Pollinator webs, plant communities and the conservation of rare plants: arable weeds as a case study. *Journal of Applied Ecology*, **43**, 246–257.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S. & Knight, M.E. (2005) Causes of rarity in bumblebees. *Biological Conservation*, **122**, 1–8.

Grass, I., Albrecht, J., Jauker, F., Diekötter, T., Warzecha, D., Wolters, V. & Farwig, N. (2016) Much more than bees - Wildflower plantings support highly diverse flower-visitor communities from complex to structurally simple agricultural landscapes. *Agriculture, Ecosystems and Environment*, **225**, 45–53.

Hannon, L.E. & Sisk, T.D. (2009) Hedgerows in an agri-natural landscape: potential habitat value for native bees. *Biological Conservation*, **142**, 2140–2154.

Hegland, S.J. & Boeke, L. (2006) Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. *Ecological Entomology*, **31**, 532–538.

Jäger, E. J. & Werner, K. (2005) *Rothmaler, Exkursionsflora von Deutschland, Bd. 4, Gefäßpflanzen, Kritischer Band 10. Aufl.* Elsevier, Spektrum Akademischer Verlag, München, Germany.

Jauker, F., Diekötter, T., Schwarzbach, F. & Wolters, V. (2009) Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecology*, **24**, 547–555.

Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M. & Yela, J.L. (2006) Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, **9**, 243–254.

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., Adamson, N.L., Ascher, J.S., Baldi, A., Batary, P., Benjamin, F., Biesmeijer, J.C., Blitzer, E.J., Bommarco, R., Brand, M.R., Bretagnolle, V., Button, L., Cariveau, D.P., Chifflet, R., Colville, J.F., Danforth, B.N., Elle, E., Garratt, M.P.D., Herzog, F., Holzschuh, A., Howlett, B.G., Jauker, F., Jha, S., Knop, E., Krewenka, K.M., Le Feon, V., Mandelik, Y., May, E.A., Park, M.G., Pisanty, G., Reemer, M., Riedinger, V., Rollin, O., Rundlof, M., Sardinas, H.S., Scheper, J., Sciligo, A.R., Smith, H.G., Steffan-Dewenter, I., Thorp, R., Tscharntke, T., Verhulst, J., Viana, B.F., Vaissiere, B.E., Veldtman, R., Westphal, C. & Potts, S.G. (2015) Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications*, **6**, 7414.

Klein, A.M., Vaissiere, 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**, 303–313.

Korpela, E.-L., Hyvönen, T., Lindgren, S. & Kuussaari, M. (2013) Can pollination services, species diversity and conservation be simultaneously promoted by sown wildflower strips on farmland? *Agriculture, Ecosystems and Environment*, **179**, 18–24.

Lázaro, A., Lundgren, R. & Totland, Ø. (2009) Co-flowering neighbors influence the diversity and identity of pollinator groups visiting plant species. *Oikos*, **118**, 691–702.

Marshall, E.J.P., Brown, V.K., Boatman, N.D., Lutman, P.J.W., Squire, G.R. & Ward, L.K. (2003) The role of weeds in supporting biological diversity within crop fields. *Weed Research*, **43**, 77–89.

Marshall, E.J.R. & Moonen, A.C. (2002) Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture, Ecosystems and Environment*, **89**, 5–21.

Memmott, J., Carvell, C., Pywell, R.F. & Craze, P.G. (2010) The potential impact of global warming on the efficacy of field margins sown for the conservation of bumblebees. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2071–2079.

M'Gonigle, L.K., Williams, N.M., Lonsdorf, E. & Kremen, C. (2016) A tool for selecting plants when restoring habitat for pollinators. *Conservation Letters*, **10**, 105–111.

Öckinger, E. & Smith, H.G. (2007) Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, **44**, 50–59.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2015) vegan: community ecology package. *R Package Version*, **2**, 3–1.

Ovenden, G.N., Swash, A.R.H. & Smallshire, D. (1998) Agri-environment schemes and their contribution to the conservation of biodiversity in England. *Journal of Applied Ecology*, **35**, 955–960.

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**, 345–353.

Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G. & Willmer, P. (2003) Linking bees and flowers: how do floral communities structure pollinator communities?. *Ecology*, **84**, 2628–2642.

R Core Team (2014) R: A Language and Environment for Statistical Computing. R Core Team, Vienna, Austria. < http://www.r-project.org/ > 6th March 2014.

Ramseier, H., Füglistaller, D., Lädrach, C., Ramseier, C., Rauch, M. & Widmer Etter, F. (2016) Blühstreifen fördern Honig- und Wildbienen. *Agrarforschung Schweiz*, **6**, 276–283.

Robinson, R.A. & Sutherland, W.J. (2002) Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*, **39**, 157–176.

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

Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G. & Kleijn, D. (2013) Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss—a meta-analysis. *Ecology Letters*, **16**, 912–920.

Scheper, J., Reemer, M., van Kats, R., Ozinga, W.A., van der Linden, G.T., Schaminee, J.H., 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 of the United States of America*, **111**, 17552–17557.

Schmid-Egger, C. & Witt, R. (2014) Ackerblühstreifen für Wildbienen – Was bringen sie wirklich? *Ampulex*, **6**, 13–22.

Tschumi, M., Albrecht, M., Collatz, J., Dubsky, V., Entling, M.H., Najar-Rodriguez, A.J. & Jacot, K. (2016) Tailored flower strips promote natural enemy biodiversity and pest control in potato crops. *Journal of Applied Ecology*, **53**, 1169–1176.

Warzecha, D., Diekötter, T., Wolters, V. & Jauker, F. (2016) Intraspecific body size increases with habitat fragmentation in wild bee pollinators. *Landscape Ecology*, **31**, 1449–1455.

Westrich, P. (1989) Die Wildbienen Baden-Württembergs I, Allgemeiner Teil. *Die Nahrungspflanzen der Wildbienen*, pp. 300–391. Verlag Eugen Ulmer, Stuttgart, Germany.

Winfree, R. (2010) The conservation and restoration of wild bees. *Annals of the New York Academy of Sciences*, **1195**, 169–197.

Accepted 22 August 2017
First published online 3 October 2017

Editor: Raphael Didham
Associate editor: Peter Batáry

ANHANG KAPITEL V

Appendix 1. Supporting information.

S1: Wildflower mixtures used to for the random block design in this study. Shown is the share of seeds [%] per wildflower mixture. Composition of the plant species is based on the producer formula from 2012. Recent mixtures may be subtly different to the used ones. Plant species are arranged by their occurrence across seed mixtures visualized by grey filling.

		Seed mixture (German commercial brand names)			
		L1	VH	O2	O1
Plant species	Family	Lebensraum 1	Veitshöchheimer Bienenweide	ODIN-Blühfläche 2 - Kranichsteiner Mischung	ODIN-Blühfläche
Daucus carota	Apiaceae	1.5	2	1.2	1.7
Fagopyrum esculentum	Polygonaceae	7.5	7	10	8
Helianthus annuus	Asteraceae	5	5	9	8
Medicago sativa	Fabaceae	7.5	3	5	6
Onobrychis viciifolia	Fabaceae	15	10	6.5	8
Trifolium pratense	Fabaceae	5	4	5	6
Carum carvi	Apiaceae	2.5		2.3	1.7
Linum usitatissimum	Linaceae	8		2.8	6
Borago officinalis	Boraginaceae	0.2	5		1.7
Malva sylvestris	Malvaceae	1	2		4
Sanguisorba minor	Rosaceae	5.8	5		1.7
Achillea millefolium	Asteraceae	1	2	0.3	
Hypericum perforatum	Hypericaceae	0.1	1	1.2	
Malva moschata	Malvaceae	0.5	2	0.6	
Salvia pratensis	Lamiaceae	0.5	1	3.7	
Verbascum nigrum	Scrophulariaceae	0.1	0.2	0.3	
Anthemis tinctoria	Asteraceae	1	0.9	1.2	
Cichorium intybus	Asteraceae	2.5		4.5	
Galium verum	Rubiaceae	0.5		0.6	
Heracleum sphondylium	Apiaceae	0.4		0.6	
Pastinaca sativa	Apiaceae	0.1		4.5	
Centaurea scabiosa	Asteraceae	0.1	0.5		
Echium vulgare	Boraginaceae	0.8	3.5		
Foeniculum vulgare	Apiaceae	5	1		
Leucanthemum ircutianum	Asteraceae	0.5	1		
Lotus corniculatus	Fabaceae	2	3		
Medicago lupulina	Fabaceae	2	2		
Oenothera biennis	Onagraceae	0.5	2		
Origanum vulgare	Lamiaceae	0.1	0.9		
Reseda luteola	Resedaceae	0.1	0.5		
Silene vulgaris	Caryophyllaceae	2	0.5		

Silybum marianum	Asteraceae	1	3		
Verbascum lychnitis	Scrophulariaceae	0.1	0.2		
Trifolium incarnatum	Fabaceae			2.2	6
Vicia sepium	Fabaceae			2	8
Calendula officinalis	Asteraceae		5		1.7
Coriandrum sativum	Apiaceae		2		1.7
Centaurea cyanus	Asteraceae		3	9	
Centaurea jacea	Asteraceae		1	0.6	
Malva sylvestris ssp. Mauri.	Malvaceae		2	4.8	
Agrimonia eupatoria	Rosaceae	1			
Anthriscus sylvestris	Apiaceae	0.2			
Artemisia campestris	Asteraceae	0.1			
Artemisia vulgaris	Asteraceae	0.1			
Barbarea vulgaris	Brassicaceae	1			
Cerastium holosteoides	Caryophyllaceae	0.1			
Clinopodium vulgare	Lamiaceae	0.1			
Crepis biennis	Asteraceae	0.7			
Dipsacus fullonum	Caprifoliaceae	1			
Galium album	Rubiaceae	0.5			
Malva mauritanica	Malvaceae	0.5			
Malva verticillata	Malvaceae	0.5			
Petroselinum sativum	Apiaceae	1			
Plantago lanceolata	Plantaginaceae	0.5			
Prunella vulgaris	Lamiaceae	0.4			
Setaria italica	Poaceae	1			
Silene alba	Caryophyllaceae	1.6			
Silene dioica	Caryophyllaceae	1			
Silene-flos-cuculi	Caryophyllaceae	0.2			
Tanacetum vulgare	Asteraceae	0.2			
Trifolium hybridum	Fabaceae	0.5			
Verbascum thapsus	Scrophulariaceae	0.1			
Vicia pannonica	Fabaceae	5			
Vicia sativa	Fabaceae	2.8			
Ornithopus sativus	Fabaceae				8
Phacelia tanacetifolia	Boraginaceae				2
Sinapis alba	Brassicaceae				3
Trifolium resupinatum	Fabaceae				6
Trigonella caerulea	Fabaceae				5
Trigonella foenum graecum	Fabaceae				6
Anthoxanthum odoratum	Poaceae			2.3	
Cynosurus cristatus	Poaceae			2.3	
Galium mollugo	Rubiaceae			0.4	
Lathyrus pratensis	Fabaceae			0.1	

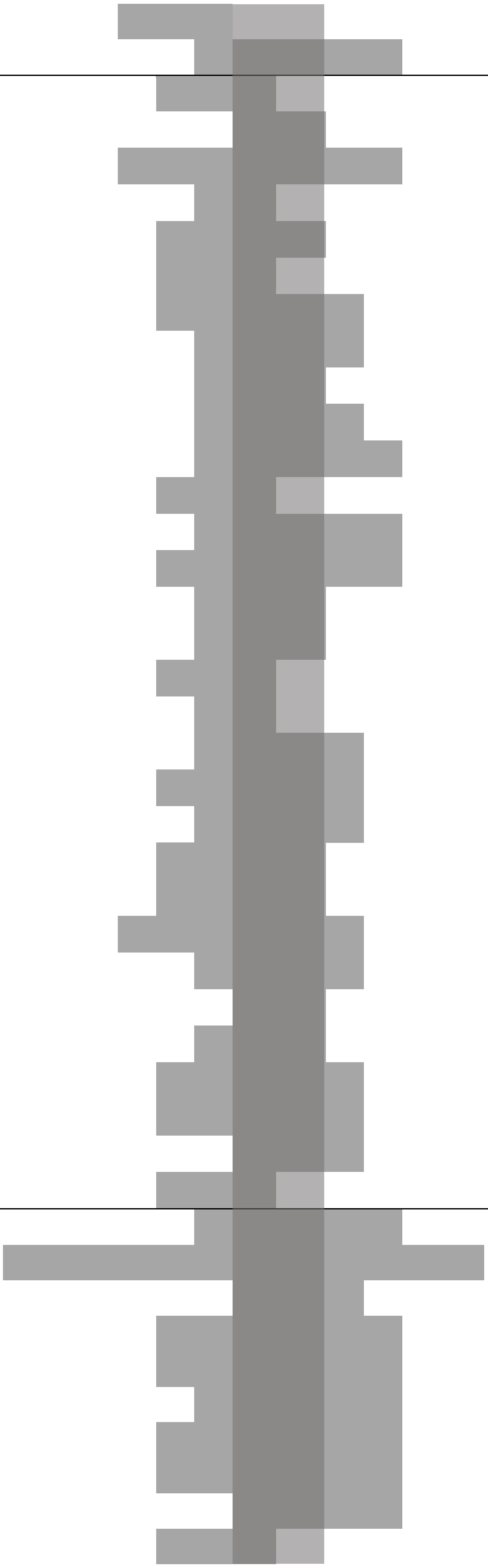
Leucanthemum vulgare	Asteraceae		1.2	
Malva alcea	Malvaceae		0.6	
Melilotus officinalis	Fabaceae		0.3	
Phleum pratense	Poaceae		5	
Poa pratensis	Poaceae		5	
Secale multicaule	Poaceae		4.7	
Verbascum phoeniceum	Scrophulariaceae		0.6	
Linum austriacum	Linaceae	1		
Anethum graveolens	Apiaceae	1		
Anthyllis vulneraria	Fabaceae	2		
Carduus nutans	Asteraceae	0.5		
Inula helenium	Asteraceae	0.1		
Leonurus cardiaca	Lamiaceae	0.5		
Myosotis arvensis	Boraginaceae	0.5		
Nigella sativa	Ranunculaceae	2		
Onobrychis arenaria	Fabaceae	4		
Papaver rhoeas	Papaveraceae	1		
Reseda lutea	Resedaceae	0.5		
Solidago virgaurea	Asteraceae	0.1		
Tanacetum corymbosum	Asteraceae	2		
Thymus pulegioides	Lamiaceae	0.5		
Trifolium montanum	Fabaceae	0.1		
Trifolium repens	Fabaceae	2		
Trifolium rubens	Fabaceae	0.5		
Verbascum densiflorum	Scrophulariaceae	0.5		

Appendix S2: Specimen sampled by slowly walking the sides of the 28 wildflower plots during flower visitor surveys. A detailed dataset including visited plant species is available from the authors upon request.

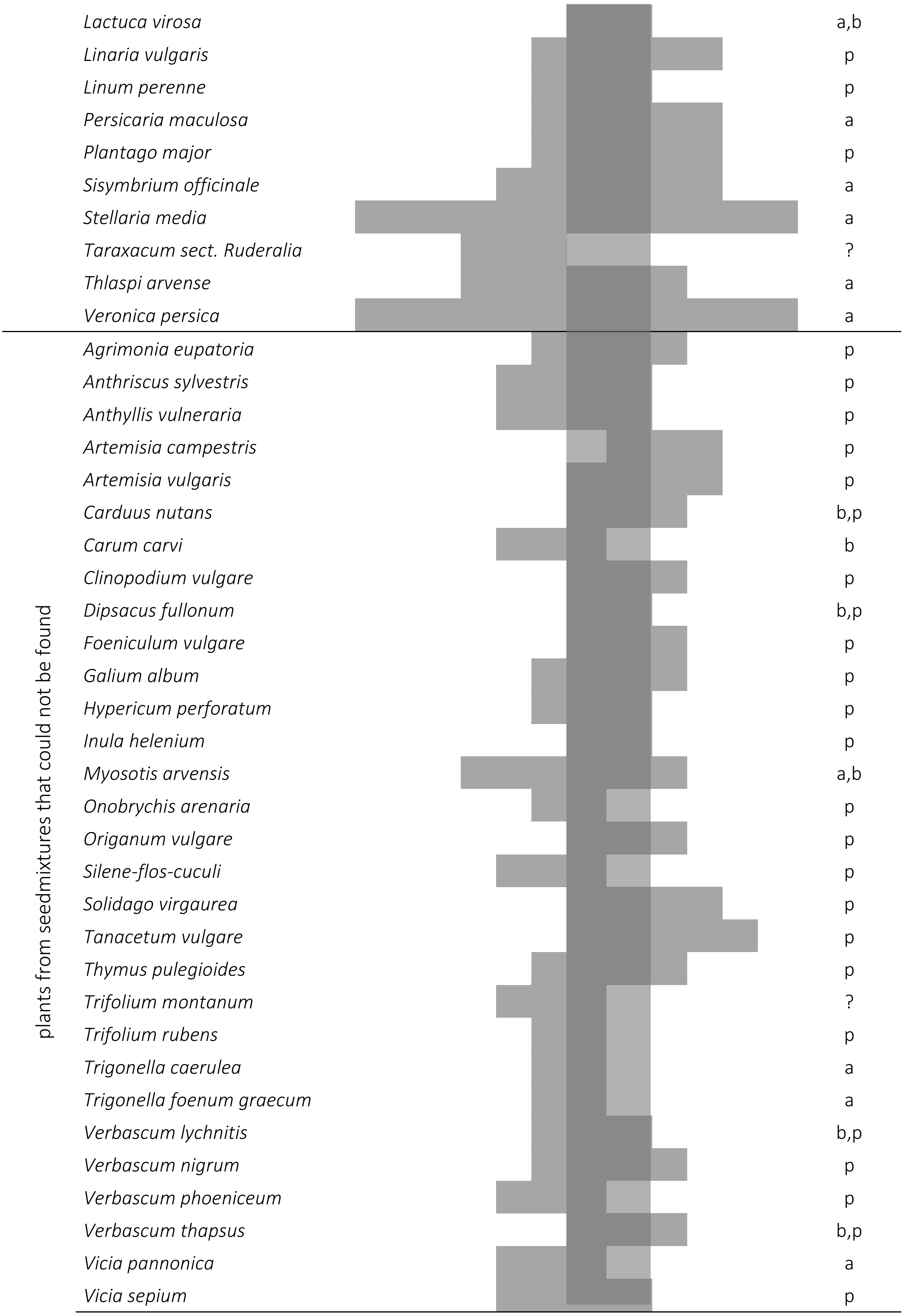
Genus	Species	n	Genus	Species	n
Andrena	*Andrena bicolor*	3		*Lasioglossum pauxillium*	39
	Andrena dorsata	10		*Lasioglossum villosulum*	1
	Andrena flavipes	121	*Megachile*	*Megachile alpicola*	2
	Andrena minutula	9		*Megachile centuncularis*	13
	Andrena minutuloides	9		*Megachile rotundata*	2
	Andrena ovatula	1	*Stelis*	*Stelis breviuscula*	1
	Andrena saundersella	1		*Stelis punctulatissima*	1
Anthophora	*Anthophora aestivalis*	1	*Cheilosia*	*Cheilosia pagana*	1
Bombus	*Bombus barbutellus*	1		*Cheilosia uviformis*	1
	Bombus hortorum	9	*Episyrphus*	*Episyrphus balteatus*	280
	Bombus lapidarius	304	*Eristalis*	*Eristalis arbustorum*	14
	Bombus pascuorum	74		*Eristalis pertinax*	1
	Bombus pratorum	2		*Eristalis similis*	3
	Bombus ruderarius	3		*Eristalis tenax*	49
	Bombus soroeensis	3	*Eristrophe*	*Eristrophe cryptica*	1
	Bombus sylvarum	129	*Eupeodes*	*Eupeodes corollae*	17
	Bombus terrestris agg.	244		*Eupeodes lappanicus*	1
	Bombus vestalis	2	*Helophilus*	*Helophilus pendulus*	2
Chelostoma	*Chelostoma rapunculi*	1		*Helophilus trivitattus*	2
Colletes	*Colletes daviensanus*	10	*Heringia*	*Heringia heringi*	1
	Colletes similis	6	*Melanostoma*	*Melanostoma scalare*	65
Halictus	*Halictus maculatus*	3	*Myathropa*	*Myathropa florea*	5
	Halictus scabiosae	5	*Neoascia*	*Neoascia podagrica*	3
	Halictus tumulorum	22	*Paragus*	*Paragus haemorrhous*	1
Heriades	*Heriades truncorum*	9	*Platycheirus*	*Platycheirus clypeatus*	1
Hylaeus	*Hylaeus communis*	13		*Platycheirus discimanus*	1
	Hylaeus cornutus	1		*Platycheirus peltatus*	1
	Hylaeus difformis	5	*Scaeva*	*Scaeva pyrastri*	5
	Hylaeus gredleri	6	*Sphaerophoria*	*Sphaerophoria scripta agg.*	187
	Hylaeus hyalinatus	2		*Sphaerophoria rueppellii*	4
	Hylaeus nigritus	3	*Syritta*	*Syritta pipiens*	36
	Hylaeus signatus	1	*Syrphus*	*Syrphus ribesii*	6
	Hylaeus styriacus	1		*Syrphus torvus*	1
Lasioglossum	*Lasioglossum calceatum*	25		*Syrphus vitripennis*	11
	Lasioglossum fulvicorne	1	*Xylota*	*Xylota segnis*	1
	Lasioglossum laticeps	4			
	Lasioglossum leucozonium	1	Apiformes	Sum	1134
	Lasioglossum malachurum	4	Syrphidae	Sum	701
	Lasioglossum morio	26		Pollinators total	1835

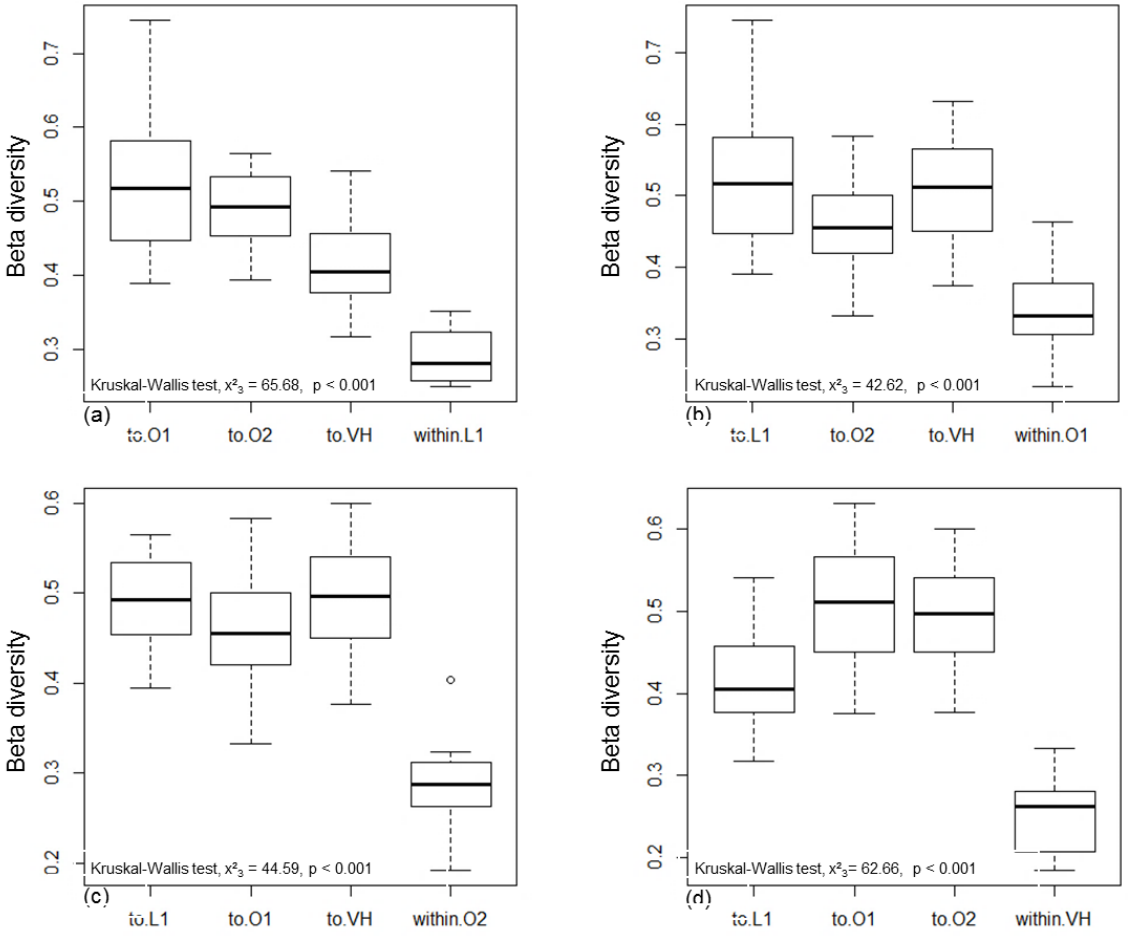
Appendix S3: Blooming periods of relevant plant species. Listed are all recorded plant species from the experimental site as well as plants from the mixtures that have not grown up. Information is taken from Jäger & Werner (2005). Longevity is given as: a = annual, b = biennial and p = perennial.

	plant species	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Longevity
key plant species	*Achillea millefolium*						▒	▓	▓	▒	▒			p
	Anthemis tinctoria						▒	▓	▓	▒				p
	Calendula officinalis						▒	▓	▓	▒	▒			a,p
	Centaurea cyanus						▒	▓	▓	▒	▒			a
	Chenopodium album							▓	▓	▒	▒			a
	Daucus carota						▒	▓	▓	▒				b,p
	Echium vulgare					▒	▒	▓	▓	▒	▒			b,p
	Fagopyrum esculentum						▒	▓	▓	▒				a
	Lactuca serriola							▓	▓	▒				a
	Linum usitatissimum						▒	▓	░					a,b
	Malva sylvestris						▒	▓	▓	▒	▒			b,p
	Persicaria hydropiper							▓	▓	▒				a
	Phacelia tanacetifolia						▒	▓	▓	▒	▒			a
visited plant species	*Anethum graveolens*							▓	▓	▒				a
	Borago officinalis						▒	▓	░					a
	Centaurea jacea						▒	▓	▓	▒	▒			p
	Cichorium intybus							▓	▓	▒	▒			p
	Erigeron annuus						▒	▓	▓	▒				b,a,p
	Helianthus annuus					▒	▒	▓	▓	▒	▒			a
	Lamium purpureum			▒	▒	▒	▒	▓	▓	▒	▒			a
	Leucanthemum ircutianum						▒	▓	▓	▒	▒			p
	Lotus corniculatus						▒	▓	▓					p
	Malva moschata						▒	▓	▓	▒	▒			p
	Malva verticillata							▓	▓	▒				a
	Matricaria chamomilla					▒	▒	▓	▓					a
	Medicago sativa						▒	▓	▓	▒				p
	Melilotus officinalis						▒	▓	▓	▒				a,b
	Onobrychis viciifolia					▒	▒	▓	░					p
	Ornithopus sativus						▒	▓	▓					a
	Pastinaca sativa							▓	▓	▒				b
	Plantago lanceolata					▒	▒	▓	▓	▒				p
	Silene latifolia						▒	▓	▓	▒				p
	Sinapis alba				▒	▒	▒	▓	▓					a
	Solanum nigrum						▒	▓	▓	▒	▒			a
	Sonchus asper						▒	▓	▓	▒	▒			a
	Sonchus oleraceus						▒	▓	▓	▒	▒			a
	Trifolium incarnatum						▒	▓	▓					a
	Trifolium pratense						▒	▓	▓	▒				p,b

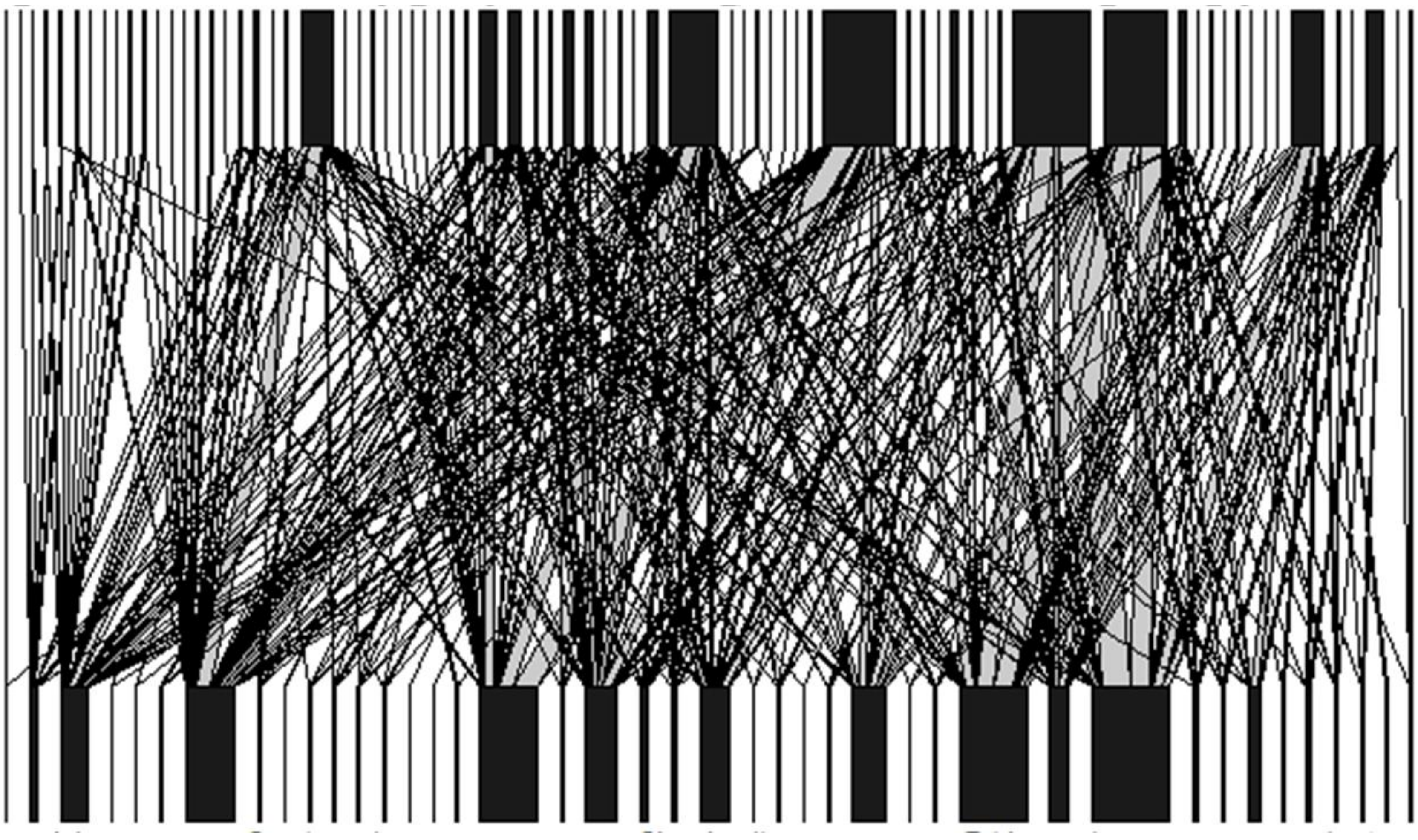


	Trifolium resupinatum	a
	Tripleurospermum perforatum	a
plants originated from seedmixtures without recorded visits	*Barbarea vulgaris*	b
	Centaurea scabiosa	p
	Cerastium holosteoides	p
	Coriandrum sativum	a
	Crepis biennis	b,p
	Galium mollugo	p
	Galium verum	p
	Heracleum sphondylium	p
	Lathyrus pratensis	p
	Leonurus cardiaca	p
	Leucanthemum vulgare	p
	Linum austriacum	p
	Malva alcea	p
	Medicago lupulina	a,p
	Nigella sativa	a
	Oenothera biennis	v
	Papaver rhoeas	a
	Petroselinum sativum	b
	Prunella vulgaris	p
	Reseda lutea	a,b
	Reseda luteola	a,b
	Salvia pratensis	p
	Sanguisorba minor	p
	Silene dioica	p
	Silene vulgaris	p
	Silybum marianum	a,b
	Tanacetum corymbosum	p
	Trifolium hybridum	p
	Trifolium repens	p
	Verbascum densiflorum	b,p
	Vicia sativa	a
plants originated from seedbank without recorded visits	*Berteroa incana*	a,b
	Capsella bursa-pastoris	a
	Cirsium arvense	p
	Fumaria officinalis	a
	Galinsoga ciliata	a
	Galium aparine	a
	Geranium pyrenaicum	b,p
	Geranium robertianum	a
	Glebionis segetum	a
	Hesperis matronalis	b,p


Lactuca virosa a,b
Linaria vulgaris p
Linum perenne p
Persicaria maculosa a
Plantago major p
Sisymbrium officinale a
Stellaria media a
Taraxacum sect. Ruderalia ?
Thlaspi arvense a
Veronica persica a
plants from seedmixtures that could not be found
Agrimonia eupatoria p
Anthriscus sylvestris p
Anthyllis vulneraria p
Artemisia campestris p
Artemisia vulgaris p
Carduus nutans b,p
Carum carvi b
Clinopodium vulgare p
Dipsacus fullonum b,p
Foeniculum vulgare p
Galium album p
Hypericum perforatum p
Inula helenium p
Myosotis arvensis a,b
Onobrychis arenaria p
Origanum vulgare p
Silene-flos-cuculi p
Solidago virgaurea p
Tanacetum vulgare p
Thymus pulegioides p
Trifolium montanum ?
Trifolium rubens p
Trigonella caerulea a
Trigonella foenum graecum a
Verbascum lychnitis b,p
Verbascum nigrum p
Verbascum phoeniceum p
Verbascum thapsus b,p
Vicia pannonica a
Vicia sepium p



Appendix S4: Beta diversity of four different seed mixtures. Beta diversity was pairwise calculated for 24 sites as a dissimilarity matrix with the function betadiver in R. Each boxplot represents the comparison of dissimilarity data for one mixture ((a) = L1; (b) = O1; (c) = O2 and (d) = VH). The first three boxes per boxplot show the dissimilarity of the beta diversity values of the given mixture compared to any other mixtures and the last box compared within itself. The box represents the lower and upper quartile, the solid line the median and the circle the minimum or maximum observation. L1 = Lebensraum 1; VH = Veitshöchheimer Bienenweide; O2 = Odin 2; O1 = Odin 1.



Appendix S5: Graph of the total plant–pollinator network. Black rectangles represent plant (below) and flower visiting insect (above) species. Rectangle width is proportional to the number of interactions recorded per species. Lines represent links between species; line width is proportional to the frequency of interactions (number of visits recorded by a visitor species to a plant species).

KAPITEL VI – SYNTHESE

SYNTHESE

DISKUSSION

Die Ergebnisse der in dieser Arbeit vorgelegten Studien belegen, dass der Landschaftskontext sich auf die Erreichbarkeit von Blühflächen durch Wildbienen auswirkt. Eine entsprechende Reaktion innerhalb der Schwebfliegen und anderer Blütenbesucher bleibt dagegen weitestgehend aus. Folglich kann die Vernetzung innerhalb von modernen Agrarlandschaften durch die Anzahl der etablierten Blühflächen gesteuert werden. Auf lokaler Ebene zeigen zudem Wildbienen und Schwebfliegen deutliche und teils kontrastierende Reaktionen auf die Zusammensetzung der untersuchten Blühmischungen. So könnte die Implementierung meiner Ergebnisse in eine standortoptimierte Anlage von Blühflächen, die sowohl den Landschaftskontext, die Konfiguration der Blühflächen untereinander sowie angepasste Blühmischungen umfassen, dazu beitragen, die Effizienz dieser Maßnahme besonders für die sensiblen Wildbienen zu steigern.

Biodiversität (im Landschaftskontext)

Mit dem Nachweis von rund einem Viertel der hessischen Wildbienen- und Schwebfliegenarten auf den untersuchten Blühflächen wird deutlich, welche Artenvielfalt selbst landwirtschaftlich genutzte Regionen heute noch beherbergen können. Während vormals extensive bewirtschaftete Kulturlandschaften flächendeckend reich an Wildbienen waren (Westrich 2019), finden sie heute nur noch auf vereinzelten naturnahen Habitatinseln geeignete Bedingungen vor und offenbaren den Bedarf an geeigneten Fördermaßnahmen für diese Lebensräume (Librán-Embid *et al.* 2021). Da Wildbienen eine intensive Brutpflege betreiben, dazu häufig zwischen unterschiedlichen Teillebensräumen zum Nisten und zur Nahrungsversorgung pendeln (Westrich 1996) und daher nur einen kleinen Aktionsradius aufweisen (Gathmann & Tscharntke 2002; Zurbuchen *et al.* 2010b; Wright *et al.* 2015), reagieren sie deutlich empfindlicher auf die Fragmentierung der Landschaft als bspw. Schwebfliegen (Jauker *et al.* 2009; Aguirre-Gutiérrez *et al.* 2015). Auch bei der Besiedlung von Blühflächen machen sich diese Unterschiede bemerkbar. So konnte ich nachweisen, dass Wildbienen eine deutliche Reaktion auf den Landschaftskontext zeigten (KAPITEL II, III & IV), während dies für Schwebfliegen und andere Gruppen nicht gefunden wurde (KAPITEL II & III) und Hypothese 1 bestätigen. Dies deckt sich mit den Ergebnissen von Boetzl *et al.* (2021). Die vergleichsweise hohen Artenzahlen auf Blühflächen in einfachen und fragmentierten Landschaften entsprechen dabei den Befunden bisheriger Studien (Scheper *et al.* 2013; Batáry *et al.* 2015). In diesen sonst eher ressourcenarmen Landschaften entwickeln Blühflächen eine regelrechte Sogwirkung auf nahrungssuchende Insekten und verdeutlichen den Bedarf nach mehr Blüten in Agrarregionen. Die Gemeinschaften bestehen dabei aus ausbreitungsstarken sowie zufällig vorkommenden lokalen Arten (Librán-Embid *et al.* 2021). Entsprechend ist eine Nutzung der Blühflächen nur möglich, wenn ausreichend Quellhabitate in der näheren Umgebung vorhanden sind (Suding 2011).

Eine hohe Biodiversität drückt sich nicht nur in Form hoher Artenvielfalt aus, sondern beinhaltet auch eine hohe genetische Vielfalt innerhalb einer Population und damit eine große Variabilität der phänotypischen Plastizität. Indem die Landschaft als Filter für das Ausbreitungsvermögen intraspezifisch größere Individuen einer Population selektiert, könnten die Gemeinschaften somit in ihrer Diversität reduziert werden, ohne dass es über Untersuchungen der Gemeinschaftszusammensetzung augenscheinlich wird (KAPITEL IV). Dieses Phänomen ist bisher noch kaum verstanden (Jauker 2020), hält aber immer stärker Einzug in die aktuelle Forschung (Van Reeth *et al.* 2018, Grab *et al.* 2019; Grass *et al.* 2021). Die Analysen der Pollenhöschen unterschiedlich großer Weibchen der Gewöhnlichen Bindensandbiene *Andrena flavipes* aus Studie drei (KAPITEL IV) zeigt, dass größere Weibchen Pollen von deutlich weniger Pflanzenarten sammelten als kleinere Individuen eines Standortes. Es ist dabei unklar, woher diese Verschiebung des Pollensammelverhaltens resultiert. Denkbar wäre, dass sich die Größe der Bienen auf das Handling der Blüten auswirkt, wodurch nur noch eine eingeschränkte Auswahl von Pflanzen genutzt werden könnte. Es könnte aber auch sein, dass diese Individuen aufgrund des erhöhten Ausbreitungspotentials gezielt längere Sammelflüge zu ihren bevorzugten Nahrungspflanzen in Kauf nehmen. Anzunehmen ist jedoch, dass in beiden Fällen eine Reduktion der Größenvariabilität gravierende ökologische Folgen mit sich bringt, weil dadurch die Vielfalt an bestäubten Pflanzenarten eingeschränkt würde. Denn Wildbienen sind sowohl für den Erhalt der Wildpflanzendiversität (Biesmeijer *et al.* 2006; Ollerton *et al.* 2011) als auch für die wirtschaftliche Nutzung von großer Bedeutung (Klein *et al.* 2007; Winfree 2010; Garibaldi *et al.* 2013). Wenngleich Honigbienen lange als die wichtigsten Bestäuber von Kulturpflanzen galten (Southwick & Southwick 1992), belegen Studien, dass der Beitrag anderer Insekten wie Wildbienen (Kremen 2005; Klein *et al.* 2007; Bommarco *et al.* 2012) und Schwebfliegen (Larson *et al.* 2001; Fontaine *et al.* 2006; Jauker & Wolters 2008; Jauker *et al.* 2012) erheblich ist oder sogar höher sein kann (Breeze *et al.* 2011; Garibaldi *et al.* 2013; Woodcock *et al.* 2013). Doch auch die Effektivität der Bestäubung scheint durch die intraspezifische Körpergröße beeinflusst zu werden (Jauker *et al.* 2016). Entgegen der Behauptung, die Bestäubung stelle einen unzureichenden Grund für den Artenschutz dar, da nur wenige dominante Arten je Standort dafür ausschlaggebend sind (Kleijn *et al.* 2015), verdeutlichen diese Ergebnisse den Stellenwert einer hohen Biodiversität auf allen Ebenen. Da zudem die Artenzusammensetzung räumlich und zeitlich stark variiert (Winfree *et al.* 2018), ist es auch im Sinne der zukünftigen Nahrungssicherheit wichtig, eine möglichst hohe Vielfalt zu erhalten.

Konnektivität

Nicht nur der Anteil an wertvollen Lebensräumen (Komposition) ist ausschlaggebend für das Vorkommen einer Art, sondern auch deren Anordnung (Konfiguration; Martin *et al.* 2019). Die Anlage mehrerer Blühflächen steigert die Konnektivität in zweifacher Weise: benachbarte Blühflächen scheinen ökologisch miteinander verknüpft zu sein und als eine Einheit zu funktionieren, gleichzeitig tragen sie auch zu einer besseren Vernetzung potenzieller Teillebensräume bei (KAPITEL II & III). Dies bestätigt Hypothese 2. So ließ sich in Bezug auf die Konnektivität in der zweiten Studie (KAPITEL III) zeigen, dass in einfachen Landschaften die Anlage mehrerer Blühflächen in räumlicher Nähe zueinander die Wildbienendiversität auf „vernetzten“ Flächen um 50 % im Vergleich zu „isolierten“ Flächen erhöht. Sie tragen somit zur Vernetzung mit vorhandenen (Teil-) Lebensräumen bei und verbessern damit besonders für Wildbienen deren Erreichbarkeit. Ein positiver Effekt der Konnektivität auf Wildbienen (speziell die Gattung *Bombus* – der Hummeln) konnte ebenfalls in der ersten Studie (KAPITEL II) nachgewiesen werden. Auch für die Wespen, die ich während der Beprobung innerhalb von Studie zwei (KAPITEL III) miterfasst, die jedoch separat ausgewertet wurden, konnte ein positiver Vernetzungseffekt nachgewiesen werden (Bendixen *et al.* eingereicht). Hier setzte die vermehrte Anlange von Blühflächen den Landschaftseffekt außer Kraft (siehe dazu auch Boetzl *et al.* 2021), so dass die Artenzahl unabhängig von der Landschaftskomplexität blieb.

Die Bedeutung der Konnektivität von Habitatelementen wird auf höherer Skalenebene immer offensichtlicher. So zeigt der beobachtete Rückgang der Fluginsekten in Naturschutzgebieten (Hallmann *et al.* 2017), dass eine Begrenzung des Schutzes auf diese Gebiete nicht ausreicht, um dem Artenrückgang entgegenzuwirken. Dafür ist die Fläche sowohl der Naturschutzgebiete als auch die anderer wertvoller naturnaher Landschaftselemente viel zu gering (Garibaldi *et al.* 2021). Zudem liegen diese Flächen meist isoliert in intensiv genutzten Landschaften. Da die intensive Landnutzung in einem weitläufigen Umfeld einen besonders negativen Einfluss auf die Artenvielfalt in Offenlandlebensräumen hat (Seibold *et al.* 2019), sollte zur Förderung von Bestäubern wie Wildbienen eine Landschaft nötig sein, in der mindestens 20 % der Fläche aus natürlichen Habitaten besteht. Dieser Schwellenwert hat sich als Mindestmaß zur Gewährleistung der Nahrungssicherheit als auch der besseren Konnektivität und Effektivität von geschützten Lebensräumen erwiesen (Garibaldi *et al.* 2021). Während eine umfangreiche Umstrukturierung der Landschaft nicht ad hoc umsetzbar wäre, führt bereits eine Verringerung der Schlaggröße zu einer höheren Biodiversität als sämtliche Änderungen der Bewirtschaftung (Batáry *et al.* 2020; Martin *et al.* 2020), indem mehr Randbereiche entstehen und dadurch eine bessere Vernetzung der Lebensräume erreicht wird. Ein höherer Vernetzungsgrad reduziert zudem die mit der Ausbreitung verbundenen Kosten (Zurbuchen *et al.* 2010a) und erleichtert die Besiedlung neu geschaffener Lebensräume (Griffin & Haddad 2021). Nicht nur für Wildbienen wäre daher ein Netzwerk aus mehreren kleinen Lebensräumen (Blühstreifen, Randstreifen, Brachen etc.) in Kombination mit einigen großen (Dauergrünland) erstrebenswert (Rösch *et al.* 2015; Cole *et al.* 2020, Boetzl *et al.* 2021).

Ressourcenverfügbarkeit

Durch ihre Abhängigkeit von Pollen und Nektar als Nahrung für sich oder ihren Nachwuchs sind blütenbesuchende Insekten wie Wildbienen und Schwebfliegen auf die Verfügbarkeit von ausreichend Blüten angewiesen (Biesmeijer *et al.* 2006). Im Vergleich der innerhalb des HIAP-Programms gängigen Blühmischungen zeigten Wildbienen und Schwebfliegen unterschiedliche Präferenzen. Dafür war jedoch nicht die Pflanzenvielfalt per se entscheidend, sondern das Vorkommen spezieller Schlüsselarten, die ein breites Spektrum an Pflanzenfamilien abdecken (KAPITEL V). Somit konnte die Annahme, dass artenreiche Blühmischungen eine größere Anzahl an Wildbienenarten ansprechen (Hypothese 3), im Rahmen meiner Untersuchungen nur teilweise bestätigt werden. Da lediglich für etwa die Hälfte der vorhandenen Pflanzen überhaupt ein Besuch dokumentiert werden konnte, scheint die Pflanzenauswahl zudem nicht optimal auf die Zieltaxa ausgerichtet zu sein. Innerhalb der Schlüsselpflanzen zeigten sich ebenfalls taxonspezifische Präferenzen. Schwebfliegen bevorzugten wie erwartet Pflanzen mit offenen und gut zugänglichen Blüten (Branquart & Hemptinne 2000, Scheper *et al.* 2021), während Wildbienen, und hier vor allem Hummeln, auch geschlossene Blüten wie die des Klees besuchten (Scheper *et al.* 2021). Allerdings stammen diese Daten auf einem einzigen Landschaftsausschnitt in urbaner Randlage, so dass von einem eingeschränkten Artenspektrum am Versuchsstandort auszugehen ist. In einem größeren Untersuchungsgebiet könnte also eine hohe Pflanzenvielfalt auf Blühflächen durchaus entscheidend für eine höhere Wildbienenvielfalt sein (Wood *et al.* 2017; Neumüller *et al.* 2020; Lane *et al.* 2021). Dafür spricht die Berechnung der Beta-Diversität in Studie zwei (KAPITEL III). So bewirkten die steigende Pflanzenvielfalt auf Blühflächen und der Anteil naturnaher Habitate der umgebenden Landschaft, dass sich Wildbienen Gemeinschaften benachbarter Blühflächen unähnlicher wurden. Dies lässt darauf schließen, dass durch die vermehrte Anlage von Blühflächen auch das verfügbare Pflanzenspektrum erhöht wurde und es zur Aufspaltung der Artengemeinschaften entsprechend artspezifischer Präferenzen kommt. Folglich dürften die Ansprüche an die Zusammensetzung der Mischungen in Abhängigkeit der Landschaftskomplexität steigen. Bei den Schwebfliegen sank die Beta-Diversität mit der Pflanzendiversität hingegen, während sich eine hohe Vielfalt auf Ebene der Pflanzenfamilien positiv auswirkte. Schwebfliegen besuchen vorrangig Pflanzen der Familien Ranunculaceae, Rosaceae, Apiaceae und Asteraceae, zeigen dann aber keine stärkere Spezialisierung, sondern nutzen vielmehr die am häufigsten vorkommenden Arten (Branquart & Hemptinne 2000). Solch dominante Bestände dürften jedoch zugunsten einer höheren Diversität zurückgegangen sein.

Rund ein Drittel der Wildbienenarten zeigen eine Spezialisierung auf bestimmte Pollenpflanzen zur Brutversorgung (Westrich 2019). Diese spezifischen Pollenpflanzen werden jedoch bisher bei der Zusammenstellung der Mischungen kaum berücksichtigt. Der Hauptgrund dafür dürfte die ursprüngliche und wenig spezielle Ausrichtung auf Honigbienen und Hummeln sein, deren Nahrungspflanzenwahl vorrangig über deren Quantität erfolgt (Leonhardt and Blüthgen 2012). Die dichte Vegetation der gewählten Stauden soll zudem Deckung für Wild- und Vogelarten bieten. Auch meine Studien (KAPITEL II und IV) zeigen, dass diese generalistischen Gruppen den Hauptteil der nachgewiesenen Individuen ausmachen. Die Tatsache, dass in der ersten Studie (KAPITEL II) nur 2,6 % der Individuen andere Wildbienen waren und in Studie vier (KAPITEL V) zwei Drittel der Individuen zu den vier häufigsten Hummelarten gehörten, zeigt, dass die Maßnahme an Wildbienen weitestgehend vorbeigeht und in erster Linie häufige Arten fördert (Kleijn *et al.* 2006). Die Mehrheit der Wildbienen sind typische Bewohner von Offenlandlebensräumen wie Wiesen unterschiedlichster Ausprägung sowie Brachen und Ruderalstandorten (Westrich 2019). Von diesen Lebensräumen unterscheiden sich Blühflächen sowohl in ihrer Pflanzenartenzusammensetzung als auch in ihrer Struktur. Viele der charakteristischen Pflanzenarten von Wiesen, die häufig wichtige Ressourcen für spezialisierte Arten darstellen, sind nicht Bestandteil der Mischungen oder im Kontext der restlichen Mischung zu konkurrenzschwach. Hierrunter fallen etwa Arten aus der Gruppe der Glockenblumen (Campanula). So ist es auch nicht verwunderlich, dass blütenreiche Habitatelemente wie Randstreifen und Hecken (von Königslöw *et al.* 2021) sowie Kalkmagerasen (Boetzel *et al.* 2021) selbst im gleichen Landschaftskontext und direkten Vergleich deutlich abweichende Wildbienengemeinschaft beherbergen als Blühflächen. Dies zeigt aber auch, dass der starke Einfluss der Pflanzenzusammensetzung auf die Gemeinschaftsstruktur von Wildbienen (Purvis *et al.* 2020; Lane *et al.* 2021) für Blühflächen bisher zu wenig untersucht wurde. Entsprechend dürften viele der von mir erfassten Wildbienenarten, und hier vor allem die Spezialisten, ohne Match mit den von ihnen benötigten Wirtspflanzen, die Blühflächen überwiegend zum Nektarerwerb aufgesucht und den dringend benötigen Pollen an anderen Standorten gesammelt haben (Wood *et al.* 2017). Die Umwandlung von Grünflächen hin zu Einheitsblühflächen mit dem Ziel Wildbienen zu fördern dürfte sich folglich eher negativ auf deren Bestände auswirken.

PERSPEKTIVEN FÜR DIE ANWENDUNG UND WEITERFÜHRENDE FORSCHUNG

Trotz umfangreicher Naturschutzbemühungen wie den Agrarumweltmaßnahmen scheint der Artenrückgang vor allem bei Insekten in den Lebensräumen der Agrarlandschaft sowie in anderen Kulturlandschaften stärker voranzuschreiten als beispielsweise im urbanen Umfeld (Theodorou *et al.* 2020) oder in Wäldern (Seibold *et al.* 2019). Auch wenn davon auszugehen ist, dass die Berücksichtigung der hier vorgestellten Ergebnisse bei der Anlage von Blühflächen zu einer gesteigerten Effizienz für die Förderung der untersuchten Taxa der Wildbienen und Schwebfliegen beiträgt, bleiben noch einige Forschungsfragen offen. Ebenso wichtig ist die Übertragung der aktuellen Forschung in die Praxis. Denn obwohl viele Landwirte sich ihrer Bedeutung für den Schutz der Biodiversität bewusst sind und entsprechende Maßnahmen in ihre Bewirtschaftung gezielt integriert haben (Busse *et al.* 2021), fehlt es oft an Unterstützung dafür, die passenden Maßnahmen für den jeweiligen Standort und die zu fördernden Arten aus dem breiten Angebot an Möglichkeiten auszuwählen (Ekroos *et al.* 2014).

Aufgrund ihres hohen öffentlichen Ansehens fällt die Maßnahmenwahl häufig auf die Anlage von Blühflächen (Haaland *et al.* 2011). Doch auch unter Berücksichtigung der hier diskutierten Forschungsergebnisse bieten Blühflächen in ihrer jetzigen Form alleine nur einen eingeschränkten Nutzen für den Schutz blütenbesuchender Insekten und besonders von Wildbienen. Gleichzeitig mindert die gängige Praxis die potenzielle Effektivität. So ist etwa die Rückführung ehemaliger Blühflächen in die landwirtschaftliche Nutzung nach einer Verweildauer von fünf Jahren sehr aufwendig und stellt viele Landwirte vor große Probleme. Aufgrund dessen bevorzugen Landwirte verstärkt die Anlage von einjährigen Blühflächen. Behörden folgen häufig dieser Tendenz und empfehlen diese vermehrt, obgleich von ihnen eine geringere Effektivität für die Biodiversität zu erwarten ist. Der größte Nutzen einjähriger Flächen scheint dabei in Form einer Ablenktracht für Honigbienen in der Nähe blütenreicher natürlicher Lebensräume zu liegen, weil dies den Konkurrenzdruck auf Wildbienen reduziert. Denn die Tatsache, dass in den hier zusammengefassten Untersuchungen und in denen von Neumüller *et al.* (2021) keine Bestandszunahmen nachgewiesen werden konnte, ist sehr wahrscheinlich auf den kurzen Beobachtungszeitraum von zwei Jahren zurückzuführen. Andere Studien zeigen, dass positive Effekte Zeit benötigen, und dass die damit verbundenen Bestandsentwicklungen möglicherweise erst verzögert sichtbar werden (Iles *et al.* 2018, Purvis *et al.* 2020). Während Hummeln mit ein bis vier Jahren noch verhältnismäßig schnell auf die Wiederherstellung von Wiesen ansprachen, dauert dies bei den restlichen Wildbienenarten fünf bis zehn Jahre (Purvis *et al.* 2020). Auch bei Blühflächen wirkt sich die Kontinuität positiv auf die Artenvielfalt und –zusammensetzung aus. Auf aufgefrischten Blühflächen mit einer Verweildauer von bis zu zehn Jahren (im Rahmen der ökologischen Vorrangflächen) näherte sich die Zusammensetzung der Wildbienengemeinschaften älterer Flächen an die wertvoller Kalkmagerasen an (Boetzl *et al.* 2021). Damit einher gehen ökosystemare Dienstleistungen wie Bestäubung (Krimmer *et al.* 2019, Albrecht *et al.* 2020) oder Schädlingsbekämpfung (Krimmer *et al.* 2021), die erst nach einigen Jahren von Blühflächen ausgehen. So nahm auch auf den von mir untersuchten Flächen die Abundanz der Wespen über die drei Untersuchungsjahre zu – und das am stärksten in einfachen Landschaften mit vernetzten Blühflächen (Bendixen *et al.* eingereicht). Von der längerfristigen Verfügbarkeit der Wirtspflanzen in Blühstreifen profitieren zudem Schmetterlinge, die dort sämtliche Entwicklungsstadien durchlaufen können (Kolkman *et al.* 2021) und in intensiv genutzten Landschaften vor allem durch das Fehlen von Puppenstuben bedroht sind (Wintergerst *et al.* 2021).

Der mit der Persistenz von Blühflächen einhergehende deutliche Rückgang der Pflanzenvielfalt als Folge der voranschreitenden Sukzession wird von Praktikern häufig bemängelt. Auch bei meinen Untersuchungen machte sich dies in einer gesunkenen Beta-Diversität im dritten Jahr und damit ähnlicheren Wildbienengemeinschaften zwischen den Flächen bemerkbar (KAPITEL III). Dem können allerdings Pflegemaßnahmen entgegenwirken. So zeigten Untersuchungen, dass zeitlich versetzte und partielle Pflegeschnitte die Pflanzenvielfalt erhalten und die Attraktivität für Wildbienen sogar noch erhöhen (Neumüller *et al.* 2021). Anders als im HIAP sind im Folgeprogramm HALM Pflegeschnitte einmal jährlich gestattet. Wichtig ist hier vor allem die abschnittsweise Pflege, damit die Blütenverfügbarkeit durchgehend gegeben ist. Denn potentielle Blühlücken könnten die Entwicklung oder Vollendung des Lebenszyklus beeinträchtigen (Memmott *et al.* 2010, Burkle *et al.* 2013, Wintergerst *et al.* 2021). Die positive Wirkung der Pflegemaßnahmen auf Wildbienen könnte ferner nicht nur ein Resultat der gesteigerten Pflanzenvielfalt sein, sondern ist möglicherweise auch auf die veränderte Habitatstruktur zurückzuführen. Durch die im Zuge der Sukzession allmählich zunehmende Verdichtung der Vegetation und das Ausbleiben der Bodenbearbeitung verschwinden vegetationsarme Bereiche, die von unterirdisch nistenden Wildbienenarten für die Nestanlage benötigt werden. Auch in meinen Untersuchungen fanden sich Hinweise darauf, dass sich die Wildbienengemeinschaften im Laufe der Zeit von Bodennistern hin zu Hohlraumnistern verschiebt (KAPITEL III). Denn gerade unter den bodennistenden Arten waren nicht zuletzt die regelmäßigen Störungen durch die ehemals extensive Landwirtschaft für deren ehemals hohe Artenvielfalt mitverantwortlich (Westrich 2019).

Bei der im Abschnitt *Ressourcenverfügbarkeit* angeführten Notwendigkeit, Blühmischungen zur Förderung von Spezialisten artenreicher zu gestalten, ergibt sich jedoch das praktische Problem, dass sich viele wünschenswerte Pflanzenarten nicht auf den nährstoffreichen Böden ansiedeln oder nicht gegen die lokale Samenbank konkurrieren können. So wurde auch in meinen Untersuchungen deutlich, dass standortspezifische Faktoren wie die Samenbank (KAPITEL V) sowie die Sukzession (KAPITEL III) einen erheblichen Einfluss auf die tatsächliche Ressourcenverfügbarkeit auf Blühflächen haben. Dabei unterschied sich die vorgefundene Pflanzenzusammensetzung zum Teil deutlich von der verwendeten Blühmischung (Scheper *et al.* 2021). Bei einer sehr üppig ausgestatteten Samenbank ist daher auf eine intensive Bodenbearbeitung zu achten, damit sich auch konkurrenzschwächere Pflanzen der Mischungen etablieren können. Sollten Wildkräuter, die hervorragende Futterpflanzen für Wildbienen sind (Westrich 2019), für die umliegenden Anbauflächen unproblematisch sein, empfiehlt es sich, diese durchwachsen lassen, da sie sich bei den lokalen Insektenarten als sehr beliebt erwiesen haben (KAPITEL V). Zudem scheinen sich Mischungen, die stärker auf Wildpflanzen statt auf Kulturarten setzten, tendenziell besser etablieren zu lassen (Schmidt *et al.* 2020, Kolkman *et al.* 2021). Auch die Praxiserfahrung der letzten Jahre hat zu einer Anpassung von Blühmischungen geführt, die jedoch vor allem das Entfernen problematischer Pflanzen zu Folge hatte. Dabei sollen vor allem Fruchtfolgekrankheiten (z.B. Kohlhernie durch Kreuzblütler), schwer bekämpfbarer Arten in problematischen Fruchtfolgen (z.B. Buchweizen in Zuckerrüben) sowie ein anschließend erhöhter Herbizid-aufwand (Malven, Mariendistel u.a. sollten gar nicht mehr ausgesät werden) vermieden werden (Landesbetrieb Landwirtschaft Hessen 2021).

Dennoch stellt sich die Frage, inwieweit man Blühflächen wirklich attraktiver als bisher gestalten sollte. Blühflächen stellen für Insekten einen neuartigen und künstlich geschaffenen Lebensraum dar, der zwar einerseits divers wie eine artenreiche Wiese ist und idealerweise ein ähnlich attraktives Pflanzenspektrum beherbergt, andererseits jedoch durch das kompakte Blütenangebot eher mit Massentrachten wie Raps vergleichbar ist. Bedingt durch die konzentrierte Blütenverfügbarkeit sind Blühflächen sehr attraktiv für ein breites Spektrum an blütenbesuchenden Insekten (KAPITEL II) und deren Prädatoren (Hoffmann *et al.* 2020). Aufgrund dieser Lockwirkung ergeben sich jedoch Fragen, die bisher wenig berücksichtigt wurden. So ist unklar, wie sich die Anlage von Blühflächen auf die Bestäubung und den Fortbestand natürlich vorkommender Blütenpflanzen in den umliegenden Lebensräumen auswirkt. Biesmeijer *et al.* (2006) haben gezeigt, dass Pflanzen, die auf die Bestäubung durch Insekten angewiesen sind, parallel mit diesen zurückgegangen sind. Da Grünländer immer blütenärmer werden (Wesche *et al.* 2012, Eichenberg *et al*. 2020), vor allem in Agrarsystemen mit wenig Bestäubern (Clough *et al.* 2014), ist nicht auszuschließen, dass diese Tendenz wegen der Attraktivität der Blühflächen durch einen Rückkopplungseffekt verstärkt wird, weil die Bestäuber aus ihren ursprünglichen Nahrungshabitaten abgezogen werden. Solch negative Effekte auf naturnahe Lebensräume (Holzschuh *et al.* 2016) und Wildpflanzen (Holzschuh *et al.* 2011) konnte für Massentrachten wie Raps bereits gezeigt werden.

Der Kontrast zwischen der begrenzten Wirksamkeit von Blühflächen und deren Beliebtheit verlangen nach einer gezielten Umsetzung und der Kombination unterschiedlicher Maßnahmen im Rahmen der Agrarumwelprogramme der GAP. Jedoch zeichnet sich auch für die Überarbeitung der GAP für den Zeitraum nach 2020 ab, dass es weiterhin an klar definierten Optionen und Richtlinien für die Umsetzung fehlt (Cole *et al.* 2020). Dies könnte die Schutzwirkung entsprechend reduzieren (Pe'er *et al.* 2019). Ein Ansatz, der verschiedene Maßnahmen innerhalb der Agrarumweltmaßnahmen vereint und dadurch nicht nur die Habitat Quantität, sondern auch Qualität erhöht, ist nötig, um Wildbienen optimal zu fördern (Cole *et al.* 2020). Denn bisher limitieren suboptimale Kombinationen von Maßnahmen deren Potential (Nilsson *et al.* 2019, Pe'er *et al.* 2019). Ein interessanter Ansatz für die Erarbeitung alternativer Lösungen innerhalb des HALM ist etwa die Möglichkeit einer Zusammenarbeit mit anderen Akteuren wie den Landschaftspflegeverbänden (Förderung der Zusammenarbeit (HALM A)). Ein Beispiel für ein solches Projekt ist das im Frühjahr 2021 gestartete „Wildbienen-Netzwerk-Agrarlandschaft", in dem ein Netzwerk aus speziell auf die Bedürfnisse von Wildbienen angepassten Ansaaten und der Anlage geeigneter Nistmöglichkeiten mit möglichst langem Bestand etabliert und Pflegemaßnahmen erarbeitet wurden. Die Effizienz dieses Ansatzes wird aktuell gemonitort (Main-Kinzig-Kreis 2021). Sollten diese Bemühungen erfolgreich sein, ist zu hoffen, dass entsprechende Umsetzungskonzepte Einzug in zukünftige Programme halten, um nicht ausschließlich auf Eigeninitiative zur Verfügung zu stehen, sondern auch weiteren Landwirten zugänglich gemacht werden können.

Bei allen Maßnahmen, die die Blütenverfügbarkeit in der Agrarlandschaft steigern, stellt sich nicht zuletzt die Frage, welchen Anteil die Verwendung von Pestiziden an den ausbleibenden Erfolgen haben. So kommt etwa der Einsatz dieser standortbedingt auf Blühflächen potenziell stärker zum Tragen als in artenreichen Grünländern. Die Böden können als ehemalige Ackerfläche bereits durch die bisherige Nutzung Schadstoffe akkumuliert haben und gleichzeitig ist durch benachbarte Nutzflächen mit einer Drift der Mittel zu rechnen. So könnte die Belastung der Blühflächen mit Pestiziden im Vergleich zu naturnahen Lebensräumen deutlich erhöht sein. Die große Mehrzahl (97%) der belasteten Pollen in Honigbienenvölkern stammte zum Beispiel von Wildpflanzen (Botías *et al.* 2015), von denen einige auch zu den gängigen Arten in Blühstreifen gehören (wie Malven oder Buchweizen). Bekannt ist zudem, dass die Westliche Honigbiene *Apis mellifera* und die Dunkle Erdhummel *Bombus terrestris* Nektar, der mit den Neonicotinoiden Imidacloprid (IMD) und Thiamethoxam (TMX) behandelt wurde, unbelastetem Nektar vorzogen (Kessler *et al.* 2015). Neonicotinoidbelastungen wirken sich zudem negativ auf das Blütenbesuchsverhalten aus, indem die Bienen insgesamt weniger Nahrung zu sich nehmen (Kessler *et al.* 2015) und weniger Blüten je Sammelflug anfliegen. Letzteres liegt an längeren Aufenthalten sowie Suchzeiten zwischen zwei Blütenbesuchen (Straub *et al.* 2021). Zudem hebt der Einsatz von Pestiziden in umliegenden Feldern wie Raps den positiven Effekt der Schädlingsbekämpfung aus Blühflächen auf (Krimmer *et al.* 2021). Dies verdeutlicht den negativen Einfluss der Umweltgifte auf die Gemeinschaften von Blühflächen. Hier besteht noch deutlicher Forschungs- und Handlungsbedarf.

SCHLUSSFOLGERUNG

Es konnte gezeigt werden, dass der Landschaftskontext einer der entscheidenden Faktoren für die standortgerechte Optimierung von Blühflächen ist. Vielmehr noch verdeutlichen die Ergebnisse dieser Arbeit den Filtereffekt der durch den Menschen veränderten Landschaft auf blütenbesuchende Insekten und vor allem auf die besonders empfindlichen Wildbienen. Blühflächen bieten in einer modernen und blütenarmen Agrarlandschaft schnelle Unterstützung durch die Bereitstellung von Nahrungsressourcen (vor allem in einfachen Landschaften). Zudem tragen sie zur Verknüpfung mit anderen Teillebensräumen bei und haben das Potential Konkurrenzsituationen (selbst in komplexen Landschaften) sowie den Selektionsdruck auf Artebene abzumildern. Der hohe Pflegeaufwand für eine effiziente Anlage sowie die kurze Bestanddauer und die damit verbundene Unstetigkeit für ihre Besucher legen jedoch nahe, dass Blühflächen vorrangig als unterstützende Sofortmaßnahme für Insekten zu verstehen sind. Auch stellt es sich als schwierig dar, im Rahmen der mit der Maßnahme verbundenen Auflagen und der standörtlichen Gegebenheiten Pflanzengemeinschaften zu etablieren, die den Bedürfnissen der Breite der Wildbienen gerecht wird. Naturschutzbemühungen sollten sich daher zukünftig verstärkt auf die Erhaltung, Renaturierung und Schaffung längerfristig bestehender naturnaher Lebensräume wie artenreiche Grünländer und Randstrukturen fokussieren. Hierfür bieten die Agrarumweltprogramme ein großes Repertoire an Möglichkeiten, die – spezifisch auf zu fördernde Zielarten ausgerichtet – einen effizienteren Bestäuberschutz ermöglichen. Hierfür müssen jedoch aktuelle Forschungsergebnisse Einzug in die Praxis halten. Zukünftige Forschung sollte zudem verstärkt negative Nebeneffekte, die aus der Anlage von Blühflächen resultieren, in den Blick nehmen und ermitteln, wie diese vermieden werden könnten.

LITERATUR

LITERATUR

Aguirre-Gutiérrez J, Biesmeijer JC, van Loon EE, Reemer M, WallisDeVries MF, Carvalheiro LG (2015) Susceptibility of pollinators to ongoing landscape changes depends on landscape history. Diversity and Distributions 21: 1129–1140.

Albrecht M, Kleijn D, Williams NM, Tschumi M, Blaauw BR, Bommarco, R, Campbell AJ, Dainese M, Drummond FA, Entling MH, Ganser D, Arjen de Groot G, Goulson D, Grab H, Hamilton H, Herzog F, Isaacs R, Jacot K, Jeanneret P, Jonsson M, Knop E, Kremen C, Landis DA, Loeb GM, Marini L, McKerchar M, Morandin L, Pfister SC, Potts SG, Rundlöf M, Sardiñas H, Sciligo A, Thies C, Tscharntke T, Venturini E, Veromann E, Vollhardt IM, Wäckers F, Ward K, Westbury DB, Wilby A, Woltz M, Wratten S, Sutter L (2020) The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: a quantitative synthesis. Ecology Letters 23: 1488–1498.

Baldock KCR, Goddard MA, Hicks DM, Kunin WE, Mitschunas N, Osgathorpe LM, Potts SG, Robertson KM, Scott AV, Stone GN, Vaughan IP, Memmott J (2015) Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. Proceedings: Biological Sciences 282: 20142849.

Batáry P, Báldi A, Ekroos J, Gallé R, Grass I, Tscharntke T (2020) Biologia Futura: landscape perspectives on farmland biodiversity conservation. Biologia Futura 71: 9–18.

Batáry P, Báld, A, Kleijn D, Tscharntke T (2011) Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. Proceedings of the Royal Society B: Biological Sciences 278: 1894–1902.

Batáry P, Dicks LV, Kleijn D, Sutherland WJ (2015) The role of agri-environment schemes in conservation and environmental management. Conservation Biology 29: 1006–1016.

Baulechner D, Diekötter T, Wolters V, Jauker F (2019) Converting arable land into flowering fields changes functional and phylogenetic community structure in ground beetles. Biological Conservation 231: 51–58.

Bendixen US, Jauker F, Wolters V, Warzecha D, Diekötter T (eingereicht) Increased spatial connectivity of sown wildflower strips boosts their benefits to biodiversity.

Beyer N, Gabriel D, Westphal C (2021) Contrasting effects of past and present mass-flowering crop cultivation on bee pollinators shaping yield components in oilseed rape. Agriculture, Ecosystems & Environment 319: 107537.

Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J, Kunin WE (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313: 351–354.

Bignal EM, McCracken DI (1996) Low-Intensity Farming Systems in the Conservation of the Countryside. The Journal of Applied Ecology 33: 413–424.

Billeter R, Liira J, Bailey D, Bugter R, Arens P, Augenstein I, Aviron S, Baudry J, Bukacek R, Burel F (2008) Indicators for biodiversity in agricultural landscapes: a pan-European study. Journal of Applied Ecology 45: 141–150.

Boetzl FA, Krauss J, Heinze J, Hoffmann H, Juffa J, König S, Krimmer E, Prante M, Martin EA, Holzschuh A, Steffan-Dewenter I (2021) A multitaxa assessment of the effectiveness of agri-environmental schemes for biodiversity management. Proceedings of the National Academy of Sciences 118: e2016038118.

Bommarco R, Marini L, Vaissière BE (2012) Insect pollination enhances seed yield, quality, and market value in oilseed rape. Oecologia 169: 1025–1032.

Botías C, David A, Horwood J, Abdul-Sada A, Nicholls E, Hill E, Goulson D (2015) Neonicotinoid Residues in Wildflowers, a Potential Route of Chronic Exposure for Bees. Environmental Science & Technology 49: 12731–12740.

Branquart E, Hemptinne J–L (2000) Selectivity in the exploitation of floral resources by hoverflies (Diptera: Syrphinae). Ecography 23: 732–742.

Brian AD (1954) The Foraging of Bumble Bees Part I. Foraging Behaviour. Bee World 35: 61–67.

Breeze TD, Bailey AP, Balcombe KG, Potts SG (2011) Pollination services in the UK: How important are honeybees? Agriculture, Ecosystems & Environment 142: 137–143.

Brook BW, Sodhi NS, Bradshaw CJA (2008) Synergies among extinction drivers under global change. Trends in Ecology & Evolution 23: 453–460.

Buhk C, Oppermann R, Schanowski A, Bleil R, Ludemann J, Maus C (2018) Flower strip networks offer promising long term effects on pollinator species richness in intensively cultivated agricultural areas. BMC Ecology 18: 55.

Burkle LA, Marlin JC, Knight TM (2013) Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. Science 339: 1611–1615.

Busse M, Zoll F, Siebert R, Bartels A, Bokelmann A, Scharschmidt P (2021) How farmers think about insects: perceptions of biodiversity, biodiversity loss and attitudes towards insect-friendly farming practices. Biodiversity and Conservation 30: 3045–3066.

Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque J-F, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Morcillo MH, Oldfield TEE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vié J-C, Watson R (2010) Global biodiversity: indicators of recent declines. Science 328: 1164–1168.

Clough Y, Ekroos J, Báldi A, Batáry P, Bommarco R, Gross N, Holzschuh A, Hopfenmüller S, Knop E, Kuussaari M, Lindborg R, Marini L, Öckinger E, Potts SG, Pöyry J, Roberts SPM, Steffan-Dewenter I, Smith HG (2014) Density of insect-pollinated grassland plants decreases with increasing surrounding land-use intensity. Ecology Letters 17: 1168–1177.

Cardoso P, Barton PS, Birkhofer K, Chichorro F, Deacon C, Fartmann T, Fukushima CS, Gaigher R, Habel JC, Hallmann CA, Hill MJ, Hochkirch A, Kwak ML, Mammola S, Noriega JA, Orfinger AB, Pedraza F, Pryke JS, Roque FO, Settele J, Simaika JP, Stork NE, Suhling F, Vorster C, Samways MJ (2020) Scientists' warning to humanity on insect extinctions. Biological Conservation 242: e108426.

Carvell C (2002) Habitat use and conservation of bumblebees (Bombus spp.) under different grassland management regimes. Biological Conservation 103: 33–49.

Carvell C, Meek WR, Pywell RF, Goulson D, Nowakowski M (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. Journal of Applied Ecology 44: 29–40.

Carvell C, Meek WR, Pywell RF, Nowakowski M (2004) The response of foraging bumblebees to successional change in newly created arable field margins. Biological Conservation 118: 327–339.

Carvell C, Roy DB, Smart SM, Pywell RF, Preston CD, Goulson D (2006a) Declines in forage availability for bumblebees at a national scale. Biological Conservation 132: 481–489.

Carvell C, Westrich P, Meek WR, Pywell RF, Nowakowski M (2006b) Assessing the value of annual and perennial forage mixtures for bumblebees by direct observation and pollen analysis. Apidologie 37: 326–340.

Cole LJ, Kleijn D, Dicks LV, Stout JC, Potts SG, Albrecht M, Balzan MV, Bartomeus I, Bebeli PF, Bevk D, Biesmeijer JC, Chlebo R, Dautartė A, Emmanouil N, Hartfield C, Holland JM, Holzschuh A, Knoben NTJ, Kovács-Hostyánszki A, Mandelik Y, Panou H, Paxton RJ, Petanidou T, Pinheiro de Carvalho MAA, Rundlöf M, Sarthou J-P, Stavrinides MC, Suso MJ, Szentgyörgyi H, Vaissière BE, Varnava A, Vilà M, Zemeckis R, Scheper J (2020) A critical analysis of the potential for EU Common Agricultural Policy measures to support wild pollinators on farmland. Journal of Applied Ecology 57: 681–694.

Dramstad WE, Fjellstad WJ, Strand GH, Mathiesen HF, Engan G, Stokland JN (2002) Development and implementation of the Norwegian monitoring programme for agricultural landscapes. Journal of Environmental Management 64: 49–63.

Dramstad WE, Fry G (1995) foraging activity of bumblebees (Bombus) in relation to flower resources on arable land. Agriculture Ecosystems & Environment 53: 123–135.

Eichenberg D, Bowler DE, Bonn A, Bruelheide H, Grescho V, Harter D, Jandt U, May R, Winter M, Jansen F (2021) Widespread decline in Central European plant diversity across six decades. Global Change Biology 27: 1097–1110.

Ekroos J, Olsson O, Rundlöf M, Wätzold F, Smith HG (2014) Optimizing agrienvironment schemes for biodiversity, ecosystem services or both? Biological Conservation 172: 65–71.

Librán-Embid F, Grass I, Emer C, Ganuza C, Tscharntke T (2021) A plant–pollinator metanetwork along a habitat fragmentation gradient. Ecology Letters 24: 2700– 2712.

Fitzpatrick U, Murray TE, Paxton RJ, Brown MJF (2007) Building on IUCN regional red lists to produce lists of species of conservation priority: a model with Irish bees. Conservation Biology 21: 1324–1332.

Foley JA, Defries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder PK (2005) Global consequences of land use. Science 309: 570–574.

Foley JA, Ramankutty N, Brauman KA, Cassidy ES, Gerber JS, Johnston M, Mueller ND, O'Connell C, Ray DK, West PC, Balzer C, Bennett EM, Carpenter SR, Hill J, Monfreda C, Polasky S, Rockström J, Sheehan J, Siebert S, Tilman D, Zaks DPM (2011) Solutions for a cultivated planet. Nature 478: 337–342.

Fontaine C, Dajoz I, Meriguet J, Loreau M (2006) Functional diversity of plant-pollinator interaction webs enhance the persistence of plant communities. PLoS Biology 4: 129–135.

Franzen M, Nilsson SG (2008) How can we preserve and restore species richness of pollinating insects on agricultural land? Ecography 31: 698–708.

Fussell M, Corbet SA (1992) Flower Usage by Bumble-Bees: A Basis for Forage Plant Management. Journal of Applied Ecology 29: 451–465.

Gámez-Virués S, Perović DJ, Gossner MM, Börschig C, Blüthgen N, de Jong H, Simons NK, Klein A-M, Krauss J, Maier G, Scherber C, Steckel J, Rothenwöhrer C, Steffan-Dewenter I, Weiner CN, Weisser W, Werner M, Tscharntke T, Westphal C (2015) Landscape simplification filters species traits and drives biotic homogenization. Nature Communications 6: e8568.

Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, Cunningham SA, Kremen C, Carvalheiro LG, Harder LD, Afik O, Bartomeus I, Benjamin F, Boreux V, Cariveau D, Chacoff NP, Dudenhöffer JH, Freitas BM, Ghazoul J, Greenleaf S, Hipólito J, Holzschuh A, Howlett B, Isaacs R, Javorek SK, Kennedy CM, Krewenka KM, Krishnan S, Mandelik Y, Mayfield MM, Motzke I, Munyuli T, Nault BA, Otieno M, Petersen J, Pisanty G, Potts SG, Rader R, Ricketts TH, Rundlöf M, Seymour CL, Schüepp C, Szentgyörgyi H, Taki H, Tscharntke T, Vergara CH, Viana BF, Wanger TC, Westphal C, Williams N, Klein A-M (2013) Wild pollinators enhance fruit set of crops regard-less of honey bee abundance. Science 339: 1608–1611.

Garibaldi LA, Oddi FJ, Miguez FE, Bartomeus I, Orr MC, Jobbágy EG, Kremen C, Schulte LA, Hughes AC, Bagnato C, Abramson G, Bridgewater P, Gomez Carella D, Díaz S, Dicks LV, Ellis EC, Goldenberg M, Huaylla CA, Kuperman M, Locke H, Mehrabi Z, Santibañez F, Zhu C-D (2021) Working landscapes need at least 20% native habitat. Conservation Letters 14: e12773.

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

Geiger F, Bengtsson J, Berendse F, Weisser WW, Emmerson M, Morales MB, Ceryngier P, Liira J, Tscharntke T, Winqvist C, Eggers S, Bommarco R, Pärt T, Bretagnolle V, Plantegenest M, Clement LW, Dennis C, Palmer C, Oñate JJ, Guerrero I, Hawro V, Aavik T, Thies C, Flohre A, Hänke S, Fischer C, Goedhart PW, Inchausti P (2010) Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic and Applied Ecology 11: 97–105.

Goulson D, Stout JC (2001) Homing ability of the bumblebee Bombus terrestris (Hymenoptera: Apidae). Apidologie 32: 105–111.

Grab H, Brokaw J, Anderson E, Gedlinske L, Gibbs J, Wilson J, Loeb G, Isaacs R, Poveda K (2019) Habitat enhancements rescue bee body size from the negative effects of landscape simplification. Journal of Applied Ecology 56: 2144– 2154.

Grass I, Albrecht J, Farwig N, Jauker F (2021) Plant traits and landscape simplification drive intraspecific trait diversity of Bombus terrestris in wildflower plantings. Basic and Applied Ecology 57: 91–101.

Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. Oecologia 153: 589–596.

Griffin SR, Haddad NM (2021) Connectivity and edge effects increase bee colonization in an experimentally fragmented landscape. Ecography 44: 919–927.

Haaland C, Naisbit RE, Bersier LF (2011) Sown wildflower strips for insect conservation: A review. Insect Conservation and Diversity 4: 60–80.

Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Müller A, Sumser H, Hörren T, Goulson D, de Kroon H (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS ONE 12: e0185809.

Hannon LE, Sisk TD (2009) Hedgerows in an agri-natural landscape: Potential habitat value for native bees. Biological Conservation 142: 2140–2154.

Hartmann E, Thomas F, Luick R, Bierer J, Poppinga O (2003) Kurzfassungen der nach der Verordnung EG 1257/1999 kofinanzierten Agrarumweltprogramme der Bundesländer. BfN-Skripten 87

Haslett JR (1989) Interpreting patterns of resource utilization - randomness and selectivity in pollen feeding by adult hoverflies. Oecologia 78: 433–442.

Heard MS, Carvell C, Carreck NL, Rothery P, Osborne JL, Bourke AFG (2007) Landscape context not patch size determines bumble-bee density on flower mixtures sown for agri-environment schemes. Biology Letters 3: 638–641.

Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: A review of 22 years of recommendations. Biological Conservation 142: 14–32.

Hodge I, Hauck J, Bonn A (2015) The alignment of agricultural and nature conservation policies in the European Union. Conservation Biology 29: 996–1005.

Hoffmann US, Jauker F, Diehl E, Mader V, Fiedler D, Wolters V, Diekötter T (2020) The suitability of sown wildflower strips as hunting grounds for spider-hunting wasps of the genus Trypoxylon depends on landscape context. Journal of Insect Conservation 24: 125–131.

Hofmann MM, Zohner CM, Renner SS (2019) Narrow habitat breadth and late-summer emergence increases extinction vulnerability in Central European bees. Proceedings of the Royal Society B: Biological Sciences 286: e20190316.

Holland, J.M., Bianchi FJ, Entling MH, Moonen A-C, Smith BM, Jeanneret P (2016) Structure, function and management of semi-natural habitats for conservation biological control: a review of European studies. Pest Management Science 72: 1638–1651.

Holzschuh A, Dainese M, González-Varo JP, Mudri-Stojnić S, Riedinger V, Rundlöf M, Scheper J, Wickens JB, Wickens VJ, Bommarco R, Kleijn D, Potts SG, Roberts SPM, Smith HG, Vilà M, Vujić A, Steffan-Dewenter I (2016) Massflowering crops dilute pollinator abundance in agricultural landscapes across Europe. Ecology Letters 19: 1228–1236.

Holzschuh A, Dormann CF, 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: 3444–3451.

Iles DT, Williams NM, Crone EE (2018) Source-sink dynamics of bumblebees in rapidly changing landscapes. Journal of Applied Ecology 55: 2802–2811.

Jauker F (2020) Bee body size and global change: Growing with the task? Global Change Biology 26: 1940–1941.

Jauker B, Krauss J, Jauker F, Steffan-Dewenter I (2013) Linking life history traits to pollinator loss in fragmented calcareous grasslands. Landscape Ecology 28: 107–120.

Jauker F, Bondarenko B, Becker HC, Steffan-Dewenter I (2012) Pollination efficiency of wild bees and hoverflies provided to oilseed rape. Agricultural and Forest Entomology 14: 81–87.

Jauker F, Diekötter T, Schwarzbach F, Wolters V (2009) Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landscape Ecology 24: 547–555.

Jauker F, Jauker B, Grass I, Steffan-Dewenter I, Wolters V (2019) Partitioning wild bee and hoverfly contributions to plant–pollinator network structure in fragmented habitats. Ecology 100: 1–3.

Jauker F, Speckmann M, Wolters V (2016) Intra-specific body size determines pollination effectiveness. Basic and Applied Ecology 17: 714–719.

Jauker F, Wolters V (2008) Hover flies are efficient pollinators of oilseed rape. Oecologia 156: 819–823.

Kearns CA, Oliveras DM (2009) Environmental factors affecting bee diversity in urban and remote grassland plots in Boulder, Colorado. Journal of Insect Conservation 13: 655–665.

Kessler S, Tiedeken E, Simcock K, Derveau S, Mitchell J, Softley S, Radcliffe A, Stout JC, Wright GA (2015) Bees prefer foods containing neonicotinoid pesticides. Nature 521: 74–76.

Kevan PG, Baker HG (1983) Insects as flower visitors and pollinators. The Annual Review of Entomology 28: 407–53.

Kleijn D, Baquero RA, Clough Y, Díaz M, De Esteban J, Fernández F, Gabriel D, Herzog F, Holzschuh A, Jöhl R, Knop E, Kruess A, Marshall EJP, Steffan-Dewenter I, Tscharntke T, Verhulst J, West TM, Yela JL (2006) Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecology Letters 9: 243–254.

Kleijn D, Winfree R, Bartomeus I, Carvalheiro LG, Henry M, Isaacs R, Klein A-M, Kremen C, M'Gonigle LK, Rader R, Ricketts TH, Williams NM, Adamson NL, Ascher JS, Báldi A, Batáry P, Benjamin F, Biesmeijer JC, Blitzer EJ, Bommarco R, Brand MR, Bretagnolle V, Button L, Cariveau DP, Chifflet R, Colville JF, Danforth BN, Elle E, Garratt MPD, Herzog F, Holzschuh A, Howlett BG, Jauker F, Jha S, Knop E, Krewenka KM, Le Féon V, Mandelik Y, May EA, Park MG, Pisanty G, Reemer M, Riedinger V, Rollin O, Rundlöf M, Sardiñas HS, Scheper J, Sciligo AR, Smith HG, Steffan-Dewenter I, Thorp R, Tscharntke T, Verhulst J, Viana BF, Vaissière BE, Veldtman R, Ward KL, Westphal C, Potts SG (2015) Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. Nature Communication 6: 7414.

Klein A-M Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B - Biological Sciences 274: 303–313.

Kolkman A, Dopagne C, Piqueray J (2021) Sown wildflower strips offer promising long term results for butterfly conservation. Journal of Insect Conservation [online].

Korpela E-L, Hyvönen T, Lindgren S, Kuussaari M (2013) Can pollination services, species diversity and conservation be simultaneously promoted by sown wildflower strips on farmland? Agriculture, Ecosystems and Environment 179: 18–24.

Kremen C (2005) Managing ecosystem services: what do we need to know about their ecology? Ecology Letters 8: 468–479.

Kremen C, Williams NM, Thorp RW (2002) Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Sciences 99: 16812–16816.

Krimmer E, Martin EA, Holzschuh A, Krauss J, Steffan-Dewenter I (2021) Flower fields and pesticide use interactively shape pollen beetle infestation and parasitism in oilseed rape fields. Journal of Applied Ecology [online].

Krimmer E, Martin EA, Krauss J, Holzschuh A, Steffan-Dewenter I (2019) Size, age and surrounding semi-natural habitats modulate the effectiveness of flower-rich agrienvironment schemes to promote pollinator visitation in crop fields. Agriculture, Ecosystems and Environment 284: 106590.

Landesbetrieb Landwirtschaft Hessen (2021) Neue Empfehlungen für Blühmischungen [online] https://llh.hessen.de/umwelt/biodiversitaet/bluehflaechen/neue-empfehlungen-fuer-bluehmischungen/ (Stand 29.10.2021).

Lane IG, Portman ZM, Herron-Sweet CH, Pardee GL, Cariveau DP (2021) Differences in bee community composition between restored and remnant prairies are more strongly linked to forb community differences than landscape differences. Journal of Applied Ecology [online].

Larson BMH, Kevan PG, Inouye DW (2001) Flies and flowers: taxonomic diversity of anthophiles and pollinators. The Canadian Entomologist 133: 439–465.

Leonhardt SD, Blüthgen N (2012) The same, but different: pollen forag-ing in honeybee and bumblebee colonies. Apidologie 43: 449–464.

Le Feon V, Schemann-Legionnet A, Delettre Y, Aviron S, Billeter R, Bugter R, Hendrickx F, Burel F (2010) Intensification of agriculture, landscape composition and wild bee communities: A large scale study in four European countries. Agriculture Ecosystems & Environment 137: 143–150.

Main-Kinzig-Kreis (2021) Projektstart Wildbienen-Netzwerk-Agrarlandschaft [online] https://www.mkk.de/aktuelles/pressemitteilungen_1/pressemitteilung_1771585.html (Stand 29.10.2021).

Marshall EJR, Moonen AC (2002) Field margins in northern Europe: their functions and interactions with agriculture. Agriculture, Ecosystems and Environment 89: 5–21.

Martin AE, Dainese M, Clough Y, Baldi A, Bommarco R, Gagic V, Garratt MPD, Holzschuh A, Kleijn D, Kovács-Hostyánszki A, Marini L, Potts SG, Smith HG, Al Hassan D, Albrecht M, Andersson GKS, Asís JD, Aviron S, Balzan MV, Baños-Picón L, Bartomeus I, Batáry P, Burel F, Caballero-López B, Concepción ED, Coudrain V, Dänhardt J, Diaz M, Diekötter T, Dormann CF, Duflot R, Entling MH, Farwig N, Fischer C, Frank T, Garibaldi LA, Hermann J, Herzog F, Inclán D, Jacot K, Jauker F, Jeanneret P, Kaiser M, Krauss J, Le Féon V, Marshall J, Moonen A-C, Moreno G, Riedinger V, Rundlöf M, Rusch A, Scheper J, Schneider G, Schüepp C, Stutz S, Sutter L, Tamburini G, Thies C, Tormos J, Tscharntke T, Tschumi M, Uzman D, Wagner C, Zubair-Anjum M, Steffan-Dewenter I (2019) The interplay of landscape composition and conguration: new pathways to manage functional biodiversity and agroecosystem services across Europe. Ecology Letters 22: 1083–1094.

Martin AE, Collins SJ, Crowe S, Girard J, Naujokaitis-Lewis I, Smith AC, Lindsay K, Mitchell S, Fahrig L (2020) Effects of farmland heterogeneity on biodiversity are similar to—or even larger than—the effects of farming practices. Agriculture, Ecosystems & Environment 288: 106698.

Meeus JHA (1993) The transformation of agricultural landscapes in Western-Europe. Science of the Total Environment 129: 171–190.

Memmott J, Carvell C, Pywell RF, Craze PG (2010) The potential impact of global warming on the efficacy of field margins sown for the conservation of bumblebees. Philosophical Transactions of the Royal Society B: Biological Sciences 365: 2071–2079.

Mittelbach GG, Schemske DW (2015) Ecological and evolutionary perspectives on community assembly. Trends in Ecology & Evolution 30: 241–247.

Neumüller U, Burger H, Krausch S, Blüthgen N, Ayasse M (2020) Interactions of local habitat type, landscape composition and flower availability moderate wild bee communities. Landscape Ecology 35: 2209–2224.

Neumüller U, Burger H, Schwenninger HR, Hopfenmüller S, Krausch S, Weiß K, Ayasse M (2021) Prolonged blooming season of flower plantings increases wild bee abundance and richness in agricultural landscapes. Biodiversity Conservation 30: 3003–3021.

Nilsson L, Clough Y, Smith HG, Olsson JA, Brady MV, Hristov J, Olssona P, Skantzed k, Ståhlberg D, Dänhardt J (2019) A suboptimal array of options erodes the value of CAP ecological focus areas. Land Use Policy 85: 407– 418.

Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? Oikos 120: 321–326.

Pe’er G, Zinngrebe Y, Moreira F, Sirami C, Schindler S, Müller R, Bontzorlos V, Clough D, Bezák P, Bonn A, Hansjürgens B, Lomba A, Möckel S, Passoni G, Schleyer C, Schmidt J, Lakner S (2019) A greener path for the EU Common Agricultural Policy. Science 365: 449–451.

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution 25: 345–353.

Purvis EEN, Vickruck JL, Best LR, Devries JH, Galpern P (2020) Wild bee community recovery in restored grassland-wetland complexes of prairie North America. Biological conservation 252: 108829.

Pywell RF, Warman EA, Hulmes L, Hulmes S, Nuttall P, Sparks TH, Critchley CNR, Sherwood A (2006) Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. Biological Conservation 129: 192–206.

Rabbinge R, van Diepen CA (2000) Changes in agriculture and land use in Europe. European Journal of Agronomy 13: 85–99.

Redpath N, Osgathorpe LM, Park K, Goulson D (2010) Crofting and bumblebee conservation: The impact of land management practices on bumblebee populations in northwest Scotland. Biological Conservation 143: 492–500.

Regierungspräsidium Gießen (2020) Biodiversität, Landschaftspflege [online] https://rp-giessen.hessen.de/umwelt-natur/forsten-naturschutz/biodiversit%C3%A4t/hessisches-programm-f%C3%BCr-agrarumwelt-und (Stand 31.05.2010).

Robinson RA, Sutherland WJ (2002) Post-war changes in arable farming and biodiversity in Great Britain. Journal of Applied Ecology 39: 157–176.

Rösch V, Tscharntke T, Scherber C, Batáry P (2015) Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments. Oecologia 179: 209–222.

Sánchez-Bayo F, Wyckhuys KAG (2019) Worldwide decline of the entomofauna: A review of its drivers. Biological Conservation 232: 8–27.

Scheper J, Bommarco R, Holzschuh A, Potts SG, Riedinger V, Roberts SPM, Rundlöf M, Smith HG, Steffan-Dewenter I, Wickens JB, Wickens VJ, Kleijn D (2015) Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. Journal of Applied Ecology 52: 1165–1175.

Scheper J, Bukovinszky T, Huigens ME, Kleijn D (2021) Attractiveness of sown wildflower strips to flower-visiting insects depends on seed mixture and establishment success. Basic and Applied Ecology 56: 401–415.

Scheper J, Holzschuh A, Kuussaari M, Potts SG, Rundlöf M, Smith HG, Kleijn D (2013) Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – a meta-analysis. Ecology Letters 16: 912–920.

Scheper J, Reemer M, van Kats R, Ozinga WA, van der Linden GTJ, Schaminée JHJ, Siepel H, Kleijn D (2014) Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. PNAS 111: 17552–17557.

Schmidt A, Kirmer A, Kiehl K, Tischew S (2020) Seed mixture strongly affects species-richness and quality of perennial flower strips on fertile soil. Basic and Applied Ecology 42: 62–72.

Seibold S, Gossner MM, Simons NK, Blüthgen N, Müller J, Ambarlı D, Ammer C, Bauhus J, Fischer M, Habel JC, Linsenmair KE, Nauss T, Penone C, Prati D, Schall P, Schulze ED, Vogt J, Wöllauer S, Weisser WW (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574: 671–674.

Shelly TE, Buchmann SL, Villalobos EM, O'Rourke MK (1991) Colony ergonomics for a desert-dwelling bumblebee species (Hymenoptera: Apidae). Ecological Entomology 16: 361–370.

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

Steffan-Dewenter I, Tscharntke T (1999) Effects of habitat isolation on pollinator communities and seed set. Oecologia 121: 432–440.

Stoate C, Boatman ND, Borralho RJ, Carvalho CR, de Snoo GR, Eden P (2001) Ecological impacts of arable intensification in Europe. Journal of Environmental Management 63: 337–365.

Straub F, Orih IJ, Kimmich J, Ayasse M (2021) Negative Effects of the Neonicotinoid Clothianidin on Foraging Behavior and Antennal Sensitivity in Two Common Pollinator Species, Osmia bicornis and Bombus terrestris. Frontiers in Ecology and Evolution 9: 697355.

Southwick EE, Southwick L (1992) Estimating the Economic Value of Honey Bees (Hymenoptera: Apidae) as Agricultural Pollinators in the United States. Journal of Economic Entomology 85: 621–633.

Suding KN (2011) Toward an era of restoration in ecology: Successes, failures, and opportunities ahead. Annual Review of Ecology, Evolution, and Systematics 42: 465–487.

Theodorou P, Radzevičiūtė R, Lentendu G, Kahnt B, Husemann M, Bleidorn C, Settele J, Schweiger O, Grosse I, Wubet T, Murray TE, Paxton RJ (2020) Urban areas as hotspots for bees and pollination but not a panacea for all insects. Nature Communications 11: 576.

Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, Bengtsson J, Clough Y, Crist TO, Dormann CF, Ewers RM, Fründ J, Holt RD, Holzschuh A, Klein AM, Kleijn D, Kremen C, Landis DA, Laurance W, Lindenmayer D, Scherber C, Sodhi N, Steffan-Dewenter I, Thies C, van der Putten WH, Westphal C (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biological Reviews 87: 661–685.

Van Reeth C, Caro G, Bockstaller C, Michel N (2018) Current and previous spatial distributions of oilseed rape fields influence the abundance and the body size of a solitary wild bee, *Andrena cineraria*, in permanent grasslands. PLoS ONE 13: e0197684.

Von Königslöw V, Mupepele A-C, Klein A-M (2021) Overlooked jewels: Existing habitat patches complement sown flower strips to conserve pollinators. Biological Conservation 261: 109263.

Wesche K, Krause B, Culmsee H, Leuschner C (2012) Fifty years of change in Central European grassland vegetation: Large losses in species richness and animal-pollinated plants. Biological Conservation 150: 76–85.

Westphal C, Steffan-Dewenter I, Tscharntke T (2003) Mass flowering crops enhance pollinator densities at a landscape scale. Ecology Letters 6: 961–965.

Westrich P (1996) Habitat requirements of central European bees and the problems of partial habitats, in: Matheson A., Buchmann S.L., O'Toole C., Westrich P., Williams I.H. (Eds.), The Conservation of Bees. Academic Press, London, Seiten 1–16.

Westrich P (2019) Die Wildbienen Deutschlands, zweite Auflage. Ulmer, Stuttgart.

Williams NM, Crone EE, Roulston TH, Minckley RL, Packer L, Potts SG (2010) Ecological and life-history traits predict bee species responses to environmental disturbances. Biological Conservation 143: 2280–2291.

Wilson JB, Peet RK, Dengler J, Partel M (2012) Plant species richness: the world records. Journal of Vegetation Science 23: 796–802.

Winfree R (2010) The conservation and restoration of wild bees. Year in Ecology and Conservation Biology 2010 1195: 169–197.

Winfree R, Aguilar R, Vazquez DP, LeBuhn G, Aizen MA (2009) A meta-analysis of bees' responses to anthropogenic disturbance. Ecology 90: 2068–2076.

Winfree R, Reilly JR, Bartomeus I, Cariveau DP, Williams NM, Gibbs J (2018) Species turnover promotes the importance of bee diversity for crop pollination at regional scales. Science 359: 791–793.

Wintergerst J, Kästner T, Bartel M, Schmidt C, Nuss M (2021) Partial mowing of urban lawns supports higher abundances and diversities of insects. Journal of Insect Conservation 25: 797–808.

Wood TJ, Holland JM, Hughes WHO, Goulson D (2015) Targeted agri-environment schemes significantly improve the population size of common farmland bumblebee species. Molecular Ecology 24: 1668–1680.

Wood TJ, Holland JM, Hughes WHO, Goulson D (2017) Providing foraging resources for solitary bees onfarmland: current schemes for pollinators benefit alimited suite of species. Journal of Applied Ecology 54: 323–333.

Woodcock BA, Edwards M, Redhead J, Meek WR, Nuttall P, Falk S, Nowakowski M, Pywell RF (2013) Crop flower visitation by honeybees, bumblebees and solitary bees: Behavioural differences and diversity responses to landscape. Agriculture, Ecosystems & Environment 171: 1–8.

Wray JC, Elle E (2015) Flowering phenology and nesting resources influence pollinator community composition in a fragmented ecosystem. Landscape Ecology 30: 261–272.

Wright IR, Roberts SPM, Collins BE (2015) Evidence of forage distance limitations for small bees (Hymenoptera: Apidae). European Journal of Entomology 112: 303–310.

Zurbuchen A, Cheesman S, Klaiber J, Mueller A, Hein S, Dorn S (2010a) Long foraging distances impose high costs on offspring production in solitary bees. Journal of Animal Ecology 79: 674–681.

Zurbuchen A, Landert L, Klaiber J, Müller A, Hein S, Dorn S (2010b) Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biological Conservation 143: 669–676.

DANKSAGUNG

DANKSAGUNG

Ohne die Unterstützung einer Reihe von Menschen wäre diese Arbeit nicht möglich gewesen, ihnen allen gilt von Herzen mein Dank! Als erstes möchte ich meinem Doktorvater *Prof. Dr. Volkmar Wolters* herzlich dafür danken, dass er die Betreuung meiner Arbeit übernommen hat und ich diese als Mitglied seiner Arbeitsgruppe anfertigen durfte. In dieser Zeit habe ich sehr viel von ihm lernen können und habe die konstruktiven Ratschläge sehr zu schätzen gewusst. Ganz besonderer Dank gilt *Tim Diekötter* und *Frank Jauker*, die mich ermutigt und dabei unterstützt haben den Projektantrag zu schreiben und die Arbeit fachlich betreut haben, aber auch für den zusätzlichen Aufwand den die Begutachtung dieser Arbeit und der Manuskripte mit sich gebracht hat. Danke euch, dass ihr mich mit eurer herzlichen Art für das Thema begeistert habt und sich die Arbeit immer angefühlt hat wie seinem größten Hobby nachzugehen. An dieser Stelle möchte ich auch *Birgit Jauker* danken, dass du und Frank mich darin unterstütz habt den Weg in Richtung Museum zu gehen. Ohne euch wäre das sicher nicht so erfolgreich gewesen und ich kann nicht in Worte ausdrücken wie dankbar ich dafür bin. Liebe Birgit, gemeinsames Bienenbestimmen macht mit keinem mehr Spaß als mit dir.

Die Feldarbeit wurde besonders durch die Unterstützung von *Uta Bendixen*, *Patricia Schmidt*, *Anton Müller*, *Aziza Bouffara*, *Stefanie Ettling* und *Jonathan Lanzen* nie langweilig, euch und vielen weiteren Studierenden, die bei der Feldarbeit und Probenaufbereitung geholfen haben, sei an dieser Stelle gedankt! Mein Dank gilt zudem Frau Weiß und Herrn Zerbe vom Amt für Ländlichen Raum in Marburg-Biedenkopf und allen Landwirten die uns den Zugang zu ihren Flächen gewährt haben oder uns mit einem Abschleppdienst zur Seite standen. Die Zeit in Gießen wäre nicht die gleiche gewesen ohne all die wunderbaren Kolleg*innen der Arbeitsgruppe Tierökologie: *Andrea Früh-Müller*, *Andrey Zaytsev*, *Birgit Aue*, *Christian Krippes*, *Elisabeth Pohlon*, *Elvira Sereda*, *Eva Diehl*, *Keiko Sasaki*, *Klaus Birkhofer*, *Klemens Ekschmitt*, *Nora Rütz*, *Ralf Sauerbrei* und *Viktoria Mader*. Ganz besonders möchte ich meinen ehemaligen Zimmernachbar*innen *Katharina John* und *Dennis Baulechner* für die konstruktiven Diskussionen und die schöne Zeit danken, die wir miteinander verbracht haben.

Diese Arbeit wurde durch ein Promotionsstipendium der deutschen Bundesstiftung Umwelt (DBU) gefördert. Für ihre stets ermutigende Art möchte ich hier ganz herzlich meiner Referentin *Hedda Schlegel-Starmann* danken. *Lisa Thill* und *Natalie Körte*, dank euch sind die gemeinsamen DBU Seminare in besonders positiver Erinnerung geblieben. *Uli Frommer*, *Stefan Tischendorf* und *Wolfgang Dorow* danke ich, dass sie mich bei der Einarbeitung in die Bestimmung der Bienen unterstützt haben und mir immer mit Rat zur Seite standen. *Paul Westrich* danke ich für die vielen Stunden gemeinsamer und unterhaltsamer Gespräche, bei denen wir Probleme diskutiert und er mir tiefere Einblicke in die Ökologie der Bienen gewährt hat.

Meiner Familie danke ich für die Unterstützung mit dem richtigen Maß an Nachfragen und Ermutigen. Von Herzen Danke ich *Daniel* und meiner Tochter *Mina Clementine*, dem wohl schönsten Grund für eine Verzögerung bei der Fertigstellung dieser Arbeit.

CURRICULUM VITAE

PUBLIKATIONEN

PUBLIKATIONEN

PEER-REVIEWED:

Bendixen US, Jauker F, Wolters V, Warzecha D, Diekötter T (eingereicht) Increased spatial connectivity of sown wildflower strips boosts their benefits to biodiversity.

Warzecha D, Diekötter T, Wolters V, Jauker F (2021) Spatial configuration and landscape context of wildflower areas determine their benefits to pollinator α- and β-diversity. Basic and Applied Ecology 56: 335–344.

Warzecha D, Diekötter T, Wolters V, Jauker F (2018) Attractiveness of wild-flower mixtures for wild bees and hoverflies depends on some key plant species. Insect Conservation and Diversity 11: 32–41.

Hoffmann U S, Jauker F, Lanzen J, Warzecha D, Wolters V, Diekötter T (2018) Prey-dependent benefits of sown wildflower strips on solitary wasps in agroecosystems. Insect Conservation and Diversity 11: 42–49.

Grass I, Albrecht J, Jauker F, Diekötter T, Warzecha D, Wolters V, Farwig N (2016) Much more than bees – Wildflower plantings support highly diverse flower-visitor communities from complex to structurally simple agricultural landscapes. Agriculture, Ecosystems & Environment 225: 45–53.

Warzecha D, Diekötter T, Wolters V, Jauker F (2016) Intraspecific body size increases with habitat fragmentation in wild bee pollinators. Landscape Ecology 31: 1449–1455.

ANDERE:

Warzecha D (2021) Möglichkeiten und Grenzen der Beteiligung von Bürgern und Bürgerinnen bei der Erfassung von Insektendaten – Erfahrungsberichte aus dem Bereich der Stechimmenforschung. Bundesamt für Naturschutz: Citizen Science und Insekten – Welchen Beitrag kann bürgerschaftliches Engagement für das Insektenmonitoring leisten? Dokumentation des gleichnamigen Workshops. BfN-Skripten.

Bauer T, Warzecha D, Höfer H, Verhaagh M (2019) Stadt.Wiesen.Mensch. - Natur und Biodiversität vor der eigenen Haustür. Natur im Museum 9: 101–104.

Frommer U, Tischendorf S, Flügel H-J unter Mitarbeit von Dorow WHO, Warzecha D (2017) Kommentierte Rote Liste der „Dolchwespenartigen" Hessens. – Hess. Min. f. Umwelt, Klimaschutz, Landwirtschaft und Verbraucherschutz 77 S., Wiesbaden.

Warzecha D, Frommer U, Wolters V (2016) Nachweise der Furchenbiene *Lasioglossum pauperatum* (Brullé, 1832) aus der Region Marburg-Biedenkopf in Hessen (Hymenoptera, Apidae). – Hessische Faunistische Briefe 35 (1/3): 41–47.

Warzecha D, Diehl E (2015) Der Feldentomologe, (k)eine aussterbende Species. Nachrichten der Gesellschaft für Ökologie 45(1): 6–7.

KONFERENZBEITRÄGE:

Warzecha D, Bauer T, Verhaag M, Jauker F (2017) Bees in the city – The role of relict populations and connectivity for wild bees in urban green spaces. Ecology Across Borders, Ghent 2017 – Poster

Warzecha D, Diekötter T, Wolters V, Jauker F (2016) Pollinator communities can be effectively supported by seed mixtures with only few attractive plant species. Jahrestagung der Gesellschaft für Ökologie 46 – Vortrag

Warzecha D, Diekötter T, Jauker F, Wolters V (2015) Benefits of flowering fields to pollinators in relation to landscape context. Jahrestagung der Gesellschaft für Ökologie 45 – Vortrag

EIDESSTAATLICHE ERKLÄRUNG

EIDESSTAATLICHE ERKLÄRUNG:

Ich erkläre: Ich habe die vorgelegte Dissertation selbstständig und ohne unerlaubte fremde Hilfe und nur mit den Hilfen angefertigt, die ich in der Dissertation angegeben habe. Alle Textstellen, die wörtlich oder sinngemäß aus veröffentlichten Schriften entnommen sind, und alle Angaben, die auf mündlichen Auskünften beruhen, sind als solche kenntlich gemacht. Bei den von mir durchgeführten und in der Dissertation erwähnten Untersuchungen habe ich die Grundsätze guter wissenschaftlicher Praxis, wie sie in der „Satzung der Justus-Liebig-Universität Gießen zur Sicherung guter wissenschaftlicher Praxis“ niedergelegt sind, eingehalten.

____________________________	____________________________
(Daniela Warzecha)	Ort, Datum