Landsc Ecol (2025) 40:19
https://doi.org/10.1007/s10980-024-02027-3

REVIEW ARTICLE

Crop diversification for pollinator conservation

Thijs P. M. Fijen · Maxime Eeraerts · Julia Osterman · Nicole Beyer · Annika Hass · Ola Lundin · Catrin Westphal

Received: 27 June 2024 / Accepted: 16 December 2024

Abstract
Context Intensive agriculture drives insect decline impacting insect-mediated ecosystem services that support production. Crop diversification shows promise in increasing crop productivity and enhancing ecosystem services, however, the impact on biodiversity conservation, particularly of pollinators, is unclear.
Objectives Here, we synthesize the mechanisms and current evidence base of how increasing the spatial and temporal diversity of crops within and across agricultural fields can benefit pollinator biodiversity.
Methods We focus on research in the highly intensified agricultural regions, in Western Europe and North America, from which we know a lot about pollinator decline, but use inspiration from tropical regions.
Results We find that higher crop diversity, with sequentially flowering cultivars, intercropping practices, and a larger coverage of flowering crops, for example through integrating the cultivation of forgotten, novel, and woody crops increases flower resource availability throughout the active flight period of pollinators. All practices can increase landscape heterogeneity, which is further enhanced by decreasing field sizes. As a result, the functional connectivity increases, which improves the flower accessibility within the foraging ranges of pollinators.
Conclusions Our review highlights the potential benefit of various crop diversification measures for

Collection: Effects of agricultural landscapes on biodiversity, ecosystem services, and yield.

T. P. M. Fijen (✉)
Plant Ecology and Nature Conservation Group, Department of Environmental Sciences, Wageningen University & Research, Wageningen, The Netherlands
e-mail: thijs.fijen@wur.nl

M. Eeraerts
Forest and Nature Lab, Department of Environment, Ghent University, 9090 Melle-Gontrode, Belgium

J. Osterman
Nature Conservation and Landscape Ecology, University of Freiburg, 79106 Freiburg, Germany

J. Osterman
Department of Biological and Environmental Sciences, University of Gothenburg, 413 90 Gothenburg, Sweden

J. Osterman
Gothenburg Global Biodiversity Centre, University of Gothenburg, 431 90 Gothenburg, Sweden

N. Beyer · A. Hass · C. Westphal
Functional Agrobiodiversity & Agroecology, Department of Crop Sciences, University of Göttingen, Göttingen, Germany

O. Lundin
Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

C. Westphal
Centre of Biodiversity and Sustainable Land Use (CBL), University of Göttingen, 37077 Göttingen, Germany

Published online: 11 January 2025

supporting pollinating insects without taking land out of production, as well as the limitations, including that only a subset of pollinator species may benefit. Empirical evidence suggest that diversification practices could benefit pollinators, but landscape-wide studies are needed to properly evaluate the true potential of crop diversification for pollinator conservation as part of the solution for bending the curve of pollinator decline.

Keywords Agriculture · Biodiversity conservation · Crop diversity · Flower resources · Hoverflies · Landscape diversity · Wild bees

Introduction

Agricultural intensification and landscape simplification are among the main drivers of insect biodiversity decline within agricultural landscapes (Goulson 2021; Priyadarshana et al. 2024). Yet, crop production benefits from insect-mediated ecosystem services, such as natural pest control and crop pollination (Kleijn et al. 2019). Diversifying agricultural systems could increase ecosystem service delivery, yield stability and resource use efficiency (Tamburini et al. 2020). Establishing non-crop habitats like buffer strips, wildflower strips and high-quality landscape features is considered essential for biodiversity conservation (Batáry et al. 2015; Pe'er et al. 2017), but uptake of these measures depends largely on subsidies, and is relatively low because they take land out of production (Pe'er et al. 2017; Kleijn et al. 2019). Instead, crop diversification might be a more acceptable option to support biodiversity and crop productivity (Kovacs-Hostyanszki et al. 2017). Here, we define crop diversification as increasing the spatial and temporal diversity of crops within and across agricultural fields, compared to specialized and simplified cropping systems (Hufnagel et al. 2020). Indeed, there is growing evidence that diversification practices, such as intercropping or wider crop rotation, can increase crop yield, and multiple ecosystem services supporting crop yield, such as soil fertility, nutrient cycling and weed, pest and disease control (Tamburini et al. 2020). However, it is unclear whether these crop diversification practices also have the potential to halt or reverse biodiversity decline in agricultural landscapes. Specifically, there is a crucial knowledge gap on how crop diversification affects insect pollinator conservation (Tamburini et al. 2020; Beillouin et al. 2021).

Over several decades, agricultural landscapes in Europe and North America have changed drastically from diverse landscapes with small-scaled fields and many natural elements, to landscapes with relatively large-scaled fields of intensively managed monocultures, resulting in substantial habitat loss and landscape homogenization (Batary et al. 2017; Goulson 2021; Hemberger et al. 2021). As a result, flower resource availability and continuity is greatly reduced (Goulson 2021). The remaining flowers are scattered widely in the landscape, making large parts of the landscape unsuitable for most pollinators. If crop diversification practices involve adding flowers (e.g. through flowering crops, temporary grasslands with flowers, or weeds), nesting sites, or improve the accessibility of resources (i.e. reduce the distance between reproduction and foraging sites; including increased landscape heterogeneity), these practices have the potential to reverse the negative pollinator trends (Raderschall et al. 2021). For example, flowering crops provide ample food resources throughout their short flowering period, thereby supporting pollinator abundance and diversity (Holzschuh et al. 2013; Dainese et al. 2018), population growth (Westphal et al. 2003, 2009; Schweiger et al. 2022) and sometimes reproduction (Rundlöf et al. 2014).

Crop diversification has the largest conservation potential for those pollinators that visit crops, but other species can benefit too. Only a small proportion of all pollinators is expected to visit crops (Senapathi et al. 2015). A field study in Italy showed that about 10% of the local pollinator species pool will visit any flowering crop, and cumulatively, 36% of all pollinator species encountered in non-crop areas in the study area were also observed on flowering crops (Martínez-Núñez et al. 2022). With increasing crop diversity, this percentage will most certainly increase (Martins et al. 2018; Winfree et al. 2018). On top of that, crop diversification measures that additionally increase the amount of semi-natural habitat (e.g. non-productive margins between fields) will also benefit non-crop pollinators (Sutter et al. 2017; Fijen et al. 2019). Furthermore, pollinator populations in agricultural landscapes usually consist of relatively common species (Kleijn et al. 2015), but it is exactly those species that are declining the most (van Klink et al. 2024) and therefore need supporting interventions as these species often contribute considerably to crop pollination (Kleijn et al. 2015).

Here, we qualitatively review the literature on the emerging research field of how crop diversification can promote pollinator conservation, and highlight research opportunities to better understand the benefits of crop diversification practices to insect pollinators (notably wild bees and hoverflies). Such insights can help target research agendas, and inform policies (e.g. EU Pollinator Initiative, or U.S.A. Conservation Reserve Program) on which crop diversification measures are most beneficial for pollinator conservation. We focus mainly on research conducted in Europe and North America, from which we know a lot about pollinator decline (Wagner 2020). More specifically we focus on Western Europe, because Eastern Europe is a greatly understudied region. Yet, we use additional examples from tropical regions, where there is a strong history in crop diversification measures (Altieri 2013).

Four main mechanisms through which crop diversification can support pollinators

Crop diversification increases *flower resource availability* if flowering crops are added [e.g., fruit, oil or leguminous crops, flowering temporary grassland; (Hufnagel et al. 2020); Fig. 1]. Therefore increased flower resource availability is a main mechanism through which crop diversification can contribute to enhanced pollinator conservation (Table 1). The most abundant insect pollinator groups in intensified agricultural systems in Europe and North America are bees and hoverflies (Rader et al. 2016). Both groups are highly diverse and show large differences in life history. Yet, a shared trait is their usage of flowers for nectar for self-maintenance in the adult stage, and bees also collect pollen for their brood (Westrich 1996; Rotheray and Gilbert 2011). Hoverflies can

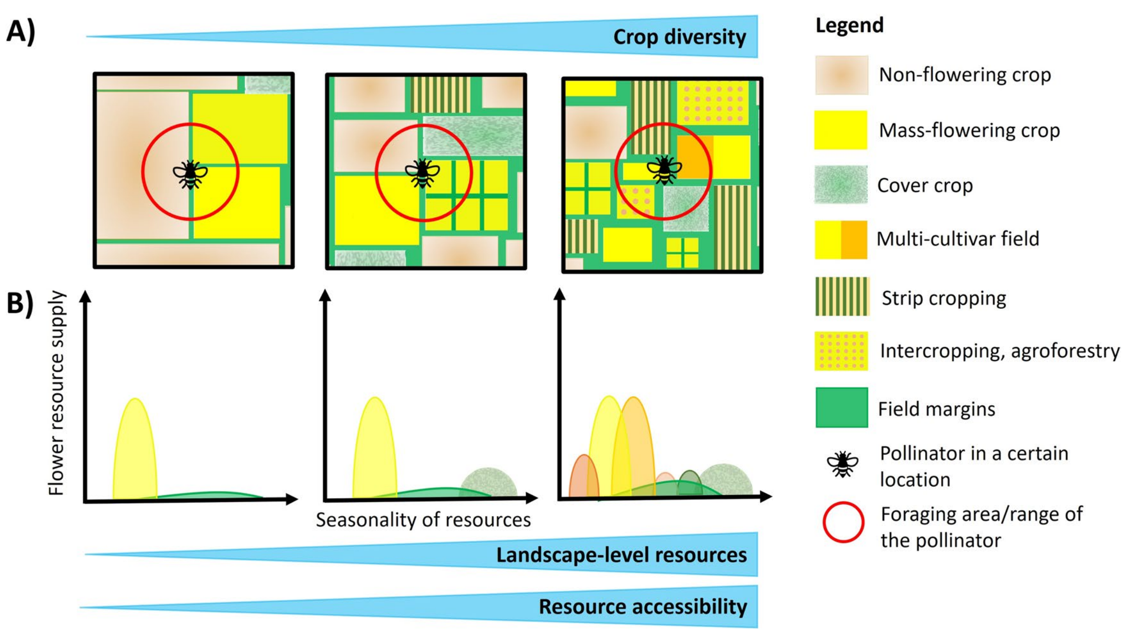

Fig. 1 Schematic figure of increasing spatial and temporal resource availability and accessibility at the landscape-scale with increasing crop diversification practices (i.e., going from left to right). **A** Landscapes with increasing uptake of different crop diversification practices. In these hypothetical landscapes, pollinators can extract resources within their foraging range. **B** The corresponding effect of diversification practices on the flower resource abundance, diversity and continuity throughout time within the pollinators' foraging range, which is expected to benefit pollinator populations. Smaller crop fields also lead to higher landscape functional connectivity, and when non-productive field margins increase, also enhanced nesting habitat availability

Table 1 Overview of the crop diversification practices and how they would contribute to the mechanisms that would lead to increased pollinator conservation

Diversification practice	Increased flower availability	Increased flower resource continuity	Increased flower accessibility within foraging range (i.e. flight distance reduced)	Increased landscape functional connectivity (i.e. permeability of the landscape)
Sequential crop cultivar flowering	±	+++	±	±
Intercropping practices	+++	+/++	++	±
Flowering cover crops	+/++	+	±	±
Re-introducing forgotten crops	+++	+	±	±
Introducing novel crops	++	+	±	±
Introducing woody crops	++	++	±	++
Reducing crop field size	+	±	+++	+++

Effects are evaluated and qualitatively scored based on the empirical evidence found in the literature (+ somewhat positive, ++ positive, +++ strongly positive, ± neutral)

additionally benefit from non-flowering crops for larval food resources (e.g. aphids or decaying organic matter) and oviposition sites (Rotheray and Gilbert 2011). As each crop species has a specific (flower) morphology and phenology, they can benefit different pollinator species by providing additional resources (e.g. flowers, nesting and oviposition sites), thereby complementing the resources provided by pre-existing non-crop habitat (Mallinger et al. 2016; Martínez-Núñez et al. 2022).

Another main mechanism of increased diversity of flowering crops is an expected increased *flower resource continuity* at the landscape scale (Fig. 1). A longer food supply can substantially extend the longevity of hoverflies (Pinheiro et al. 2013), but effects on wild bees are less clear (Straka et al. 2014; Malfi et al. 2019). Two recent empirical studies using reared colonies of bumblebees indicate that gaps between flower resource pulses can have negative effects on reproductive outputs (Hemberger et al. 2022; Schweiger et al. 2022). However, landscape studies on the explicit effect of sequentially flowering crops on wild pollinator populations are virtually lacking (but see Martins et al. 2018; Hemberger et al. 2023), and effects of landscape-scale crop diversity on pollinator diversity are ambiguous (Mallinger et al. 2016; Martínez-Núñez et al. 2022). Future landscape-scale studies should be specifically designed to investigate the effect of enhanced crop diversification on resource complementarity and continuity, and, subsequently, on pollinator populations. With increasing crop diversification, we expect to have an enhanced spatio-temporal availability and continuity of flower resources at the landscape scale (Fig. 1), which is particularly important to suit more pollinator species, and the social species (mainly European honeybees *Apis mellifera*, and bumblebees *Bombus* sp.) that build up colonies during the year (Bishop et al. 2024).

Crop diversification practices may also enhance the spatial *availability of flower resources within the foraging ranges of pollinators* (Hemberger et al. 2022) if field sizes are reduced (Fig. 1). Reduced field sizes in diversified farming systems can be expected through the introduction of specific practices, such as intercropping, or splitting of fields to grow more crops in the same area. This is specifically relevant for wild bees because they are central place foragers with their nests typically located outside agricultural fields, requiring them to find food within their foraging range. Wild bees can have limited foraging ranges of less than a hundred meters (Greenleaf et al. 2007), and even species that can fly further have better reproduction success if food availability is higher close by (Ganser et al. 2021).

In addition to increasing the resource availability within pollinator foraging ranges, higher crop diversity and measures that reduce field sizes are promising spatial diversification measures to boost pollinator conservation through *increased landscape functional connectivity*. Large-scale, multi-taxa studies aiming at disentangling the effects of composition and configuration found that reducing field size at the landscape scale enhances multi-taxa diversity including bees, hoverflies and butterflies

(Priyadarshana et al. 2024; Sirami et al. 2019). More crop edges can benefit functional connectivity for pollinators even without any addition of non-crop habitat. For example, a phytometer experiment showed that pollen transfer between cornflowers (*Centaurea cyanus*) was four times higher along crop-crop edges than from the crop edge into a cereal crop, and along a crop-semi-natural habitat edge, and the effect was stronger when the crops were structurally contrasting (Hass et al. 2018). This shows that increasing crop-crop edge density can facilitate the movement of pollinators, thereby increasing the functional connectivity. Although not being a crop diversification practice per se, more heterogeneous landscapes often have a larger amount of pollinator-attractive linear structures at field edges, like grassy margins, headlands or hedgerows (Fig. 1). These structures also increase landscape connectivity and therefore pollinator movement across the landscape (Hass et al. 2018), which can be especially beneficial for pollinators specialized on non-crop resources, with low dispersal ability, or free-ranging species (e.g. hoverflies). The features themselves also provide complementary food and nesting/oviposition sites for pollinators compared to crop resources (Eeraerts et al. 2021; Martínez-Núñez et al. 2022).

Crop diversification practices

Below we will discuss crop diversification practices that are increasingly being promoted in intensive agricultural landscapes, and how they contribute to the four main mechanisms that support pollinator conservation (Table 1).

Increasing cultivar diversity

In most intensive cropping systems, almost all field crops consist of a single cultivar (Hufnagel et al. 2020). Yet, especially in fruit crops, it can be common to combine several cultivars to extend the production period, to facilitate cross-pollination or both (MacInnis and Forrest 2019; Eeraerts 2022; Anders et al. 2023). Growing multiple cultivars could extend the flowering period of a crop (i.e. higher resource continuity) or provide cultivars with variable flower traits (Kirsch et al. 2023). Different pollinator species can be attracted to different cultivars because they vary in flower morphology (Courcelles et al. 2013; Ferguson et al. 2021), floral rewards (Estravis-Barcala et al. 2021) and floral attractants (Ceuppens et al. 2015; Prasifka et al. 2018). This could result in a higher overall species richness of pollinators in fields with multiple compared to single cultivars. Only few studies investigated the effects of different cultivars on pollinator communities, finding complementary pollinator communities visiting different cultivars in sunflower (*Helianthus annuus*) and sweet cherry (*Prunus avium*; (Ferguson et al. 2021; Eeraerts 2022)), but not in faba bean (*Vicia faba*; Kirsch et al. (2023)). Yet, studies on this topic with adequate site replication, and that explore the mechanisms are lacking. Expanding the concept of multi-cultivar crops to more field crops could yield larger benefits to pollinators, but depending on the production system, it might be more challenging for farmers to harvest and sell cultivar mixtures (Chabert et al. 2024).

Intercropping practices

Rather than having fields of single crops, more than one crop could be grown in a field simultaneously, i.e. intercropping (Vandermeer 1992; Hufnagel et al. 2020). The spatial degree of crop mixing can vary, from strip or pixel cropping where each crop is grown in alternating strips or small-scale plots (e.g. 1 m^2), to mixed intercropping where crops are freely mixed without any fixed spatial arrangement. Likewise, the temporal degree of mixing can vary from synchronous establishment and harvest, to relay cropping where a second crop is established during growth of the first crop (i.e., undersowing; Gardarin et al. (2022)). The effect of these practices on pollinator conservation has only recently gained attention. Intercropping at the (experimental) field level increases pollinator densities relative to the sole non-flowering crop when harvestable flowering crops (Hüber et al. 2022; Brandmeier et al. 2023), or cover crops are added (Norris et al. 2018; Boetzl et al. 2023), or when two or more flowering crops are combined (Dingha et al. 2021; Grof-Tisza et al. 2024). Furthermore, a study at the experimental plot level found that faba bean intercropped with wheat (*Triticum aestivum*; grown in alternating rows) had similar pollinator densities as faba bean sole crops, even though the faba bean sowing density was reduced by 50% when intercropped (Kirsch et al. 2023). This results suggests that intercropping at the field scale can translate to disproportionate benefits for pollinators at the landscape scale when intercropping flowering crops in 50–50% coverage on all fields, compared to growing 50% of the landscape with flowering sole crops.

Flowering cover crops

Resources for pollinators in agricultural landscapes can be enhanced through pollinator-attractive cover crops (Mallinger et al. 2019). As cover crops are already regularly implemented by farmers (Pe'er et al. 2017; Kleijn et al. 2019), flowering cover crops can serve as a tool for promoting pollinators. Red clover (*Trifolium pratense*) might be such a high-potential flowering cover crop, especially for bumblebees (*Bombus* spp.), as it provides high quality food for hibernating queens (Riggi et al. 2021; Cole et al. 2022). Summer cover crops, which are more common in arid areas in North America and in the Mediterranean in Europe, have shown great potential for pollinators (Mallinger et al. 2019), but the benefit of winter cover crops for pollinators is clearly understudied (Shackelford et al. 2019). In temperate regions, many winter cover crops do not come into flowering, or only very early or late in the season, limiting the potential benefits for pollinators. Strips of undestroyed winter cover crops in spring sown crop fields seem to be effective for pollinator conservation (Triquet et al. 2024), but farmers did not prefer to apply this (Kleijn et al. 2019). One option to align cover crop flowering with the phenology of pollinators in temperate regions could be to establish cover crops as living mulches in spring sown crops.

Re-introducing forgotten crops

The large-scale adoption of synthetic fertilizer in intensive agriculture has strongly reduced the number of crops in the crop rotation, especially the cultivation of many nitrogen-fixing leguminous crops (Zander et al. 2016; Hemberger et al. 2021). In parallel, pollinators that prefer, or specialize on these lost crops also show the strongest declines (Scheper et al. 2014). For example, a retrospective pollen-analysis showed that most of the threatened, once common, bumblebee species made extensive use of red clover, vetch (*Vicia* sp.), and lupins (*Lupinus* sp.; Kleijn and Raemakers (2008)), which used to be commonly cultivated, mainly as fodder or cover crops (Zander et al. 2016). Some of these forgotten crops (Padulosi et al. 2002), both leguminous and non-leguminous, are still being consumed (e.g. buckwheat (*Fagopyrus esculentum*), lupins, camelina (*Camelina sativa*), and black chokeberry (*Aronia melanocarpa*)), or can be used again or more extensively by applying new technologies (e.g. food protein extraction from grass and clover). Reintroducing them locally, could have potential benefits for pollinators (Fijen et al. 2022). However, very little is known about the specific benefits of (re-)introducing crops for pollinator biodiversity (Fijen et al. 2022; Bishop et al. 2025), mainly because of logistic and practical bottlenecks during cultivation. A first step would be to characterize the local pollinator communities visiting these crops (Fijen et al. 2021, 2022), so that we can better predict which species could potentially benefit from re-introducing forgotten crops. A recent study introduced 1ha lupin fields to landscapes without history of lupin cultivation, and compared measured pollinator populations with agricultural landscapes without lupin. They found that lupin cultivation significantly increased bumblebee populations (the main lupin-pollinators) after bloom, but effects did not carry over to the second year (Bishop et al. 2025). This suggests that while reintroducing a single crop has the potential to boost pollinator populations, more additional conservation measures are needed to sustainably benefit pollinators.

Novel crops

Nowadays, many of the most important crops are already cultivated outside their region of origin (Khoury et al. 2016), and there is still potential for introduction of novel crops. Novel crops can be wild plants that are introduced or bred to become established crops, or crops originating from other geographical regions (Brown and Cunningham 2019). As only a small fraction of possible useful plants are currently grown as crops there is also great potential to diversify cropping systems with new crops through crop domestication (Krug et al. 2023). One example of a novel crop that support pollinators is the cup plant (*Silphium perfoliatum* L.), which now can be cultivated commercially as an alternative energy crop, providing more pollen and nectar than maize (*Zea mays*; Mueller et al. (2020)). Such relatively recently domesticated crops can aid the population persistence and range expansion of their associated pollinators when cultivated in or close to the crops' native range. For example, the domestication of squash (*Cucurbita pepo*) from Mexico to the whole of northern America has facilitated the range expansion of the squash bee (*Peponapis pruinosa*; Lopez-Uribe et al. (2016)). However, introducing non-native crops might not always contribute much to pollinator conservation, as they are visited by fewer bee genera than within their region of origin (Brown and Cunningham 2019), and could become invasive and have net-negative effects on pollinators due to outcompeting the natural flowering resources (Ramula and Sorvari 2017). Non-native novel crops therefore have the potential to benefit pollinator conservation but need careful consideration. Crops that attract generalist pollinators or have their origin relatively close-by are probably most promising.

Woody and perennial crops

Many agronomically important flowering crops are perennial trees (e.g., almond *Prunus amygdalus*, apple *Malus domesticus*), shrubs (e.g. blueberry *Vaccinium* sp., raspberry *Rubus idaeus*), or forbs (e.g. strawberries *Fragaria x ananassa*). They provide important food sources, especially for pollinator species that are active early in the year (Mallinger et al. 2016; Bänsch et al. 2020; Eeraerts et al. 2021). Additionally, in perennial crops the soil is less often disturbed compared to field crops, which most likely increases nesting site availability for pollinators (Antoine and Forrest 2021). Old branches of shrubs, like bramble and raspberry, can also provide nesting sites for cavity nesting bees (Coates et al. 2022), which are otherwise mainly found in semi-natural habitats (Eeraerts et al. 2021).

Interspersing woody crops with non-woody crops or livestock (i.e. agroforestry) therefore can aid pollinator conservation. This agricultural system has strong roots in the tropics, but has only recently gained attention in temperate regions. A recent review found mixed effects of agroforestry on pollinator diversity (Centeno-Alvarado et al. 2023), resulting potentially from a range of different types of agroforestry. A meta-analysis dominated by Mediterranean studies in Europe showed that arthropod biodiversity (including pollinators) in silvo-arable systems (cropland + trees) was higher compared to cropland, but not for silvo-pastoral (grasslands + trees) agroforestry (Mupepele et al. 2021). For example, a field study with potted California poppy showed that sites with agroforestry had higher bee abundance in silvo-arable systems compared to monocrops, and therefore had a higher seed set (Varah et al. 2020). Although relatively little is known in temperate regions (Graham and Nassauer 2019; Varah et al. 2020), it can be expected that woody plants in agroforestry systems benefit pollinators, as about 50% of the pollen collected by bees come from woody plant species (Wood et al. 2018; Bertrand et al. 2019; Schweiger et al. 2022).

Reducing field size

Reducing field sizes does not does not only increase spatial availability of floral resources and landscape functional connectivity (see mechanisms through which crop diversification can support pollinators), but may additionally increase the amount of floral resources available for pollinators. For example, diversity and density of flowering weed species is higher in field borders compared to the centers (Alignier et al. 2020) and therefore enhanced in landscapes with higher field border density. Species richness of weeds additionally increases in field interiors with the reduction of landscape-scale field size (Alignier et al. 2020). This indicates that small-scaled landscapes enable weeds to reach higher overall cover and probably provide more flower resources across the landscape and throughout the season, and that reducing field sizes can be an effective measure to enhance pollinator conservation as weeds are essential food resources for many pollinator species (Balfour and Ratnieks 2022). Large scale specialization of intensive agricultural systems has drastically increased field sizes at the expense of semi-natural habitats (Batary et al. 2017), because it makes agricultural management more efficient. Consequently, policy support will be needed for reducing field sizes and we discuss this further in the next section.

Future challenges in crop diversification for pollinator conservation

Many crop diversification practices are in essence 'old farming practices' that need to find a place in modern times. There are still many barriers that slow down uptake, and they are the focus of many other papers (Vanbergen et al. 2020; Carlisle et al. 2022; Brannan et al. 2023). Nevertheless, there are a few outstanding barriers related to the crop diversification practices for pollinator conservation that we would like to highlight. A lack of crop management knowledge and seed availability is a relatively easy problem to overcome, but the highly specialized character of intensive agricultural areas (for example the 'corn belt' in USA; Green et al. (2018)) is limiting crop diversification uptake, unless these practices are legislated, subsidized, or recognized as beneficial to the farmer (e.g. cover crops). Many crop diversification practices require access to special machinery for crop management or post-harvest processing, or adjustments to crop protection practices. Smaller fields may, for example, lead to increased management costs, as well as increased opportunity costs if non-crop field margins are introduced (Kirchweger et al. 2020). These costs may not always be fully compensated by benefits through enhanced pollination services (Scheper et al. 2023), or only on the longer term because pollinator populations need time to build up (Blaauw and Isaacs 2014; Morandin et al. 2016). Therefore, these issues require technological adaptations, and higher farmer rewards (Scheper et al. 2023), because crop diversification can benefit society as a whole through public benefits such as water conservation, soil preservation and biodiversity conservation (Tamburini et al. 2020).

Implementing crop diversification with flowering crops that depend on crop pollinators also requires careful spatial and multi-year planning to increase uptake by farmers. When a single crop covers large areas of the landscape, crop pollinators are dispersed across flowering fields, resulting in reduced pollinator densities and dilution of pollination services (Holzschuh et al. 2016; Eeraerts et al. 2017; Grab et al. 2019; Lajos et al. 2021; Riggi et al. 2024). This pollinator dilution could limit the crop yields to a point where the yield is not high enough to be profitable. Such effects could diminish over the years (Magrach et al. 2023) because pollinator populations need to build up (Beyer et al. 2021a; Neira et al. 2024). Indeed, inn a space-for-time study, a longer history of flowering crop cultivation increased the density of crop pollinators, suggesting that the crop pollinator population grows over the years (Beyer et al. 2021b). Furthermore, different crop species that flower at the same time might compete for the same pollinator communities: flowering apple orchards have shown to draw away pollinators from nearby strawberry fields, reducing strawberry yields (Grab et al. 2017). Two recent studies have shown that such effects largely depend on the crop-crop combination and differ between functional pollinator groups (Bänsch et al. 2020; Osterman et al. 2021). The drivers of these patterns are not entirely clear, but it is likely that sociality (social bees tend to prefer high resource density; Rollin et al. (2013)), species-specific floral or nutritional preferences (Petanidou et al. 2006), as well as displacement of pollinators play a role (Grab et al. 2017; Bänsch et al. 2020; Osterman et al. 2021).

Displacement of pollinators can also be an indication that there is resource competition between managed bees, such as European honeybees (*Apis mellifera*) and mason bees (*Osmia* sp; (LeCroy et al. 2020)), and wild pollinators. There is ample evidence that managed honeybees can outcompete wild pollinators for flower resources (Henry and Rodet 2018; Wignall et al. 2020; Bommarco et al. 2021; Page and Williams 2023) with negative effects on pollination (Magrach et al. 2017; Page and Williams 2023). In general, competition between honeybees and wild bees is expected when flowering resources are scarce (Herbertsson et al. 2016). By increasing flowering resource availability and continuity through crop diversification, a reduction in competition can be expected. Mass-flowering crops offer so abundant floral resources, that pollinator competition for resources seems unlikely to happen (but see (Lindstrom et al. 2016)). This suggests that wild pollinators can benefit from mass-flowering crops, especially when honeybee hive placement is limited (Fijen et al. 2022). Furthermore, hives need to be removed after flowering of the crop, because they otherwise might undo any benefits that the mass-flowering crop had on wild pollinators (Magrach et al. 2017). However, when crops are not flowering,

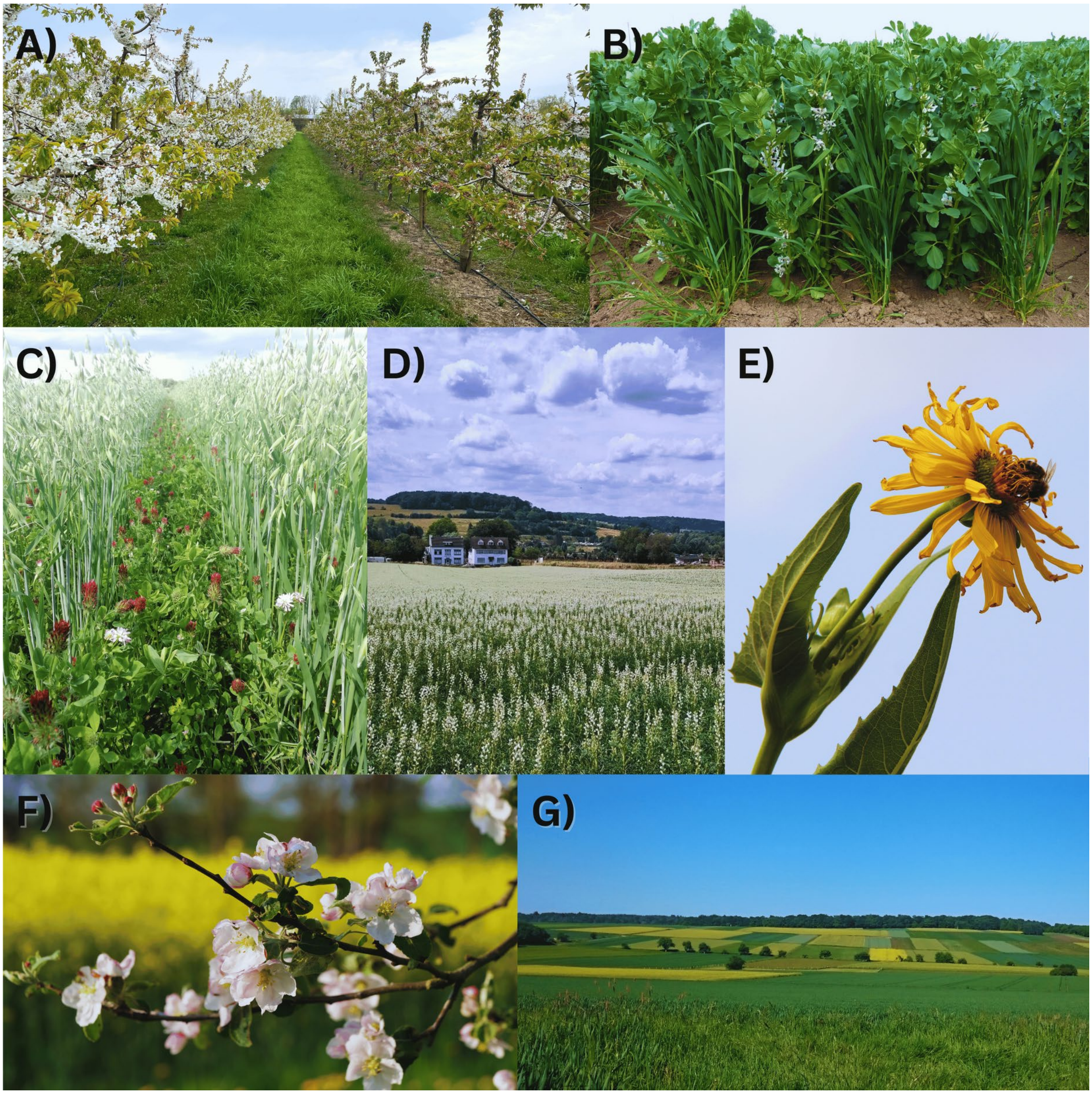

Fig. 2 Examples of crop diversification practices. **A** Cherry orchard with the two sequentially flowering cultivars Regina and Kordia, extending the availability of flower resources (photo: Wiebke Kämper); **B** faba bean-winter wheat intercropping (photo: Horst Steinmann) and **C** oats undersown with clovers, both increasing the surface with flowering crops without compromising crop yield. **D** Narrow-leaved lupin (*Lupinus angustifolius*) as an example of a forgotten crop. **E** The novel flowering crop cup plant (*Silphium perfoliatum*; photo: Lea Stringl). **F** Flowering apple trees next to flowering oilseed rape, illustrating the complementarity of woody crops to annual crops. **G** A landscape with high landscape heterogeneity and functional connectivity

there is the risk that the increasing crop pollinator populations can displace wild pollinators on wild plants too, particularly by some dominant bumblebee species such as buff-tailed bumblebees (Wignall et al. 2020).

Increased pesticide exposure could be a barrier to pollinator conservation through crop diversification and could act as an ecological trap. Pesticide use is likely to be reduced in diversified agricultural landscapes (Nicholson and Williams 2021), but it still poses both direct (lethal and sub-lethal) and indirect (e.g. loss of flowering plants through herbicide use) risks for pollinators (Goulson 2021; Wintermantel et al. 2022). Direct effects of pesticides are less worrisome if pollinators have access to high-quality food resources (Wintermantel et al. 2022), which additionally suggests that if crop diversification practices enhance high-quality food resource availability, it is likely that crop diversification results in lower negative effects of pesticide exposure (Rundlöf and Lundin 2019).

Conclusions

Crop diversification has gained momentum because of the many benefits it can have for farmers and the environment (Tamburini et al. 2020; Beillouin et al. 2021; Nicholson and Williams 2021). Crop fields are not as stable and diverse as natural habitats, and cannot replace the importance of semi-natural habitat for pollinator conservation (Batáry et al. 2015; Eeraerts 2023; Fijen et al. 2024), we highlight the potential of crop diversification practices as an additional pollinator conservation measure (Table 1; Fig. 2). Crop diversification can enhance spatio-temporal flower resource availability, continuity and accessibility without too drastic adjustments for farmers, while also improving the landscape heterogeneity and functional connectivity for pollinators. With large changes ahead in the agricultural system driven by climate change and the need for a more plant-based diet, it is essential to design long-term studies on how crop diversification can benefit wild pollinators. Outstanding questions include what crops to diversify with, and how landscape context and farming intensity can modulate the effect on crop diversification practices on wild pollinators. Combined effects of multiple crop diversification practices on wild pollinators are also virtually unknown. Crop diversification with both agricultural production and pollinator conservation in mind can provide synergies without taking a substantial part of land out of production: after all, farmers need pollinators for high yields of many crops (Turo et al. 2024), and pollinators need flowers to survive. If well-adjusted to each other, this can lead to a positive feedback loop where flowering crop cultivation boosts the pollinator populations, and these pollinators in turn boost crop yields.

Author contributions T.P.M.F., M.E, J.O., N.B., A.H., O.L., C.W. conceived the ideas and designed methodology; T.P.M.F. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Funding TPMF was funded through a private donor to University Fund Wageningen. JO was supported by the Carl Trygger foundation (CTS 21:1757), European Union Horizon Europe research and innovation programme project RestPoll (Grant Agreement No. 101082102), WildPosh (Grant Agreement No. 101135238), and Formas (Grant Nr. 2024-00298). ME was supported as a Flanders Research Foundation postdoctoral fellow (Grant No. 1210723N). OL was supported by Formas (Grant Nr. 2019-01294). CW was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation; Project Number 493487387). This paper was written during the preparations of, and inspired by, the EU Horizon project AGRI4POL (Grant Nr. 101181146).

Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

References

Alignier A, Uroy L, Aviron S (2020) The role of hedgerows in supporting biodiversity and other ecosystem services in intensively managed agricultural landscapes. Reconciling agricultural production with biodiversity conservation. Burleigh Dodds Science Publishing, Sawston, pp 177–204

Altieri MA (2013) Agroecological principles for sustainable agriculture. Agroecological innovations. Routledge, London, pp 40–46

Anders M, Grass I, Linden VMG, Taylor PJ, Westphal C (2023) Smart orchard design improves crop pollination. J Appl Ecol 60(4):624–637

Antoine CM, Forrest JR (2021) Nesting habitat of ground-nesting bees: a review. Ecol Entomol 46(2):143–159

Balfour NJ, Ratnieks FLW (2022) The disproportionate value of "weeds" to pollinators and biodiversity. J Appl Ecol 59(5):1209–1218

Bänsch S, Tscharntke T, Gabriel D, Westphal C, Requier F (2020) Crop pollination services: complementary resource use by social vs solitary bees facing crops with contrasting flower supply. J Appl Ecol 58(3):476–485

Batáry P, Dicks LV, Kleijn D, Sutherland WJ (2015) The role of agri-environment schemes in conservation and environmental management. Conserv Biol 29(4):1006–1016

Batary P, Galle R, Riesch F et al (2017) The former Iron Curtain still drives biodiversity-profit trade-offs in German agriculture. Nat Ecol Evol 1(9):1279–1284

Beillouin D, Ben-Ari T, Malézieux E, Seufert V, Makowski D (2021) Positive but variable effects of crop diversification on biodiversity and ecosystem services. Global Change Biol 27(19):4697–4710

Bertrand C, Eckerter PW, Ammann L et al (2019) Seasonal shifts and complementary use of pollen sources by two bees, a lacewing and a ladybeetle species in European agricultural landscapes. J Appl Ecol 56(11):2431–2442

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

Beyer N, Kirsch F, Gabriel D, Westphal C (2021b) Identity of mass-flowering crops moderates functional trait composition of pollinator communities. Landsc Ecol 36(9):2657–2671

Bishop GA, Fijen TPM, Raemakers I, van Kats RJM, Kleijn D (2024) Bees go up, flowers go down: increased resource limitation from late spring to summer in agricultural landscapes. J Appl Ecol 61(3):431–441

Bishop GA, Kleijn D, Vicente IGPP, Fijen TPM (2025) Mass-flowering lupin has positive, but limited, effect on wild bee conservation in agricultural landscapes. J Appl Ecol in press

Blaauw BR, Isaacs R (2014) Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. J Appl Ecol 51(4):890–898

Boetzl FA, Sundahl AD, Friberg H, Viketoft M, Bergkvist G, Lundin O (2023) Undersowing oats with clovers supports pollinators and suppresses arable weeds without reducing yields. J Appl Ecol 60(4):614–623

Bommarco R, Lindström SAM, Raderschall CA, Gagic V, Lundin O (2021) Flower strips enhance abundance of bumble bee queens and males in landscapes with few honey bee hives. Biol Conserv 263:109363

Brandmeier J, Reininghaus H, Scherber C (2023) Multispecies crop mixtures increase insect biodiversity in an intercropping experiment. Ecol Solut Evid 4(3):e12267

Brannan T, Bickler C, Hansson H, Karley A, Weih M, Manevska-Tasevska G (2023) Overcoming barriers to crop diversification uptake in Europe: a mini review. Front Sustain Food Syst 7:1107700

Brown J, Cunningham SA (2019) Global-scale drivers of crop visitor diversity and the historical development of agriculture. Proc Biol Sci 286(1915):20192096

Carlisle L, Esquivel K, Baur P et al (2022) Organic farmers face persistent barriers to adopting diversification practices in California's Central Coast. Agroecol Sustain Food Syst 46(8):1145–1172

Centeno-Alvarado D, Lopes AV, Arnan X (2023) Fostering pollination through agroforestry: a global review. Agr Ecosyst Environ 351:108478

Ceuppens B, Ameye M, Van Langenhove H, Roldan-Ruiz I, Smagghe G (2015) Characterization of volatiles in strawberry varieties "Elsanta" and "Sonata" and their effect on bumblebee flower visiting. Arthropod-Plant Interact 9(3):281–287

Chabert S, Eeraerts M, DeVetter LW, Borghi M, Mallinger RE (2024) Intraspecific crop diversity for enhanced crop pollination success. A review. Agron Sustain Dev 44(5):1–24

Coates JM, Brown J, Cunningham SA (2022) Wild bees nest in the stems of cultivated Rubus plants and act as effective crop pollinators. Agric Ecosyst Environ 325:107741

Cole LJ, Baddeley JA, Robertson D, Topp CF, Walker RL, Watson CA (2022) Supporting wild pollinators in agricultural landscapes through targeted legume mixtures. Agric Ecosyst Environ 323:107648

Courcelles D, Button L, Elle E (2013) Bee visit rates vary with floral morphology among highbush blueberry cultivars (*V. accinium corymbosum* L.). J Appl Entomol 137(9):693–701

Dainese M, Riedinger V, Holzschuh A, Kleijn D, Scheper J, Steffan-Dewenter I (2018) Managing trap-nesting bees as crop pollinators: spatiotemporal effects of floral resources and antagonists. J Appl Ecol 55(1):195–204

Dingha BN, Omaliko PC, Amoah BA, Jackai LE, Shrestha D (2021) Evaluation of cowpea in an intercropping system as pollinator enhancer for increased crop yield. Sustainability 13(17):9612

Eeraerts M (2022) Increasing wild bee richness and abundance on sequentially flowering cultivars of a pollinator-dependent crop. Agric Ecosyst Environ 325:107745

Eeraerts M (2023) A minimum of 15% semi-natural habitat facilitates adequate wild pollinator visitation to a pollinator-dependent crop. Biol Conserv 278:109887

Eeraerts M, Meeus I, Van Den Berge S, Smagghe G (2017) Landscapes with high intensive fruit cultivation reduce wild pollinator services to sweet cherry. Agr Ecosyst Environ 239:342–348

Eeraerts M, Van den Berge S, Proesmans W, Verheyen K, Smagghe G, Meeus I (2021) Fruit orchards and woody semi-natural habitat provide complementary resources for pollinators in agricultural landscapes. Landsc Ecol 36(5):1377–1390

Estravis-Barcala MC, Palottini F, Macri I, Nery D, Farina WM (2021) Managed honeybees and South American bumblebees exhibit complementary foraging patterns in highbush blueberry. Sci Rep 11(1):8187

Ferguson B, Mallinger RE, Prasifka JR (2021) Bee community composition, but not diversity, is influenced by floret size in cultivated sunflowers. Apidologie 52(6):1210–1222
Fijen TPM, Scheper JA, Boekelo B, Raemakers I, Kleijn D (2019) Effects of landscape complexity on pollinators are moderated by pollinators' association with mass-flowering crops. Proc Biol Sci 286(1900):20190387
Fijen TPM, Morra E, Kleijn D (2021) Pollination increases white and narrow-leaved lupin protein yields but not all crop visitors contribute to pollination. Agric Ecosyst Environ 313:107386
Fijen TPM, van Bodegraven V, Lucassen F (2022) Limited honeybee hive placement balances the trade-off between biodiversity conservation and crop yield of buckwheat cultivation. Basic Appl Ecol 65:28–38
Fijen TPM, Bishop GA, Ganuza C, Scheper J, Kleijn D (2024) Analyzing the relative importance of habitat quantity and quality for boosting pollinator populations in agricultural landscapes. Conserv Biol e14317
Ganser D, Albrecht M, Knop E (2021) Wildflower strips enhance wild bee reproductive success. J Appl Ecol 58(3):486–495
Gardarin A, Celette F, Naudin C et al (2022) Intercropping with service crops provides multiple services in temperate arable systems: a review. Agron Sustain Dev 42(3):39
Goulson D (2021) Silent earth: averting the insect apocalypse. Random House, London
Grab H, Blitzer EJ, Danforth B, Loeb G, Poveda K (2017) Temporally dependent pollinator competition and facilitation with mass flowering crops affects yield in co-blooming crops. Sci Rep 7:45296
Grab H, Branstetter MG, Amon N et al (2019) Agriculturally dominated landscapes reduce bee phylogenetic diversity and pollination services. Science 363(6424):282–284
Graham JB, Nassauer JI (2019) Wild bee abundance in temperate agroforestry landscapes: assessing effects of alley crop composition, landscape configuration, and agroforestry area. Agrofor Syst 93(3):837–850
Green TR, Kipka H, David O, McMaster GS (2018) Where is the USA Corn Belt, and how is it changing? Sci Total Environ 618:1613–1618
Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. Oecologia 153(3):589–596
Grof-Tisza P, Muller MH, Gónzalez-Salas R, Bustos-Segura C, Benrey B (2024) The Mesoamerican milpa agroecosystem fosters greater arthropod diversity compared to monocultures. Agric Ecosyst Environ 372:109074
Hass AL, Kormann UG, Tscharntke T et al (2018) Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. Proc R Soc B 285(1872):20172242
Hemberger J, Crossley MS, Gratton C (2021) Historical decrease in agricultural landscape diversity is associated with shifts in bumble bee species occurrence. Ecol Lett 24(9):1800–1813
Hemberger J, Witynski G, Gratton C (2022) Floral resource continuity boosts bumble bee colony performance relative to variable floral resources. Ecol Entomol 47(4):703–712
Hemberger J, Bernauer OM, Gaines-Day HR, Gratton C (2023) Landscape-scale floral resource discontinuity decreases bumble bee occurrence and alters community composition. Ecol Appl 33(7):e2907
Henry M, Rodet G (2018) Controlling the impact of the managed honeybee on wild bees in protected areas. Sci Rep 8(1):9308
Herbertsson L, Lindström SAM, Rundlöf M, Bornmarco R, Smith HG (2016) Competition between managed honeybees and wild bumblebees depends on landscape context. Basic Appl Ecol 17(7):609–616
Holzschuh A, Dormann CF, Tscharntke T, Steffan-Dewenter I (2013) Mass-flowering crops enhance wild bee abundance. Oecologia 172(2):477–484
Holzschuh A, Dainese M, Gonzalez-Varo JP et al (2016) Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. Ecol Lett 19(10):1228–1236
Hüber C, Zettl F, Hartung J, Müller-Lindenlauf M (2022) The impact of maize-bean intercropping on insect biodiversity. Basic Appl Ecol 61:1–9
Hufnagel J, Reckling M, Ewert F (2020) Diverse approaches to crop diversification in agricultural research. A review. Agron Sustain Dev 40(2):1–17
Khoury CK, Achicanoy HA, Bjorkman AD et al (2016) Origins of food crops connect countries worldwide. Proc R Soc B 283(1832):20160792
Kirchweger S, Clough Y, Kapfer M, Steffan-Dewenter I, Kantelhardt J (2020) Do improved pollination services outweigh farm-economic disadvantages of working in small-structured agricultural landscapes?—Development and application of a bio-economic model. Ecol Econ 169:106535
Kirsch F, Hass AL, Link W, Westphal C (2023) Intercrops as foraging habitats for bees: bees do not prefer sole legume crops over legume-cereal mixtures. Agric Ecosyst Environ 343:108268
Kleijn D, Raemakers I (2008) A retrospective analysis of pollen host plant use by stable and declining bumble bee species. Ecology 89(7):1811–1823
Kleijn D, Winfree R, Bartomeus I et al (2015) Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. Nat Commun 6:7414
Kleijn D, Bommarco R, Fijen TPM, Garibaldi LA, Potts SG, van der Putten WH (2019) Ecological intensification: bridging the gap between science and practice. Trends Ecol Evol 34(2):154–166
Kovacs-Hostyanszki A, Espindola A, Vanbergen AJ, Settele J, Kremen C, Dicks LV (2017) Ecological intensification to mitigate impacts of conventional intensive land use on pollinators and pollination. Ecol Lett 20(5):673–689
KrugVan Tassel DL, Warschefsky EJ AS (2023) The next era of crop domestication starts now. Proc Natl Acad Sci USA 120(14):e2205769120
Lajos K, Samu F, Bihaly ÁD, Fülöp D, Sárospataki M (2021) Landscape structure affects the sunflower visiting frequency of insect pollinators. Sci Rep 11(1):8147
LeCroy KA, Savoy-Burke G, Carr DE, Delaney DA, Roulston TH (2020) Decline of six native mason bee species following the arrival of an exotic congener. Sci Rep 10(1):18745

Lindstrom SA, Herbertsson L, Rundlof M, Bommarco R, Smith HG (2016) Experimental evidence that honeybees depress wild insect densities in a flowering crop. Proc Biol Sci 283:1843

Lopez-Uribe MM, Cane JH, Minckley RL, Danforth BN (2016) Crop domestication facilitated rapid geographical expansion of a specialist pollinator, the squash bee *Peponapis pruinosa*. Proc Biol Sci 283(1833):20160443

MacInnis G, Forrest JRK (2019) Pollination by wild bees yields larger strawberries than pollination by honey bees. J Appl Ecol 56(4):824–832

Magrach A, Gonzalez-Varo JP, Boiffier M, Vila M, Bartomeus I (2017) Honeybee spillover reshuffles pollinator diets and affects plant reproductive success. Nat Ecol Evol 1(9):1299–1307

Magrach A, Giménez-García A, Allen-Perkins A, Garibaldi LA, Bartomeus I (2023) Increasing crop richness and reducing field sizes provide higher yields to pollinator-dependent crops. J Appl Ecol 60(1):77–90

Malfi RL, Crone E, Williams N (2019) Demographic benefits of early season resources for bumble bee (*B. vosnesenskii*) colonies. Oecologia 191(2):377–388

Mallinger RE, Gibbs J, Gratton C (2016) Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods. Landsc Ecol 31(7):1523–1535

Mallinger RE, Franco JG, Prischmann-Voldseth DA, Prasifka JR (2019) Annual cover crops for managed and wild bees: optimal plant mixtures depend on pollinator enhancement goals. Agr Ecosyst Environ 273:107–116

Martínez-Núñez C, Kleijn D, Ganuza C et al (2022) Temporal and spatial heterogeneity of semi-natural habitat, but not crop diversity, is correlated with landscape pollinator richness. J Appl Ecol 59(5):1258–1267

Martins KT, Albert CH, Lechowicz MJ, Gonzalez A (2018) Complementary crops and landscape features sustain wild bee communities. Ecol Appl 28(4):1093–1105

Morandin LA, Long RF, Kremen C (2016) Pest control and pollination cost-benefit analysis of hedgerow restoration in a simplified agricultural landscape. J Econ Entomol 109(3):1020–1027

Mueller AL, Berger CA, Schittenhelm S, Stever-Schoo B, Dauber J (2020) Water availability affects nectar sugar production and insect visitation of the cup plant. J Agron Crop Sci 206(5):529–537

Mupepele AC, Keller M, Dormann CF (2021) European agroforestry has no unequivocal effect on biodiversity: a time-cumulative meta-analysis. BMC Ecol Evol 21(1):193

Neira P, Blanco-Moreno JM, Olave M, Caballero-López B, Sans FX (2024) Effects of agricultural landscape heterogeneity on pollinator visitation rates in Mediterranean oilseed rape. Agr Ecosyst Environ 363:108869

Nicholson CC, Williams NM (2021) Cropland heterogeneity drives frequency and intensity of pesticide use. Environ Res Lett 16(7):074008

Norris SL, Blackshaw RP, Critchley CNR et al (2018) Intercropping flowering plants in maize systems increases pollinator diversity. Agric Entomol 20(2):246–254

Osterman J, Theodorou P, Radzeviciute R, Schnitker P, Paxton RJ (2021) Apple pollination is ensured by wild bees when honey bees are drawn away from orchards by a mass co-flowering crop, oilseed rape. Agr Ecosyst Environ 315:107383

Padulosi S, Hodgkin T, Williams JT, Haq N (2002) Underutilized crops: trends, challenges and opportunities in the 21st century. In: Managing plant genetic diversity. Proceedings of an international conference, Kuala Lumpur, Malaysia, 12–16 June 2000. CABI Publishing, Wallingford, pp 323–338

Page ML, Williams NM (2023) Evidence of exploitative competition between honey bees and native bees in two California landscapes. J Anim Ecol 92(9):1802–1814

Pe'er G, Zinngrebe Y, Hauck J et al (2017) Adding some green to the greening: improving the EU's ecological focus areas for biodiversity and farmers. Conserv Lett 10(5):517–530

Petanidou T, Van Laere A, Ellis W, Smets E (2006) What shapes amino acid and sugar composition in Mediterranean floral nectars? Oikos 115(1):155–169

Pinheiro LA, Torres L, Raimundo J, Santos SAP (2013) Effect of floral resources on longevity and nutrient levels of *Episyrphus balteatus* (Diptera: Syrphidae). Biol Control 67(2):178–185

Prasifka JR, Mallinger RE, Portlas ZM et al (2018) Using nectar-related traits to enhance crop-pollinator interactions. Front Plant Sci 9:812

Priyadarshana TS, Martin EA, Sirami C et al (2024) Crop and landscape heterogeneity increase biodiversity in agricultural landscapes: a global review and meta-analysis. Ecol Lett 27(3):e14412

Rader R, Bartomeus I, Garibaldi LA et al (2016) Non-bee insects are important contributors to global crop pollination. Proc Natl Acad Sci USA 113(1):146–151

Raderschall CA, Bommarco R, Lindström SA, Lundin O (2021) Landscape crop diversity and semi-natural habitat affect crop pollinators, pollination benefit and yield. Agric Ecosyst Environ 306:107189

Ramula S, Sorvari J (2017) The invasive herb *Lupinus polyphyllus* attracts bumblebees but reduces total arthropod abundance. Arthropod-Plant Interact 11(6):911–918

Riggi LGA, Lundin O, Berggren Å (2021) Mass-flowering red clover crops have positive effects on bumblebee richness and diversity after bloom. Basic Appl Ecol 56:22–31

Riggi LGA, Raderschall CA, Fijen TPM et al (2024) Early-season mass-flowering crop cover dilutes wild bee abundance and species richness in temperate regions: a quantitative synthesis. J Appl Ecol 61(3):452–464

Rollin O, Bretagnolle V, Decourtye A et al (2013) Differences of floral resource use between honey bees and wild bees in an intensive farming system. Agr Ecosyst Environ 179:78–86

Rotheray GE, Gilbert F (2011) The natural history of hoverflies. Forrest Text, Tresaith, Wales

Rundlöf M, Lundin O (2019) Can costs of pesticide exposure for bumblebees be balanced by benefits from a mass-flowering crop? Environ Sci Technol 53(24):14144–14151

Rundlöf M, Persson AS, Smith HG, Bommarco R (2014) Late-season mass-flowering red clover increases bumble bee queen and male densities. Biol Conserv 172:138–145

Scheper J, Reemer M, van Kats R et al (2014) Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. Proc Natl Acad Sci USA 111(49):17552–17557

Scheper J, Badenhausser I, Kantelhardt J et al (2023) Biodiversity and pollination benefits trade off against profit in an intensive farming system. Proc Natl Acad Sci USA 120(28):e2212124120

Schweiger SE, Beyer N, Hass AL, Westphal C (2022) Pollen and landscape diversity as well as wax moth depredation determine reproductive success of bumblebees in agricultural landscapes. Agr Ecosyst Environ 326:107788

Senapathi D, Biesmeijer JC, Breeze TD, Kleijn D, Potts SG, Carvalheiro LG (2015) Pollinator conservation—the difference between managing for pollination services and preserving pollinator diversity. Curr Opin Insect Sci 12:93–101

Shackelford GE, Kelsey R, Dicks LV (2019) Effects of cover crops on multiple ecosystem services: ten meta-analyses of data from arable farmland in California and the Mediterranean. Land Use Policy 88:104204

Sirami C, Gross N, Baillod AB et al (2019) Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. Proc Natl Acad Sci USA 116(33):16442–16447

Straka J, Cerná K, Machácková L, Zemenová M, Keil P (2014) Life span in the wild: the role of activity and climate in natural populations of bees. Funct Ecol 28(5):1235–1244

Sutter L, Jeanneret P, Bartual AM, Bocci G, Albrecht M (2017) Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through complementary increase in key floral resources. J Appl Ecol 54(6):1856–1864

Tamburini G, Bommarco R, Wanger TC et al (2020) Agricultural diversification promotes multiple ecosystem services without compromising yield. Sci Adv 6(45):eaba715

Triquet C, Wezel A, Tolon V, Ferrer A (2024) Undestroyed winter cover crop strips support wild bee abundance and diversity in intensive cropping systems. Biodivers Conserv 33(1):179–204

Turo KJ, Reilly JR, Fijen TP, Magrach A, Winfree R (2024) Insufficient pollinator visitation often limits yield in crop systems worldwide. Nat Ecol Evol 8(9):1612–1622

van Klink R, Bowler DE, Gongalsky KB, Shen M, Swengel SR, Chase JM (2024) Disproportionate declines of formerly abundant species underlie insect loss. Nature 628(8007):359–364

Vanbergen AJ, Aizen MA, Cordeau S et al (2020) Chapter six—transformation of agricultural landscapes in the anthropocene: nature's contributions to people, agriculture and food security. In: Bohan DA, Vanbergen AJ (eds) Advances in ecological research. Academic Press, New York, pp 193–253

Vandermeer JH (1992) The ecology of intercropping. Cambridge University Press, Cambridge

Varah A, Jones H, Smith J, Potts SG (2020) Temperate agroforestry systems provide greater pollination service than monoculture. Agr Ecosyst Environ 301:107031

Wagner DL (2020) Insect declines in the anthropocene. Annu Rev Entomol 65:457–480

Westphal C, Steffan-Dewenter I, Tscharntke T (2003) Mass flowering crops enhance pollinator densities at a landscape scale. Ecol Lett 6(11):961–965

Westphal C, Steffan-Dewenter I, Tscharntke T (2009) Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. J Appl Ecol 46(1):187–193

Westrich P (1996) Habitat requirements of central European bees and the problems of partial habitats. In: Matheson A (ed) The conservation of bees, 18. Academic Press Limited, London, pp 1–16

Wignall VR, Brolly M, Uthoff C et al (2020) Exploitative competition and displacement mediated by eusocial bees: experimental evidence in a wild pollinator community. Behav Ecol Sociobiol 74(12):152

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(6377):791–793

Wintermantel D, Pereira-Peixoto MH, Warth N et al (2022) Flowering resources modulate the sensitivity of bumblebees to a common fungicide. Sci Total Environ 829:154450

Wood TJ, Gibbs J, Rothwell N et al (2018) Limited phenological and dietary overlap between bee communities in spring flowering crops and herbaceous enhancements. Ecol Appl 28(7):1924–1934

Zander P, Amjath-Babu TS, Preissel S et al (2016) Grain legume decline and potential recovery in European agriculture: a review. Agron Sustain Dev 36(2):1–20