The ecology of crop pollination and its integration into farm management to ensure sustainable and stable crop yields

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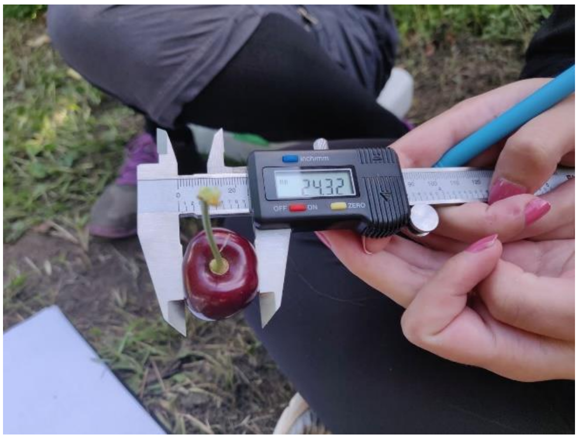
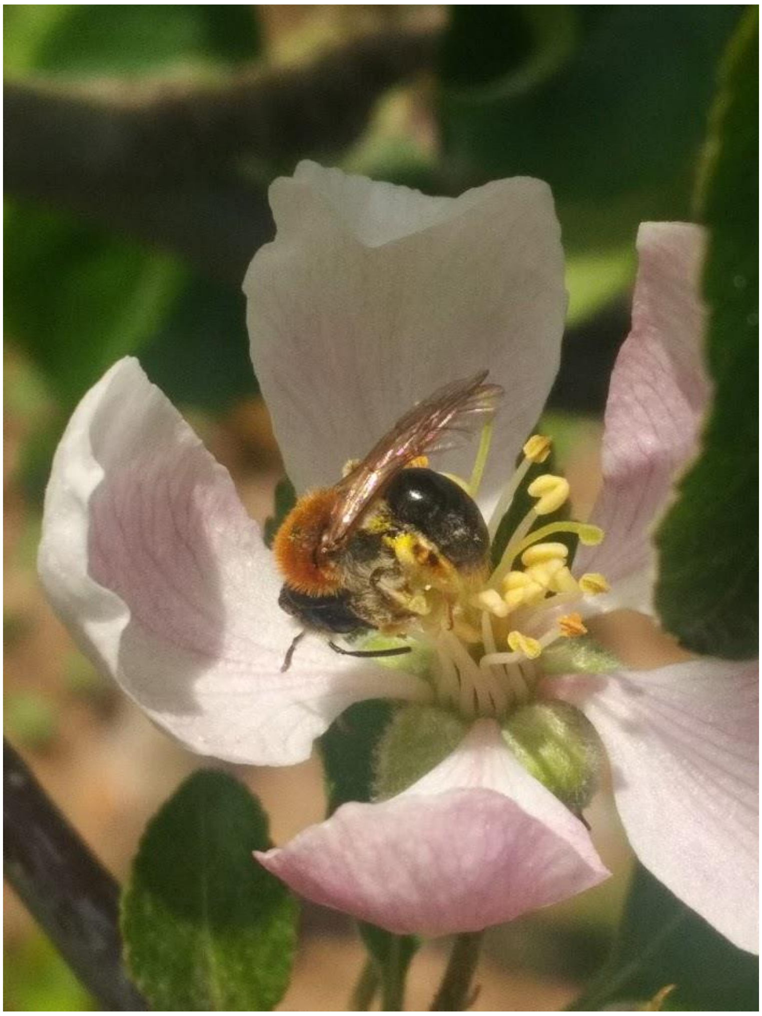
To Lima, Penelope and Freja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Abstract

More than 75% of global crops depend to some extent on insect pollination to improve yield or crop quality. Yet, many groups of pollinators are perceived as being in decline, which might consequently diminish the ecosystem service of pollination and threaten food security for a growing human population. While benefiting from insect pollinators, agriculture is thought to be one of the major drivers for their decline through landscape intensification (i.e. fragmentation and habitat loss). Ongoing changes in the agricultural landscape and production, such as the increase in cultivation of pollinator-dependent crops, warrant further understanding of landscape-scale and local drivers of pollinator abundances as well as farmer perceptions of pollinators and their management practices so as better to protect bee pollinators. In this thesis, I take on a wholesome view of pollinators and their status and contribution to food production; I review the status of managed bees, study how they contribute to crop yield in two important food crops, and investigate the farmer perception of managed and wild pollinators.

First, I investigated if pollination services in apple orchards are affected by the cultivation of oilseed rape (OSR), a co-mass-flowering crop **(Chapter I**), by performing a landscape-scale experiment in 12 commercial apple orchards. I found that the abundance of bee functional groups in apple orchards is affected by changes in OSR availability, but in different directions. While honey bees are drawn away from apple orchards to OSR fields, bumble bee abundances remain stable and other wild bees are facilitated. I suggest that wild bees compensated for the loss of honey bees, as fruit set and seed set in apple orchards remained stable and independent of OSR availability. In an increasingly pollinator-dependent agriculture, wild bees should be protected and promoted to ensure stable crop pollination.

To test whether mason bee abundance can be enhanced by providing nesting material and consequently if sweet cherry yield can be increased (**Chapter II**), I undertook a landscape-scale experiment in 17 sweet cherry orchards. I found that, by providing nesting material, mason bees abundance can be enhanced and the females predominantly collected pollen from sweet cherry flowers. Enhanced mason bees interactively with honey bees increased fruit set, but not alone. As fruit set dropped with distance to mason bee nesting material, I suggest to install nesting material every 100 m through orchards to guarantee crop pollination. My result suggest that the promotion and conservation of a wide range of pollinators should be implemented rather than relying on one single managed pollinator species.

Besides mason bees, a wide range of pollinator can be managed. However, current trends and the diversity of managed pollinators are not yet fully understood. I therefore reviewed the literature (**Chapter III**) to shed light on the range of current and potential managed pollinators. I found that the numbers of *Apis mellifera* colonies, the predominant managed pollinator, has increased by 85% since 1961. Yet, winter mortalities of *A. mellifera* remained high, with higher mortalities in North America than in other regions of the world. Thus, famers depending on a single species for pollination services are faced with uncertainties, which might have also induced the increase in managed pollinator diversity, which I report in **Chapter III**. In total, 66 pollinator species have been investigated for use as managed pollinators, of which 22 currently used. However, there are also risks associated with the use of managed pollinators which should be considered. I urge the implementation of biodiversity-friendly measures to guarantee provision of crop pollination services where possible, especially as one species alone might not enhance fruit and seed set in crops (**Chapter II**).

The implementation of biodiversity-friendly measures requires the understanding and willingness of farmers to implement on-farm mitigation measures. Despite growing evidence of local and landscape-scale drivers on pollinator abundances and their service delivery, few studies have investigated farmer perceptions and factors influencing their decision-making over pollinator management. Therefore, I investigated farmer knowledge and perception of pollinators across crops and countries (**Chapter IV**). I found that on-farm experiences shaped farmer knowledge, which - as well as external incentives - subsequently affects their management decisions. Pollination management is often already integrated into farm management, with a diverse range of measures employed by farmers beyond the current recommendations of scientists. Local knowledge is a key to co-design locally adjusted measures to protect pollinators and to adapt to a changing agricultural landscape.

In this thesis, I demonstrate that local and landscape-scale structures affect the abundance of pollinators. *Apis mellifera*, the main managed pollinator can be attracted away from a target crop by other co-flowering crops. Wild bee populations can compensate for those losses and, in combination with honey bees, secure fruit set and seed set on fruit farms. Cooperative research between farmers and scientists can be key to meeting future challenges in crop pollination and integrate crop pollination into farm management.

Keywords: Farmer knowledge, ecosystem service of pollination, nature-based solutions, landscape management, *Brassica napus*, *Malus domesticus*, *Prunus avium*

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General introduction

Importance of pollinators for agro-ecosystems

The ecosystem service of pollination is essential for crop production and critical for natural ecological processes. Up to 87.5% of wild plant species are dependent on insect pollination (Ollerton et al., 2011) and pollinators contribute to the pollination of more than 75% of globally important crops (Klein et al., 2007). Recent economic valuations of pollination services provided by bees indicate that pollinators contribute between 1 to 2 % of global GDP (Lippert et al., 2020). Pollinator-dependent crops are important for balanced human diets, as these crops are the principal source of many micronutrients, for example vitamin A and C (Eilers et al., 2011; Smith et al., 2015). While the majority of animal pollinators are insects (e.g., bees, flies, wasps, beetles, butterflies, moths and thrips), there are also vertebrate pollinators including birds, lizards and bats (Potts et al., 2016). Bees are thought to be the most important group of pollinators as they visit more than 90% of the most important 107 crops in the world (Klein et al., 2007) and dominated many crop pollinator communities both in abundances and diversity (Kleijn et al., 2015; Winfree et al., 2018; Senapathi et al., 2021). The Western honey bee (*Apis mellifera* L.), the most intensively managed pollinator, is used by farmers to increase yield of many pollinator-dependent crops (Breeze et al., 2019), but wild bee flower visitors provide an additional pollination benefit, regardless of the density of honey bees (Garibaldi et al., 2013). Also, non-bee pollinators contribute substantially to the pollination of crops (Rader et al., 2016).

Disentangling the contributions of pollinators to crop yield is complex and different parameters have to be taken into account. The role of a single species to pollination services is often considered to be a function of visitation frequency and per visit efficiency (Ne’eman et al., 2010). For many pollinator-dependent crops, wild bees have been shown to have a higher pollination efficiency per visit than honey bees (Vicens and Bosch, 2000a; Greenleaf and Kremen, 2006; Eeraerts et al., 2020b), while in other crops a reverse trend has been detected (Rader et al., 2009). Pollination efficiency of pollinators can be crop specific, with some crops even requiring special pollinator traits such as tomato flowers that have to be buzz-pollinated (bussing is a trait that honey bees do not possess; Buchmann, 1983). Also, honey bee activity is limited during inclement weather conditions (Vicens and Bosch, 2000b) and honey bees can be attracted by nearby mass-flowering crops (Bänsch et al., 2020).

Inter-species interactions and pollinator functional complementarity have been shown to positively affect pollination services to crops, explaining partly the contribution of pollinator diversity to crop yield. For instance, the presence of wild pollinator species increased honey bee pollination efficiency from around 4 seeds per visit to 12 seeds per visit in sunflower fields (Greenleaf and Kremen, 2006). In sweet cherry and almond orchards, honey bees changed rows more often with increasing wild bee abundances, which leads to improved cross-pollination by honey bees (Brittain et al., 2013; Eeraerts et al., 2020b). Hence, relationships between abundance/visitation frequency and fruit set or yield do not always have to be linear (Rollin and Garibaldi, 2019), and can be context dependent. High bee visitation rates can even have detrimental effects on fruit set (Sáez et al., 2014) and honey bees can depress wild insect densities, even in mass flowering crops (Herbertsson et al., 2016; Lindström et al., 2016). Relying on one single managed pollinator species might be considered a risks as high overwinter mortalities of *A. mellifera* colonies have been recorded over the last decades (Potts et al., 2016).

Kleijn *et al.* (2015) have argued that provision of pollination service delivery is restricted to a small number of common pollinator species and rare threatened species are rarely found on crop flowers. Therefore, the conservation of pollinator diversity might be insufficiently justified by the argument of pollination service delivery (Kleijn et al., 2015). However, this approach plainly investigated flower visitor abundances and misses out on interactive effects, as described above, species turnover across landscapes and resilience of the community over time. To reach adequate (threshold) levels of pollination per site across landscapes, many species, including rare ones, have been found to be required (Winfree et al., 2018), and wild insect diversity stabilizes crop pollinator communities across years, representing a security to climate-driven variation in pollinator activity (Senapathi et al., 2021).

These examples illustrate the complexity between flower visitor communities and the delivery of the ecosystem service of pollination in agricultural landscapes. While pollinator biodiversity is important for providing the ecosystem services of pollination in many crops (Garibaldi et al., 2013; Winfree et al., 2018), agriculture is one of the main threats to pollinators (IPBES, 2016). Long-term biodiversity changes are complex and taxonomic groups (e.g. bees) vary in the magnitude of change, in their direction and timing of change (Outhwaite et al., 2020). But insects seem to have undergone recent drastic declines in occupancy, biomass, abundance and richness (Seibold et al., 2019; Outhwaite et al., 2020; van Klink et al., 2020; Zattara and Aizen, 2021). Effects on pollinator biodiversity might differ in direction and magnitude among taxonomic groups as well as between world regions (Millard et al., 2021), with some drivers and their interactions as well the effects of practicable mitigation measures being not yet fully understood.

Challenges and trends of global agriculture and its impact on pollinators and pollination

Land use intensification

A growing global human population of almost 8 billion people, projected to reach 9.6 billion people by 2050, together with a change in dietary habits result in a need for food security (Godfray et al., 2010; Tripathi et al., 2019). Without a sharp reduction in food waste, changes in consumption, along with a decrease in postharvest losses (Seppelt et al., 2020), it is expected that within the next five decades global food production will have to increase to meet growing demands (Tripathi et al., 2019). Changes are not only expected in the future, but agricultural production has already markedly expanded in the past decades (McKenzie and Williams, 2015; Aizen et al., 2019) and at the same time led to increased productivity through conventional intensification of agricultural land, including crop monocultures with large external inputs such as plant protection products (Kovács-Hostyánszki et al., 2017).

Cropland management can have negative impacts on biodiversity, including pollinators, through expansion and intensification of cultivated land, leading to changes in landscape structure and composition (Newbold et al., 2015; Beckmann et al., 2019; Millard et al., 2021). Loss of nesting sites, foraging resources and landscape modification are linked to declines in wild bees and butterflies (Biesmeijer et al., 2006; Bommarco et al., 2014; Senapathi et al., 2015; Raderschall et al., 2021). Through the reduction of pollinator diversity and abundance, land-use changes can decrease yield, especially of highly pollinator-dependent crops (Klein et al., 2003, 20012; Holzschuh et al., 2012; Eeraerts et al., 2017).

Increasing pollinator dependency

While the total land area devoted to agriculture is steadily increasing worldwide, pollinator-dependent crops have increased disproportional, making agriculture increasingly pollinator dependent (Aizen et al., 2019). This trend is in part induced by agricultural policies that subsidize crops for biofuel production (Breeze et al., 2014). Though climate change is a key risk for food security, resulting into more frequent extreme weather events, soil deterioration and water scarcity (Campbell et al., 2016), agriculture is challenged by climate change mitigation measurements such as the production of biofuels as an alternative to fossil fuels (Banse et al., 2011; Yin et al., 2013). High demands for biofuels has inevitably led to land-use and land-cover changes, especially a substantial growth in the cultivation of pollinator-dependent crop, such as oilseed rape (OSR) (Breeze et al., 2014).

The increase in cultivation of the highly rewarding mass-flowering crop OSR in the landscape might affect the pollinator communities of co-flowering crops positively by facilitation or negatively by competition. Facilitation might occur as mass-flowering crops attract pollinators though their high density, which then also visit adjacent crops. On the other hand, mass-flowering crops could draw pollinators away from less attractive crops, with knock on effects on yield. However, the effects of variation in floral resources in the landscape on the foraging decisions of pollinator groups and the consequences for crops yield have rarely been studied (Grab et al., 2017; Bänsch et al., 2020). The few existing studies reveal that flower visitor abundance in strawberry fields was reduced when surrounded by apple orchards (Grab et al., 2017) and that OSR competes with strawberry flowers for honey bees and bumble bees, while solitary bees in strawberry fields were facilitated by OSR (Bänsch et al., 2020). Yet the effect of OSR on flower visitors in apple orchards, a commercially important crop worldwide, is unknown.

Growing crops outside of their native range and under permanent cover

The worldwide food production system has been globalizing extensively over the past 50 years and many crops are cultivated outside of their original range (Khoury et al., 2016). In many regions of the world more than 80% of food production relies on cultivating foreign crops (Khoury et al., 2016). Brown and Cunningham (2019) revealed in a meta-data analysis that crops grown outside their region of origin are visited by fewer bee genera than in the area of origin (Brown and Cunningham, 2019), with yet unknown consequences for crop yield. The higher pollinator diversity of crops in their original range could be a consequence of a home ground advantage, meaning that native-crops are more attractive to native pollinators (Brown and Cunningham, 2019). Also, pollinator communities, for example those of avocado, have been demonstrated to vary widely across regions (Dymond et al., 2021), which requires locally adapted context-dependent measures to enhance pollinator abundances and diversity. The cultivation of crops outside of their native range might have led to an increase in managed pollinators. The diversity and the extent to which pollinators are managed globally, has not yet been reviewed.

Another trend in agriculture is the increase in production under permanent covers, as they can protect from extreme weather conditions, pests and pathogens and avoid pollen contamination (Cuesta Roble, 2020). Active pollinator management is often required in crop production under permanent cover such as enclosures as wild pollinator visitations are limited in such conditions. The most important managed pollinator, *A. mellifera*, can be negatively impacted in enclosures such as decreased health and foraging actively (Evans et al., 2019; Kendall et al., 2021). Therefore new, preferable native pollinators might be considered as manageable pollinators in such agricultural systems. A synthesis of the diversity of those pollinators could give farmers an overview and guide them to make locally adapted decisions that can enhance crop pollination.

Land use intensification, increasingly pollinator-dependency, growing crops outside of their native range and cultivations under permanent covers all illustrate global changes in the agricultural landscapes, with each of them possibly affecting – positively and negatively – pollinator diversity and abundance. Integrating crop pollination into farm management to mitigate negative effects on local, landscape and global scales can be a key tool, especially when co-designed with farmers to meet their requirements and capacities.

Integrating crop pollination into farm management

Isaac *et al*. (2017) introduced the concept of Integrated Crop Pollination (ICP), which they defined as: "*The use of managed pollinator species in combination with farm management practices that support, augment, and protect pollinator populations to provide reliable and economical pollination of crops*" (Isaacs et al., 2017). ICP provides a framework to enhance provision of the ecosystem service of pollination with the prerequisite that management strategies have to be adopted to the location (i.e. local pollinator fauna), the crop grown (variations in levels of pollinator dependency, efficiency of pollinators), the landscape surrounding the farm and to farmer preferences and capacities (Isaacs et al., 2017). Two main components are included into the ICP concept: integration of practices and integration of pollinators.

Many insect pollinators can be actively managed, with unexploited opportunities to increase yield (IPBES, 2016). The most widely used pollinator species is the Western honey bee, which is used to pollinate many crops (Breeze et al., 2019). However, honey bees are not always the most effective pollinator (Vicens and Bosch, 2000a; Greenleaf and Kremen, 2006; Eeraerts et al., 2020b), they are not native in many parts of the world (Requier et al., 2019), they can suppress wild bee densities (Lindström et al., 2016) and possibly result in spill-over of pathogens from honey bees to wild bees, which might cause population declines in wild bees (Tehel et al., 2016). In addition, honey bees often struggle with ecological conditions in protected environments (Evans et al., 2019). Global changes in the agricultural landscapes, such as the increasing cultivation of mass-flowering crops and the rise in crops under permanent cover requires changes in pollinator management. Wild pollinators can ensure stable crop pollination (Garibaldi et al., 2013), of which some species can be managed or promoted (IPBES, 2016). Yet, the diversity of possible managed pollinators is not fully understood, and the number of new species under consideration increased over time (IPBES, 2016).

While some bee species have a long tradition of management, such as bumble bees for the pollination of tomatoes in greenhouses (Velthuis and Van Doorn, 2006), for most species there is limited information which can be used as a base for farmers to make decisions (Isaacs et al., 2017); their management might differ from that employed for honey bees. For instance, stingless bees in macadamia orchards were recorded within 100 meters from their natal colony, whereas honey bees were attracted by trees with the most flowers regardless of the distance to the hive (Evans et al., 2021). A more even distribution of stingless bee colonies is therefore recommended to enhance macadamia pollination and pollination management has to be appropriately adapted (Evans et al., 2021). Making practical decision to optimize pollination service delivery requires locally adapted and well communicated measures.

Apart from actively managing pollinators, farm management can be adapted to promote a diverse set of wild pollinators and the pollination services they provide. Reducing pesticide applications, enhancing habitat for food and nesting material as well as improving horticultural practices can contribute to sustainable pollination of crops (Garibaldi et al., 2017; Isaacs et al., 2017). In intensified landscapes, in which natural habitat is scares (Garibaldi et al., 2021), these measures might be an effective tool for farmers to enhance wild bee populations on their farms.

Farmer perceptions of pollinators and their management practices

In order to mitigate effects of global changes in agriculture on pollinators, pollination and crop production, crop pollination should be an integrated part of farm management strategies (Isaacs et al., 2017). This requires the willingness and the capacity of farmers to implement measures, the availability of information for farmers as well as researchers making recommendations that are practicable and profitable for farmers. While many drivers of change in pollinator abundance and diversity and the cascading effects on yields are understood, comparably little is known about farmer perceptions and knowledge of pollinators (Breeze et al., 2019). A small number of studies has investigated farmer perceptions of pollinators, suggesting differences in perceptions across regions and crops cultivated (Kasina et al., 2009; Frimpong-Anin et al., 2013; Hanes et al., 2015; Breeze et al., 2019; Hevia et al., 2021). Linking knowledge as well as external incentives to decision-making would provide a better understanding on when and how farmers implement measures (Breeze et al., 2019). Investigating local farmer knowledge and perceptions of pollinators is essential as it can make complementary perspectives available and extend scientific understanding of the temporal and spatial dynamics of pollinator biodiversity; such information can improve the deployment of measures that are adapted to local conditions (Sutherland et al., 2013).

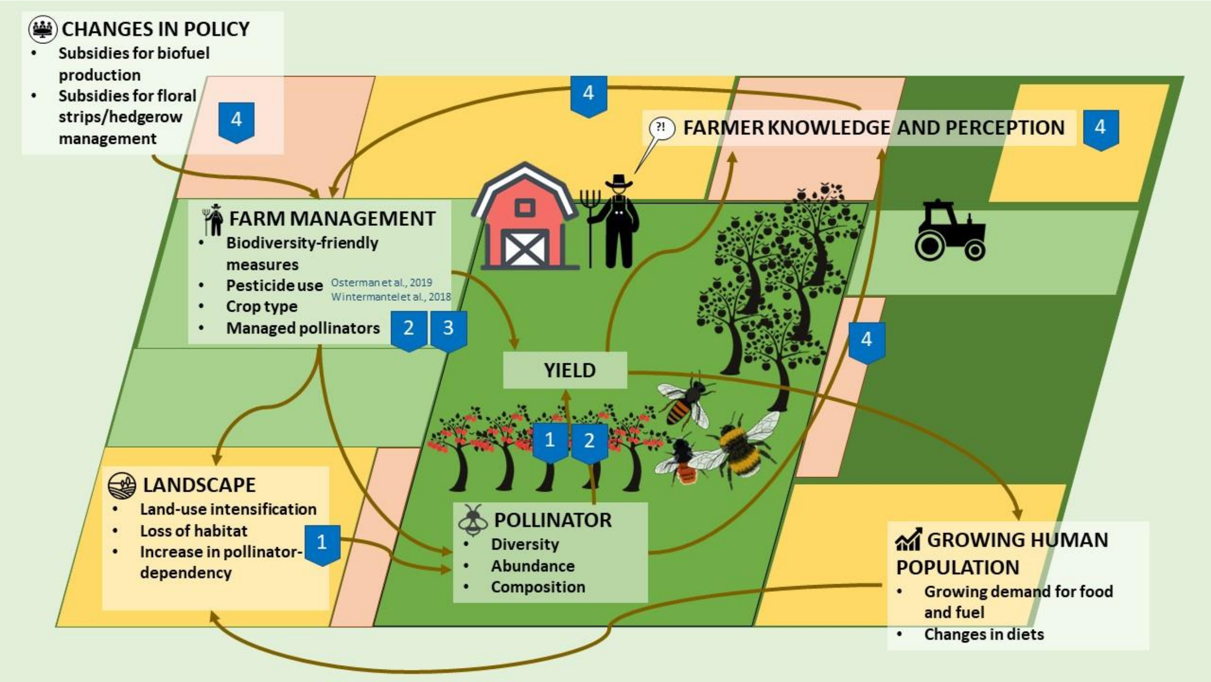

Fig. 1: Global, landscape-scale and local-scale drivers affecting pollinators in agro-ecosystems, with farmers as the key to integrate crop pollination into their farm management. Numbers represent chapters of the thesis.

Aims

While agriculture increases in pollinator dependency (Aizen et al., 2019), little is known about the effects of extensively grown mass-flowering crops on co-flowering pollinator-dependent crops. In my first chapter, I used a well replicated paired landscape-scale experiment to investigate possible facilitative and competitive interactions between two co-flowering economically important crops, oilseed rape (OSR) and apple, on flower visitor abundances in apple orchards (**Chapter I**, Fig. 1). I calculated OSR coverage in the landscape around apple orchards and tested if apple flower-visitor abundances changed with an increase in OSR abundance. By performing a pollination experiment in apple orchards, I furthermore assessed effects of OSR on fruit set and seed set in apple orchards. I aimed to give landscape-scale management recommendations for farmers to maximize yields through new insight into interactions between co-flowering crops in relation to their flower visitors.

In a changing agricultural landscape, farmers have started to actively manage insects for pollination services. In order to understand the current status and trends of managed pollinators, I reviewed the literature, collected known datasets and summarized the current scientific knowledge on managed pollinators (**Chapter II**, Fig. 1). For the most commonly used managed pollinator, the Western honey bee (*Apis mellifera*), I analysed existing data on the number of hives per year and world region, as well as synthesized data published on overwinter mortality to give an overview of honey bee health. Also, I summarised information on managed bumble bee species, stingless bees, solitary bees and non-bees and their contribution to crop pollination. I aimed to present an overview of manageable crop pollinators as well as to discuss the risks of managed pollinators in threatening wild species.

Pollination services to fruit crops are highly landscape dependent. For example, landscapes with semi-natural areas can enhance wild bee abundances in sweet cherry orchards and consequently increase pollination, fruit set and yield (Holzschuh et al., 2012). In **Chapter III**, I aimed to investigate whether the effects of land use intensification on bees can be diminished by integrated pollinator management, i.e. by providing nesting resources for wild bees to improve sustainable pollination and optimize yields in fruit orchards (**Chapter III**, Fig. 1). I studied 17 sweet cherry orchards with varying pollinator management in a highly intensified landscape in Central Germany. In all orchards, I simultaneously assessed orchard management (e.g. honey bee hive density, size of the orchard, wild bee nesting materials) and measured pollinator abundance during transect walks. By performing a pollination experiment on 20 trees per orchard, I was able to quantify the pollination services provided to quantify local effects of wild bee nesting material as well as per orchard on pollination services across sites so as to disentangle the contribution of honey bees compared to other bees. I thereby aimed to provide management recommendations for sweet cherry farmers to avoid insufficient yields in an early flowering highly pollinator-dependent crop.

Scientific understanding and evidence of the relationships between landscape composition, farming practices and provision of pollination services is rapidly growing (IPBES, 2016). Yet, farmer knowledge, their perception of pollinators and their decision-making in relation to pollinators and pollination are little explored (Breeze et al., 2019), while being a key element for implementing changes in the agricultural landscapes. In particular, little is known about farmers as knowledge holders in scientific fields that have been recently addressed by scientists, such as the contribution of non-bees and their management as crop pollinators (Rader et al., 2020, 2016). In **Chapter IV** (Fig. 1), I investigated farmer knowledge and perception of pollinator importance by interviewing farmers from 11 countries cultivating one of four important crops (apple, avocado, OSR or kiwifruit). I investigated if knowledge, perception and management actions are crop- and country-specific, which can be caused by differences in sources of information, pollinator-dependency, requirements of the crop for pollination services and external incentives (subsidies). Importantly, I aimed to link ecological knowledge with on-farm management as well as with scientific evidence as a step towards understanding and enhancing local management practices.

Chapter I. Apple pollination is ensured by wild bees when honey bees are drawn away from orchards by a mass co-flowering crop, oilseed rape

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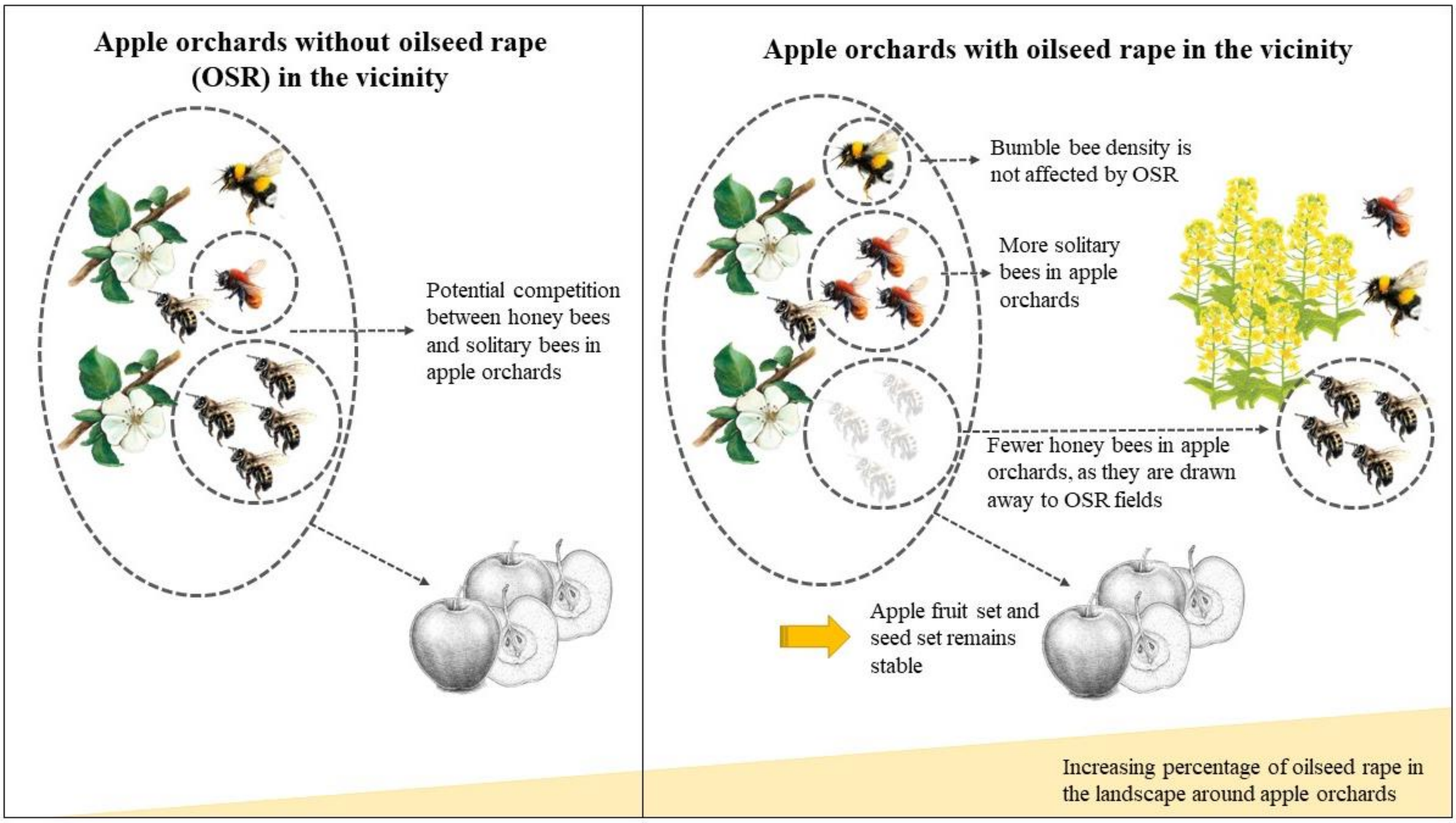
Graphical Abstract



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Highlights

- Apple orchards were pollen limited.
- Honey bees were attracted from apple orchards to co-blooming oilseed rape (OSR).
- Wild bee numbers in apple orchards increased with more OSR in the landscape.
- No effect of OSR or decreasing honey bee numbers on apple fruit or seed set.
- Wild bees might compensate the loss of honey bees.

Abstract

Over the past two decades, the cultivated area of oilseed rape (*Brassica napus* L. or OSR), a mass-flowering crop, has markedly increased in Europe in response to bioenergy demands. As well as representing a major shift in floral composition across the landscape, mass-flowering OSR may alter pollination services to other simultaneously blooming crops, either decreasing pollination via competition for pollinators or facilitating it via pollinator spill-over. Apple (*Malus domestica* Borkh.) is an economically important, obligately insect-pollinated fruit crop that co-flowers with OSR. Using twelve independent apple orchards varying in the percentage of OSR in the surrounding landscape, we investigated the effect of OSR on pollinators and pollination of co- blooming apple. We collected bees with pan traps and quantified flower visitors during transect walks in both crops and we experimentally measured pollination service provision to apple as fruit and seed set. We confirm that apples are highly dependent on animal pollination and report pollination limitation in our apple orchards. Honey bees were the numerically dominant visitors of apple flowers observed during transect walks. Though their numbers dropped with an increasing percentage of OSR in the landscape, the number of bumble bees visiting apple flowers remained stable and those of other wild bees rose. The pan trapped Shannon diversity of bees remained constant. We could not detect an effect of OSR in the landscape on apple fruit set or seed set, both of which remained stable. Local wild bee populations might compensate for the loss of honey bees in the provision of pollination services in apple, providing especially effective pollination. Our results underscore not only the dominant role of bees in apple pollination but also the importance of wild bee conservation for providing pollination insurance and stability of apple crop yields under changing agricultural policies and cropping practices.

Keywords: Ecosystem service, Landscape, Mass flowering crop, Spillover, Competition

1. Introduction

Insect pollinators, particularly bees, are a critical component of terrestrial ecosystems by pollinating many wild plants (Ollerton et al., 2011) whilst the pollination service provided by insects to crops contributes significantly to global food production and nutritional security (Klein et al., 2007; Potts et al., 2016). However, over the last two decades pollinators have been considered under threat due to reports of both wild and managed pollinator declines (Biesmeijer et al., 2006; Potts et al., 2010; Cameron et al., 2011; Powney et al., 2019; Zattara and Aizen, 2021). Agricultural intensification is thought to be one of the main global change drivers causing shifts in insect pollinator community composition, including a decrease in insect pollinator species richness and abundance (Brown and Paxton, 2009; Potts et al., 2010, 2016; González-Varo et al., 2013; Vanbergen et al., 2013) as well as functional diversity (Woodcock et al., 2014). The perceived decline in insect pollinators threatens the stability of the ecosystem service of pollination and consequently crop production in agro-ecosystems (Potts et al., 2016).

Globally, the total area of cropped land has increased by 23 % from 1961 to 2006 (Aizen et al., 2008) and, over this time, agriculture has become more pollinator-dependent (Aizen et al., 2019). In addition to food crops, there has been an expansion in biofuel production (Banse et al., 2011). In the European Union, oilseed rape (*Brassica napus* L. or OSR) is now the most common oil crop grown for biofuel (Destatis, 2018). For instance, approximately 11 % of total arable land in Germany was used for OSR production in 2016 (Destatis, 2018), a percentage that might fluctuate greatly in the future due to changes in political and agricultural policy e.g. restrictions on the use of plant protection products (e.g. neonicotinoid insecticides; Scott and Bilsborrow, 2018), climate change (e.g. droughts in spring; Pullens et al., 2019) or market forces. OSR is a mass flowering crop with bright yellow flowers that creates a large pulse of flowering resources attractive to insects for its ca. four-week-long blooming period. It can facilitate the pollination of later flowering wild plants (Herbertsson et al., 2017) and crops (Grab et al., 2017), likely by attracting many pollinators to areas with OSR grown in the vicinity. Wild plants co-flowering with OSR can also experience facilitated pollination through pollinator spillover (Kovács-Hostyánszki et al., 2013). Yet there is also the risk that they may suffer reduced pollination through competition for pollinators (Holzschuh et al., 2011; Grab et al., 2017).

While the effects of OSR on bee abundance and pollination services have been shown to vary across spatial and temporal scales (Holzschuh et al., 2011; Kovács-Hostyánszki et al., 2013; Grab et al., 2017; Herbertsson et al., 2017), OSR's impact on bees may also differ across bee taxa (Diekötter et al., 2010; Herbertsson et al., 2017; Bänsch et al., 2020a). For example, the abundance of long-tongued bumble bee spe- cies (e.g. *Bombus pascuorum* and *Bombus hortorum*) was found to decrease with increasing OSR in the landscape, while more generalist *Bombus* species increased (Diekötter et al., 2010). Moreover, it has recently been demonstrated that blooming OSR competes with nearby strawberry fields for pollinators in a taxon-specific manner, reducing honey bees and bumble bees at strawberry flowers whilst boosting numbers of other wild bees (Bänsch et al., 2020a). In the USA, strawberry yields are reduced through competition for pollinators when surrounded by co-flowering apple (Grab et al., 2017).

Apple (*Malus domestica* Borkh.) is an important fruit crop, both globally and in Europe (global production in 2014: 84.6 million tonnes; European production in 2014: 17.4 million tonnes; FAOSTAT, 2017). The predominant pollinators of apple flowers are considered to be bees and hoverflies (Delaplane and Mayer, 2000; Klein et al., 2007; Pardo and Borges, 2020). Most apple varieties are highly pollinator-dependent (Free, 1993) and need to receive pollen from a cross-compatible pollinizer cultivar for successful pollination and fruit set (Delaplane and Mayer, 2000). Seed and fruit set in apple orchards have been found to be positively correlated with an increase in wild bee species richness (Mallinger and Gratton, 2015; Blitzer et al., 2016), pollinator functional diversity (Martins et al., 2015), phylogenetic diversity (Grab et al., 2019) and abundance (Martínez-Sastre et al., 2020; Radzevičiūtė et al., 2021), suggesting that wild bees contribute considerably to apple pollination.

OSR and apple flower synchronously in many temperate localities, including Germany, and therefore OSR may impact pollinator communities in apple orchards as well as the pollination of apple. Apple flowers produce less nectar per day (e.g. 0.4− 0.6 μl nectar with a sugar concentration between 28.3 % and 36.4 % (Quinet et al., 2016)) than oilseed rape flowers (e.g. 0.9 μl nectar with a sugar concentration of 32.4 % (Carruthers et al., 2017)), which might attract pollinators away from apple orchards if oilseed rape fields are present in the vicinity of an apple orchard. Yet despite the relative abundance and importance of both crops, the extent to which co-flowering OSR facilitates apple pollination or competes with apple for pollinators remains unknown (Pardo and Borges, 2020).

Here we investigated insect pollinator communities in apple orchards and nearby OSR fields as well as quantified apple pollination to understand if OSR competes with apple for flower visitors and affects the provision of pollination services to apple crops. To do so, we used 12 commercial apple orchards with a varying percentage of OSR in the landscape (from 0 % to 30 %) in addressing the following questions: (i) does OSR in the landscape affect the pollinator community in apple orchards and, as a consequence, (ii) does co-blooming OSR impact apple pollination? We hypothesized that OSR is more attractive than apple due to its higher nectar content per flower and therefore that OSR would decrease pollination in adjacent apple orchards.

2. Methods

2.1. Study sites

In spring 2017, we selected 12 independent apple orchards in the south of the federal state of Saxony-Anhalt in Germany, a state dominated by agricultural land (60 %) (locations are highlighted in Fig. 1, coordinates are listed in Table A.1). Orchards differed in the percentage of OSR within the surrounding 1 km from the orchard border, ranging from 0% to 30 % (Table A.1, Fig. 1). Furthermore, we identified the closest OSR field to each apple orchard (mean distance between an OSR field and an apple orchard at sites was 1.1 ± 0.8 km S.D.). The closest distance between apple-OSR sites (i.e. from the closest orchard-field margin of one apple-OSR site to the next apple-OSR site) averaged 31.5 km (±17.5 km S.D., range: 2.08–69.94 km; see Fig. 1), adequate to ensure their independence (Greenleaf et al., 2007). We used Mantel tests in the R package *ade4* (Dray et al., 2017) to check for spatial autocorrelation in our data set. There was no significant spatial autocorrelation for bee biodiversity or pollination (as PSP, see definition below) across apple orchards ($P > 0.05$). Distances between crops and sites were measured in ArcMap v. 10.5 and within crops using the R statistical software (R Core Team, 2016) with the function *as.dist*.

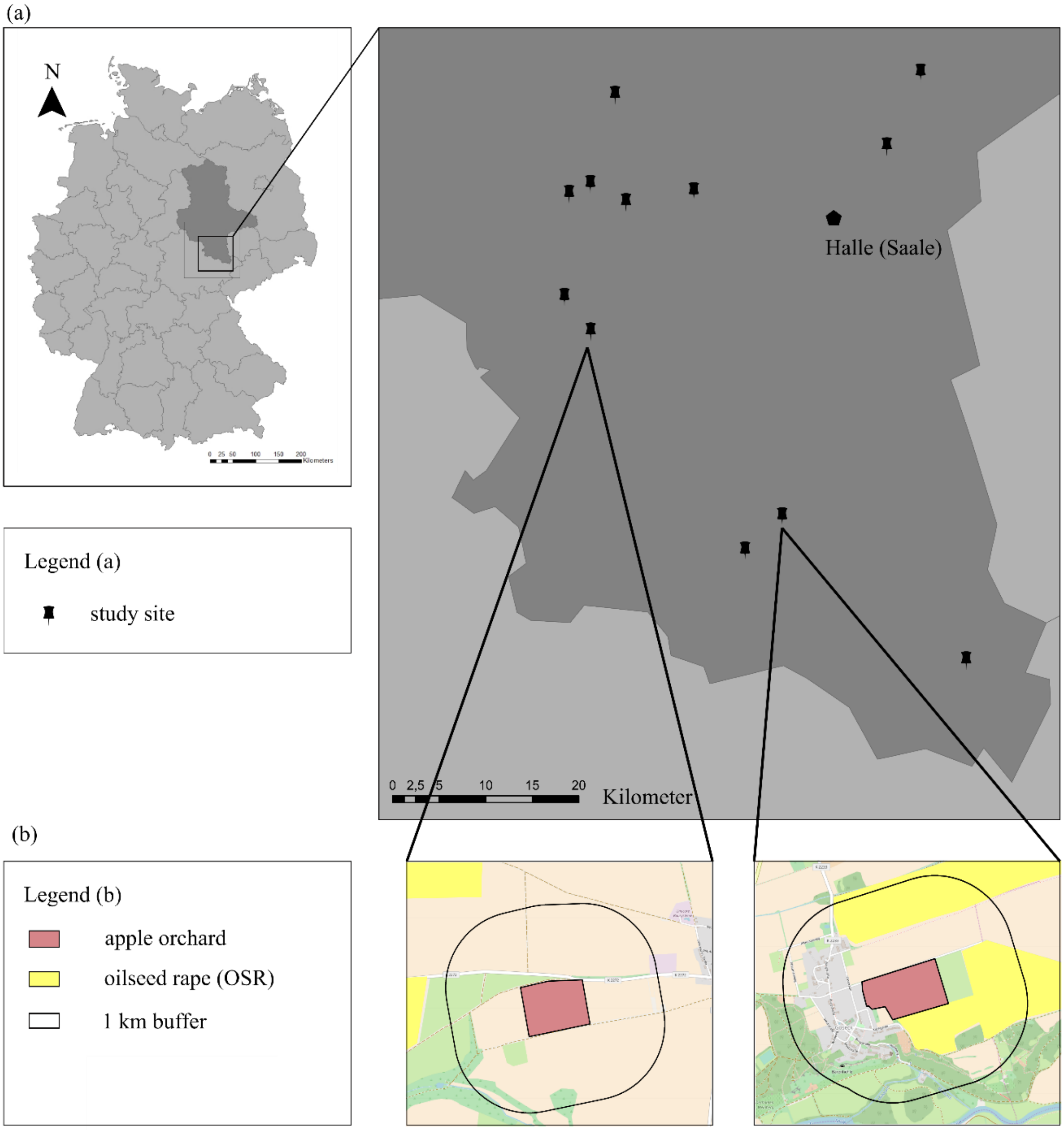

Fig. 1. (a) The twelve study sites in the federal state of Saxony-Anhalt, Germany, in the vicinity of Halle (Saale); (b) examples of two study sites, showing their percentage of oilseed rape (yellow) within a 1000 m radius buffer around each apple orchard (dark red) in 2017.

2.2. Sampling of flying insects and flower visitors

We performed a transect walk of 500 m over 30 min in apple orchards and OSR fields between 10:00 and 15:00 during the full bloom of each crop to quantify flower visitors. In apple orchards, transects ran alongside apple trees used in the pollination experiment (see below) and, in OSR fields, they ran alongside crop plants growing adjacent to pan traps (see below). During transect walks, we recorded all observed flower visitors that made contact with reproductive parts of a flower within 2 m on each side of the transect. Flower visitors observed on transect walks were identified to morpho-group: honey bees (*Apis mellifera*), bumble bees (*Bombus* spp.), other wild bees, Diptera and 'others', which included Lepidoptera and Coleoptera. In downstream analyses, we focused only on the three bee morpho-groups as they represented >95 % of all apple flower visitors (1728 of 1818 total visits, see Table A.2).

In addition, we sampled flying insects in both crops using coloured pan traps (blue, white and yellow) during full apple and OSR bloom (for sampling dates see Table A.1). Pan traps and transect walks differ in the efficiency with which they record flower-visiting insects (O'Connor et al., 2019), hence we used both methods to sample insect communities. For each site and crop, we used nine pan trap sets (three of each colour, diameter 24 cm) mounted on sticks at 70 cm in order to trap insects visiting crop flowers (Tuell and Isaacs, 2009). The pan traps were placed within a crop and at a minimum of 50 m from the orchard or field edge, with a distance of 50 m between a triplet of blue, white and yellow pan traps. In the apple orchards, a pan trap triplet was placed in a triangle with a minimum of 3 m between traps of a triplet; in OSR fields, pan traps were placed directly next to tractor tracks in a row, also with a minimum of 3 m distance between traps in a triplet. Pan traps were 2/3 filled with odour-free soapy water and exposed from 09:00 to 17:00 on the same day of full apple and OSR bloom with warm and calm spring weather. Temperature (°C) and wind speed (m/s) data were collected from the closest weather station to each site (Table A.1). Collected insects were stored in 70 % ethanol and later identified under a stereomicroscope (Olympus SZX7) using the key of Fauna Helvetica (Amiet, 1996). We identified bees down to genus (members of Halictidae to family; see Table A.2). We did not use finer taxonomic resolution as observed bee richness as well as Shannon bee diversity calculated from genus-level data correlated highly with the same matrics calculated with species-level data in an independent set of apple orchards (see Fig. A.1 and Supplementary Methodology).

2.3. Quantifying pollination service provision in apple orchards

To quantify provision of the ecosystem service of pollination in apple orchards, we performed a pollination experiment at all 12 sites. At 11 sites, we used the apple variety 'Pinova', one of the most common cultivars grown in Saxony-Anhalt. Pinova is self-sterile (S-alleles: S_2S_9) and requires cross-cultivar compatible pollen for successful seed and fruit development (Matsumoto, 2013). At one site (Eisleben Aue) the variety Pinova was absent and therefore we chose 'Elstar', another self-sterile cultivar (S_3S_5) also requiring cross-pollen to set fruit and seed (Matsumoto, 2013). Due to frost damage during Pinova flowering, we excluded two sites

(Plößnitz and Spören) from the analysis of pollination service provision, measured as fruit set and seed set.

At each site, we selected one row of trees, centrally located within the orchard. In this row, we chose 45 trees, 15 for each flower treatment, using one flower per tree (bagged, open or hand pollinated), and at least 50 m from the orchard edge adjacent to the nearest OSR field. Inflorescences at a site were on the same side of the tree row to avoid variation in shade and microclimate. At one site, the number of replicates per treatment was higher (Gatterstädt: 20 flowers per treatment). We always used the 'king bud' (i.e. the bud producing the largest, central flower of an inflorescence, which typically opens first) on a total of 465 inflorescences.

In the insect exclusion treatment (treatment 'bagged': B), we bagged in fine netting (1 mm PVC mesh) the king bud at the closed red-bud stage to prevent pollen deposition by insects, a treatment designed to represent fruit/seed set by wind pollination. King bud flowers assigned to the hand pollination treatment (treatment 'hand': H), designed to represent maximal pollination at an orchard, were manually pollinated with pollen from the freshly dehisced anthers of a flower of a compatible pollinizer from the same orchard. To do so, fresh pollen from a local compatible apple variety was collected and applied to the king bud flower at its most receptive stage (day 2–3 of anthesis) until fully covered with pollen. For pollination of the variety Pinova, we used the variety Elstar as pollinizer, and for the variety Elstar we used 'Idared' (Matsumoto, 2013). Treatment H was undertaken during peak apple bloom at the end of April/early May 2017. After manual pollen application, hand-pollinated flowers were left open for additional insect visitation. The third treatment, reflecting the actual pollination supply to apple flowers at each orchard, received unhindered pollination by insect flower visitors (treatment 'open': O). Flowers used for the three treatments were marked with coloured cable ties and cord so they could be located later to measure the fruit set and to harvest the apples so as to measure the seed set.

Pollination service provision (*PSP*) was calculated at each site using an index which we adapted from Spears' (1983) index of single-visit pollination efficiency (Spears, 1983). We define *PSP* as:

$PSP = (O - B)/ (H - B)$,

where O, B, and H are measured as either fruit set or seed set obtained from each treatment: open, bagged or hand, respectively. Theoretically, *PSP* varies between 0 (zero pollination service provision) and 1 (maximal service provision) to the crop. Note that when a flower did not set fruit, then seed set was also recorded as zero i.e. all flowers of all treatments were included in *PSP* fruit set and *PSP* seed set.

2.4. Measurement of fruit set and seed set

At the beginning of June 2017, we visited each site to record early apple fruit set, prior to commercial thinning. As only the flower arising from the king bud of each inflorescence was used for our experiment, the other apples on the same flower-bearing spur were removed. At the end of August, before commercial harvest (mid to end September for both Pinova and Elstar), all apples from the experiment were collected. Seed set, as a surrogate for fruit quality (Wu et al., 2021), was counted within 5 days of harvest.

2.5. Landscape variable

The percentage of OSR in the surrounding landscape of apple orchards was ground-truthed by determining the crop grown in each field during experiments in 2017 at six radii (250 m, 500 m, 750 m, 1000 m, 1500 m and 2000 m). The percentage of OSR within each of the six radii was then used to identify the scale at which OSR had the most power to explain insect occurrence and pollination service provision. To do so, we correlated the percentage of OSR with a range of measurements of bee biodiversity from the pan trap material and transect walks and of experimental pollination data (PSP) at each of our study sites at all six scales. Spearman rank correlation coefficients reached their greatest absolute value at a radius of 1000 m (Table A.3), which was then chosen as the spatial scale for subsequent analyses. Though honey bees and bumble bees can fly further than this distance, their main foraging ranges are less than 1000 m (Bänsch et al., 2020b).

As land use surrounding a crop is known to impact pollinator biodiversity within the crop (Kennedy et al., 2013; Martin et al., 2019), we accounted for it by quantifying the percentages of semi-natural land (nature reserve, heathland, scrub and flower-rich grassland), farmland (arable land, vineyards, orchards and intensively grazed meadows), urban cover (residential, industrial, commercial and retail) and urban green areas (park, cemetery, allotment and recreation grounds) in the landscape surrounding each apple orchard and each OSR field. Land-use data were extracted from land cover maps (Geofabrik GmbH, Germany) in ArcMap v. 10.5 at the 1000 m radius from the OSR field or orchard border. From these data, we calculated landscape diversity (H_s) for each site and crop type as:

$H_s = - \Sigma p_i \times \ln p_i$

where p_i is the proportion of each land cover type i (Krebs, 1989).

2.6. Apple orchard layout and focal field size

Within-field agronomic practices affect pollination service provision (Lundin et al., 2013; Klein et al., 2015; Marini et al., 2015). Apart from the number of insect pollinators visiting flowers (pollinator ‘quantity’), suitable pollen from a compatible variety might also limit the successful pollination of an apple flower. Therefore, we additionally mapped, in each orchard, the distance of our experimental array of trees to the nearest suitable pollinizer.

To control for the effect of field size on bee biodiversity in apple orchards and in OSR fields, we additionally estimated focal field sizes of apple orchards and OSR fields with ArcMap v. 10.5.

2.7. Statistical analysis

To investigate the effect of the percentage of OSR in the landscape on the abundance of honey bees, bumble bees and other wild bees measured by transect walks in apple orchards, we used generalised linear models (GLMs) with a negative binomial error structure implemented in the R package *MASS* (Venables and Ripley, 2002). We un- dertook this analysis for each pollinator group separately. As the presence of honey bee hives in an orchard might influence the number of honey bee flower visitors (Bartholomée et al., 2020) as well as negatively affect the number of wild bees (Herbertsson et al., 2016; Lindström et al., 2016), the presence of honey bee hives was included in all statistical models as a fixed factor (Table A.4). Landscape heteroge- neity and apple orchard size were included as explanatory variables. The same statistical approach was used to investigate the effects of apple orchards on insect abundance in OSR fields, measured by transect walks within OSR fields (Table A.5).

While transect walks are well suited to study plant-pollinator associations (Westphal et al., 2008), pan traps are an efficient, cost-effective method for sampling bee diversity excepting honey bees, which they rarely trap (O’Connor et al., 2019). From the 499 and 529 bees caught by pan traps in apple orchards and OSR fields, respectively (see Table A.2), we calculated the Shannon diversity of bees and observed bee richness per site and crop. We then used linear models (LMs) to investigate the effect of the percentage of OSR in the landscape (1000 m radius) and the percentage of apple orchard around OSR fields on observed bee richness and diversity in each crop, with the percentage of OSR/apple orchards in the landscape and the presence of honey bee hives included as fixed factors. Landscape heterogeneity as well as field size were further included as explanatory variables.

We tested the effects of pollination treatment (pollination exclusion (B) *vs*. insect pollination (O) *vs*. pollen supplementation (H)) on fruit set using a generalised linear mixed model (GLMM) with Binomial error structure. Orchard identity was included as a random factor. A Tukey post-hoc comparison was used to test for differences between treatment groups using the R package *multcomp* (Hothorn et al., 2008).

To test the effect of co-flowering OSR in the surrounding 1000 m radius on apple pollination service provision (PSP, calculated from both fruit set and seed set), we used LMs. To do so, the percentage of OSR in the landscape was used as a fixed factor and other potentially important environmental variables i.e. landscape heterogeneity, distance to the next pollinizer tree, the number of honey bees, bumble bees and other wild bees, as well as Shannon diversity of bees were used as further explanatory variables.

R.3.3.1 (R Core Team, 2016) was used for all statistical analyses. For the analyses of transect data, pan trap material and pollination service provision, we used an all-subset automated model selection approach based on the Akaike Information Criterion corrected for small sample size (AICc), with the *dredge* function (R package *MuMIn*; Bartón, 2018) and with a maximum of three predictors to avoid model overfitting. We used a cut-off of ΔAICc of 2 (Burnham and Anderson, 2002) to evaluate model fit (as no more than one model was retained in each analysis, we did not need to employ model averaging). We performed all mixed models using the package *lme4* (Bates et al., 2015). All models were checked for collinearity using variance inflation factors (VIFs) with a cut off value of 5. VIFs were lower than 5 for all predictors, indicating no major effects of collinearity. The residuals of all models were checked for spatial autocorrelation using Moran's I (Paradis et al., 2004). Residuals were not found to be autocorrelated ($P > 0.05$). All model assumptions (residuals normally distributed, homogeneity of variance, linearity, non-overdispersion) were checked visually using the package *LMERConvenienceFunctions* (Tremblay and Ransijn, 2015).

3. Results

3.1. Effects of OSR on bees in apple orchards

During spring 2017, we recorded a total of 1,818 insects during transect walks in apple orchards, of which the majority was bees (1,728, see Table A.2). In pan traps placed in apple orchards, we collected 11,235 insects in total, of which the majority was flies (10,511) and 499 were bees. While species were categorized into morphological groups during the transect walk (e.g. honey bees, bumble bees, other wild bees), bees caught by pan traps were identified to genus level. The bee genus richness ranged from 2 to 5 in the apple orchards. For a summary for insects collected in apple orchards and OSR fields, see Table A.2.

Honey bees were the dominant flower visitors we observed on transect walks in apple orchards, with a mean of 123 (± 90 S.D.) honey bees out of 152 (± 90 S.D.) total flower visits per transect. Seven out of 12 orchards in our study employed managed honey bees to increase pollination service provision and, as expected, we recorded higher numbers of honey bees on apple flowers during transect walks in orchards with hives (mean 165 ±93 S.D.) versus in orchards without hives (mean 63 ± 36 S.D.; difference between means; GLM, $t_9 = 3.361$, $P < 0.001$, $R^2_{adj} = 0.25$).

The automated model selection approach to explore the effects of OSR on the abundance of honey bees, bumble bees and other wild bees estimated by transect walks in apple orchards resulted in one best model for each bee taxon (ΔAICc < 2). Our best models included both the percentage of OSR and the presence of honey bee hives as predictors (Supplementary Table A.4). We found a negative effect of the percentage of OSR on the number of honey bees recorded on apple flowers during transect walks (GLM; $Z_9 = -3.071$, $P = 0.002$, $R^2_{adj} = 0.25$, Fig. 2a); honey bee numbers approximately halved across apple orchards with increasing OSR in the vicinity (Fig. 2a). The number of bumble bees recorded on apple flowers was not affected by the percentage of OSR in the landscape (GLM; $Z_9 = 0.897$, $P = 0.370$, $R^2_{adj} = -0.10$, Fig. 2b). The number of wild bees (excluding bumble bees) observed during transect walks in apple orchards increased with the percentage of oilseed rape in the landscape (GLM; $Z_9 = 2.123$, $P = 0.034$, $R^2_{adj} = 0.26$, Fig. 2c), approximately doubling across apple orchards with increasing OSR in the vicinity (Fig. 2c). Both the number of bumble bees and the number of other wild bees in orchards were independent of the presence of honey bee colonies (GLM; bumble bees: $Z_9 = 1.058$, $P = 0.290$, $R^2_{adj} = - 0.10$; GLM; other wild bees: $Z_9 = -0.165$, $P = 0.870$, $R^2_{adj} = 0.26$).

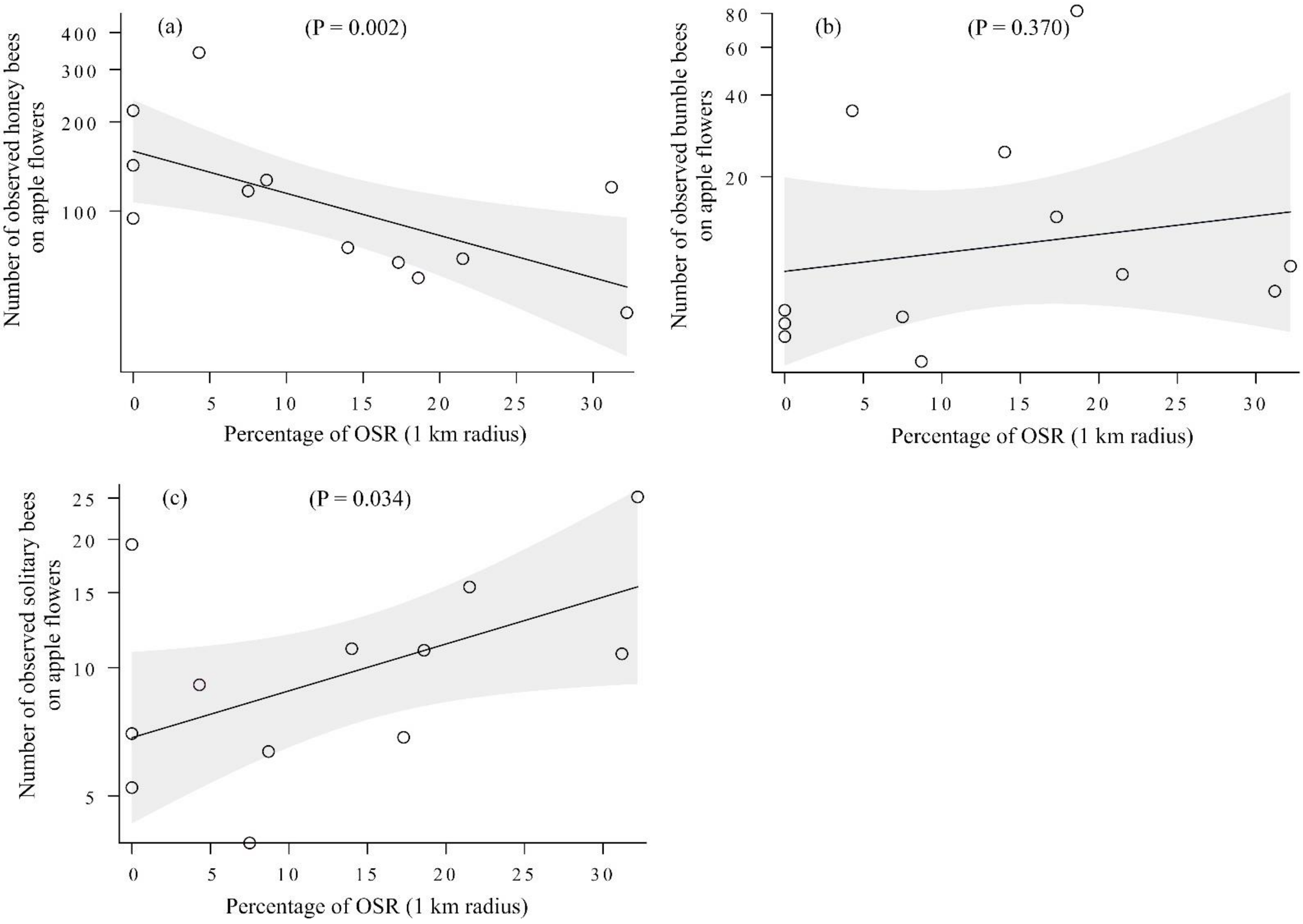

Fig. 2. Relationships between the numbers of a) honey bees, b) bumble bees and c) other wild bees as visitors of apple flowers with the % of oilseed rape within a 1000 m radius of 12 apple orchards. Plotted lines show the predicted relationships, open circles indicate negative binomial generalised linear model estimated means, shaded areas indicate the 95 % confidence intervals, and significance is shown in parentheses (negative binomial GLM).

The automated model selection approach to explore the effects of OSR on the Shannon diversity and observed bee richness of bees estimated using pan traps in apple orchards resulted in one best model for each dependent variable (ΔAICc < 2). Again, our best models included the percentage of OSR and the presence of honey bee hives (Supplementary Table A.4). Although the percentage of OSR at 1000 m radius was included as predictor in the best model, its effect on the Shannon diversity of bees was non-significant (LM; t_9 =0.423, *P* =0.682, R^2_{adj} =-0.11). We found a marginally negative effect of OSR on observed bee richness in apple orchards (LM;

t_9 = -1.968, *P* = 0.081, R^2_{adj} = 0.15). The presence of honey bee hives did not affect the Shannon diversity or observed richness of bees (LM; Shannon diversity: t_9 =0.933, *P* =0.375, R^2_{adj} = -0.11; observed richness: t_9 = -0.326, *P* = 0.752, R^2_{adj} = 0.15).

Landscape heterogeneity, the proportional cover of apple orchards or the size of apple orchards were not included as predictors in any of the best models for the abundance of bee taxa estimated using transect walks and for the and Shannon diversity and observed richness of bees estimated from pan trap material in apple orchards.

The results of the effects of apple orchards on bee abundances and bee diversity in OSR fields are presented in the Supplementary Results and Supplementary Table A.5.

3.2. Pollination in apple orchards

Bagged apple flowers (treatment B) set only 0.63 ± 0.63 S.E.M. % fruits across all sites, confirming that the studied apple varieties Pinovar and Elstar were obligately insect pollinated. Fruit set was higher for manually cross-pollinated flowers (treatment H; mean =48.32 ±4.11 S. E.M. %) compared to open flowers (treatment O; mean =18.92 ±6.88 S. E.M. %), suggesting that fruit set was pollen-limited. The three pollination treatments differed significantly from each other (GLMM; $P < 0.05$; Table A.6, Fig. 3).

Pollination service provision (*PSP*), calculated as the final fruit set, varied between -0.18 and 0.92 across sites and, calculated as seed set, it varied between 0.00 and 0.95. These values reflect considerable variation in pollination service provision across apple orchards. Values lower than zero likely arose through biological variability at orchards with extremely low pollination service provision (Open < Bagged). *PSP* (fruit set) and *PSP* (seed set, a measure of fruit quality, see Wu et al., 2021) were highly correlated (Pearson correlation: r = 0.939, *P* < 0.001, Fig. A.2).

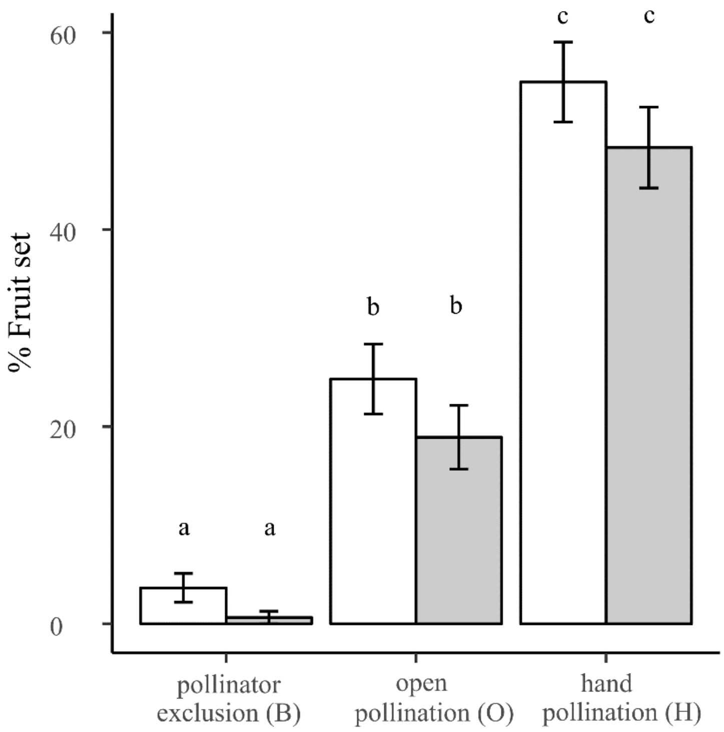

Fig. 3. Effect of pollination treatment on the initial (white) and final (grey) fruit set of apples (mean ± S.E.); means differ significantly across but not within treatments for initial (white) and final (grey) fruit set (GLMM; means with different lower case letters: *P* < 0.05; see Supplementary Table A.6).

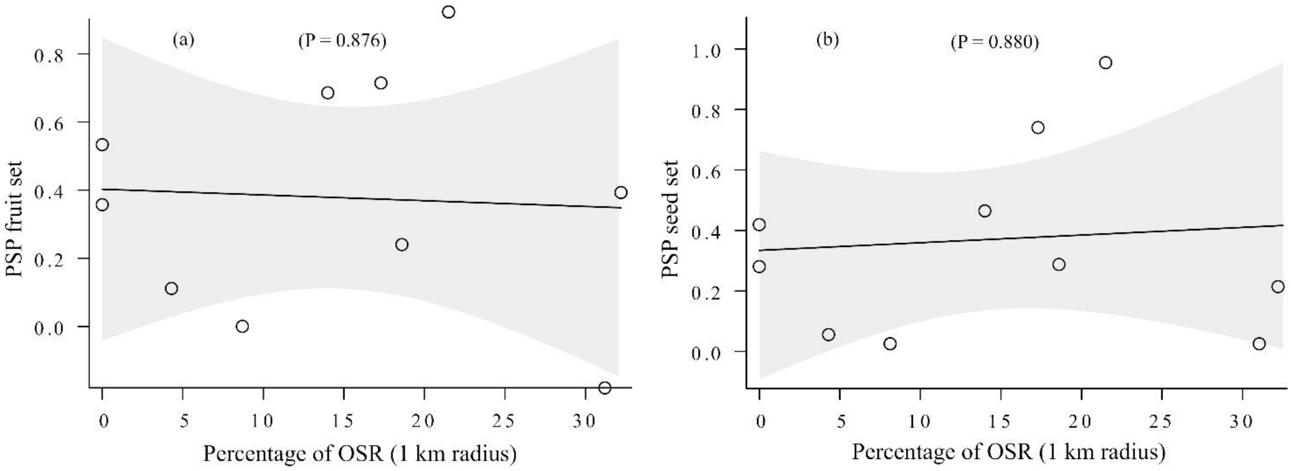

Fig. 4. Relationship between the index of pollination service provision (*PSP*) in apple orchards calculated as a) fruit set or b) seed set versus the percentage of OSR within a 1000 m radius of 10 apple orchards. Plotted lines show the predicted relationships, open circles indicate linear mixed model estimated means, shaded areas indicate the 95 % confidence intervals, and significance is shown in parentheses (LM).

3.3. Effects of oilseed rape on pollination in apple orchards

The automated model selection approach to explore the effects of OSR, landscape heterogeneity, orchard size and bee taxon abundance (i.e. honey bees, bumble bees, other wild bees each treated as separate taxa) on *PSP* resulted in one best model for each of *PSP* (fruit set) and *PSP* (seed set) (ΔAICc < 2). The percentage of OSR was the only predictor included in both best models, yet neither *PSP* (fruit set) nor *PSP* (seed set) was affected by the percentage of oilseed rape in the sur- rounding 1 km (LM; *PSP* (fruit set): t_8 =-0.161, P =0.876, R^2_{adj} =-0.12, Fig. 4a; *PSP* (seed set): t_8 = 0.156, P = 0.880, R^2_{adj} = -0.12, Fig. 4b). All other predictors explaining *PSP* (fruit set) and *PSP* (seed set), including abundances of honey bees, bumble bees and wild bees during transect walks, were excluded by our model selection process.

4. Discussion

We found that OSR, a mass flowering crop, attracted honey bees away from apple orchards such that there were fewer honey bees visiting apple flowers in orchards surrounded by OSR fields. Bumble bee densities in apple orchards were not affected and other wild bees even increased in number with increasing cultivation of OSR in the vicinity of apple orchards. Pollination of apple, measured as fruit or seed set, was not affected by the percentage of OSR in the landscape, even though the studied apple orchards were seemingly pollen limited due to lack of pollinators. We conclude that OSR, a mass flowering crop, competes with co-blooming apple for flower-visiting honey bees, but that wild bees may compensate for the loss of honey bees and ensure stability in apple yield. The observed higher wild bee densities in apple orchards surrounded by oilseed rape could be due to their release of competition with honey bees, as observed in other studies (Magrach et al., 2017).

In our study, we demonstrate again the fundamental importance of insect pollination in apple fruit set, as shown by Free (1993) and many others (reviewed in Pardo and Borges, 2020). The increase in fruit set of apple following hand pollination with compatible pollen collected from a pollinizer located in the same orchard suggests that there was a deficit in pollination service provision – as opposed to a deficit in the avail- ability of viable, compatible pollen – in our study apple orchards, as also seen in many other studies in commercial apple orchards (Garratt et al., 2014; Blitzer et al., 2016; Samnegård et al., 2019). Our treatment H remained unbagged after experimental hand pollination and was therefore exposed to the same regime of flower visitation as treatment O (open) flowers. That treatment H consistently set more fruits and seeds than treatment O suggests that O flowers did not suffer from over-pollination (e.g. due to stigmatic clogging) following an excess of flower visits (Rollin and Garibaldi, 2019). Pollination service provision was therefore likely pollinator visitation limited in our orchards.

We documented a trend for decreasing honey bee abundance observed during transect walks in apple orchards with an increasing percentage of OSR in the landscape. Pollinator management by apple orchardists often includes renting honey bee hives to enhance pollination services (Park et al., 2018). This practice might be ineffective if a competing crop like oilseed rape attracts honey bees away from apple flowers. Nevertheless, we still detected an influence of the presence of hives on the number of apple flower visits by honey bees; similarly as in France, where the presence of hives has also been found to be a good predictor of the number of honey bee flower visitors in fruit orchards (e. g. apple, pear, peach, cherry, peach; Bartholomée et al., 2020). Thus, adding honey bee hives to apple orchards still seems to have the effect of increasing honey bee visitation to apple flowers, even if OSR blooms in the vicinity and attracts honey bees from those same apple orchards.

We found that OSR co-flowering in the vicinity of commercial apple orchards seems to compete with apple for honey bee flower visitors. Previous studies have also shown that mass-flowering crops can dilute pollinator abundance in agricultural landscapes (Riedinger et al., 2015; Holzschuh et al., 2016) and co-blooming crops can compete for pollinators (Grab et al., 2017; Bänsch et al., 2020a). Yet these effects can differ between pollinator functional groups, possibly due to taxon-specific differences in pollinator flight ranges (Bänsch et al., 2020a). While we found that OSR reduced the number of flower-visiting honey bees in apple orchards, the number of bumble bees in apple or- chards remained constant whilst other wild bees even increased in abundance with more OSR in the landscape, similar to findings by Bänsch et al. (2020a) in strawberry crops co-flowering in the vicinity of OSR. The significant rise in the number of non-*Bombus* wild bees we observed in apple orchards surrounded by OSR fields might be due to reduced competition for floral resources with honey bees (Herbertsson et al., 2016; Lindström et al., 2016).

That the abundance of wild bees observed during transect walks and the Shannon diversity of bees caught by pan traps were not negatively affected by OSR in the landscape might be also a consequence of the short foraging ranges of many wild bee species (Greenleaf et al., 2007); pollinators may exhibit taxon-specific responses to the increase of OSR or other mass flowering crops in the landscape (Stanley and Stout, 2013; Bänsch et al., 2020a). The maximum foraging distances between nesting site and food patch for several solitary bee species has been estimated to be below 150 m (Hofmann et al., 2020), suggesting that local habitat structures and floral resources are more important than large-scale landscape configuration in determining their abundance and, by inference, pollination services they provide (Gathmann and Tscharntke, 2002).

We then sought to test whether the observed competition by co-blooming crops for pollinators thereby hindered pollination service provision to apple. Despite OSR fields apparently drawing honey bees from apple orchards, we could not detect a negative effect of mass flowering OSR on apple yield and apple quality; PSP (fruit set) and PSP (seed set) in apple orchards remained stable. We hypothesise that, as the percentage of OSR increases in the vicinity of an apple orchard, honey bees are drawn away from apple bloom to OSR flowers, but pollination of apple is compensated by an increase in the number of wild bee visits to apple, thus guaranteeing fruit and seed set in apple orchards. Inter- estingly, honey bee numbers approximately halved with a rise in OSR across the experiment whereas wild bee numbers doubled, though were always less numerous than honey bees on flowers, suggesting that wild bees might be more effective pollinators or indirectly enhance honey bee pollination services (Brittain et al., 2013). Mallinger and Gratton (2015) found that apple fruit set was not affected by the number of flower-visiting honey bees but significantly increased with the richness of wild bees. In Argentina, apple fruit set was reduced by half in orchards where bumble bees were absent, even when honey bees were present at high densities (Pérez-Méndez et al., 2020). These studies underpin the importance of wild bees in apple pollination. A recent meta-analysis has suggested a non-monotonic relationship between honey bee visitation rate and fruit or seed set, with an optimum of ca. eight-ten honey bee visits per flower (Rollin and Garibaldi, 2019). By attracting honey bees away from apple orchards and reducing the number of apple flower visits by honey bees, the effect on fruit or seed set might not be consequently negative, especially if the number of visits per flower are sufficient for fertilisation of all of an apple flower’s 10 ovules (Vicens and Bosch, 2000). Data on the absolute number of flower visitors would be required to test this idea, though two of our datasets: (i) our hand pollination results demonstrating good pollination by cross-compatible pollen acquired in the same orchard and lack of support for over-pollination (e.g. through stigmatic pollen clogging) and (ii) the marked decrease in honey bee visitation of apple flowers with increasing OSR in the vicinity, suggest that our orchards were limited by insufficient pollinator visits. We, therefore, conclude that in our study system the maintenance of pollination in apple orchards surrounded by co-blooming OSR is due to wild bees that compensate for the loss of honey bees to OSR.

Our study underscores the importance of wild bee conservation not only in semi-natural areas (Campbell et al., 2017) but also in agricultural landscapes that increase in pollinator dependency (Aizen et al., 2008, 2019) so as to guarantee crop pollination (Garibaldi et al., 2013). Agri-environmental measures, which have been shown to promote populations of widespread and common wild bee species (Powney et al., 2019), might compensate for the negative consequences of agricultural intensification. Further effort in wild bee conservation should be promoted to ensure stability of apple crop yields. As Nicholson et al. (2019) advocate, to promote a stable pollinator community and meet an in- crease in pollination demand, future agri-environmental schemes should aim to balance pollination demands in agriculture to avoid competition for pollinators among co-flowering crops and promote wild bee pollinators

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Chapter II. Managed mason bees enhance sweet cherry fruit set in commercial orchards

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Abstract

1. Mason bees are efficient fruit tree pollinators that can be managed to enhance their pollination. With shorter flight ranges than honey bees, management practices and recommendations might be different from those for honey bees. Optimal densities of mason bee nesting material and their distribution to increase numbers in orchards are yet still unclear. Furthermore, while mason bees have been shown to increase the yield of some crops, their effect on sweet cherry fruit set is still unknown. Furthermore, effects of mason bees and honey bees on fruit set are often investigated separately, while they can synergistically enhance crop yield.

2. We assessed the impact of mason bee management on flower visitor abundances in 17 sweet cherry orchards in Central Germany and analysed the main pollen resources they used for provisioning nests. Through a pollination experiment, we explored the interactive effect of mason bees and honey bees on yield across sites. In addition, we tested the effects of mason bees within sites by accounting for the distance between trees to bee nesting boxes to give management recommendations to farmers.

3. We found that both honey bee abundance and mason bee abundance increased with hive or nesting material density, respectively. Pollen collected by mason bees originated primarily from

the plant genus *Prunus*, suggesting that mason bees forage upon sweet cherry for floral resources (nectar and pollen).

4. Our pollination experiment demonstrated that the study orchards were pollen limited, with 28% of insect-pollinated flowers setting fruits versus 39% of hand-pollinated flowers. Sweet cherry fruit set increased across study sites synergistically with increasing mason bee and honey bee abundance while by enhancing only one of the two managed bee species sweet cherry fruit set remained low. We also show that within orchards, fruit set decreased with increasing distance to mason bee nesting material.

5. *Synthesis and application*. Providing nesting material for mason bees and employing honey bee hives enhances their abundances in sweet cherry orchards; we suggest distributing nesting material at 100 m intervals within orchards i.e. 2 boxes per ha to ensure stable pollination services within sites. By providing managed honey bees as well as enhancing wild bee populations at the same time, sweet cherry farmers can substantively boost fruit set and crop yield. To enhance pollination services, farmers should consider the benefit of biodiversity to ecosystem serivices. Managing more than one species for crop pollination can improve sweet cherry yield.

Keywords: European orchard bee, Crop pollination, Ecological intensification, *Osmia cornuta*, Pollination management

1. Introduction

For many crops, insect pollination is essential for successful fruit development (Klein et al., 2007), including sweet cherry (*Prunus avium* (L) Moench). Most sweet cherry varieties are self-sterile and they require cross-pollination (Free, 1993), to which wild pollinators are thought to contribute significantly (Holzschuh et al., 2012; Eeraerts et al., 2017, 2019a). However, habitat loss and land-use intensification due to agricultural practices are among the various human pressures that have contributed to declines in wild pollinator abundance and diversity (Potts et al., 2016). For example, intensive cherry fruit cultivation in Belgium is linked to a reduction in pollinator species richness and abundance and subsequently decreased sweet cherry fruit set (Eeraerts et al., 2017). Likewise, with the loss of wild bee habitat in the landscape surrounding German cherry orchards, visitation rates of wild bees decreased along with fruit set and yield (Holzschuh et al., 2012). Reduced fruit set of sweet cherry has been documented also in North America possibly as a consequence of a lack of pollinators (Reilly et al., 2020).

In intensified, agricultural landscapes with little natural habitat, farmers can actively engage in pollinator management or enhance local bee habitats on farms to ensure sufficient provision of crop pollination (Garibaldi et al., 2017; Osterman et al., 2021a). Worldwide, 66 species of insect can be managed for pollination services of which the Western honey bee (*Apis mellifera*) is the most prominent and used for the pollination of many crops (Osterman et al., 2021a). Also, mason bees (*Osmia* spp.) have been used as managed pollinators for many decades, especially for the pollination of rosaceous fruit trees, including cherry (Maeta and Kitamura, 1974; Torchio, 1976; Bosch and Kemp, 2001, 2002; Kornmilch, 2010; Osterman et al., 2021a). The acceptance by mason bees of multiple nesting materials (e.g. wooden blocks, bamboo, cardboard nesting material) and their gregarious nesting behaviour are important preconditions for successful mass rearing and feasible species management (Torchio, 1976). Moreover, mason bees have several traits that make them a suitable pollinator for sweet cherry varieties that flower in early spring, a time when inclement weather spells are frequent, leading to subsequent negative effects on fruit set (Roversi and Ughini, 1996). The flight activity of honey bees is limited at ambient temperatures below 12°C and therefore they might be inefficient for the pollination of an early flowering crop such as sweet cherry (Vicens and Bosch, 2000a). *Osmia* (mason bees) species can, in contrast, maintain their flight activity under low ambient temperatures, in light rain, and during windy conditions, ensuring a more uniform and consistent pollination service provision that is largely independent of inclement weather (Bosch and Kemp, 1999; Vicens and Bosch, 2000b). *Osmia cornuta* (the European orchard bee; Latreille, 1805; Megachilidae) is one of the first bees to emerge in spring in Central Europe, followed by *O. bicornis* (red mason bee; Linnaeus, 1758; Megachilidae) (Westrich, 2018); the phenology of both coincides with the flowering of sweet cherry, reinforcing their potential role in sweet cherry pollination.

Mason bees are also considered effective pollinators of sweet cherry flowers due to their putative higher efficiency (Eeraerts et al., 2020b). Their higher rate of row changes compared to honey bees or bumble bees potentially ensures good pollen transfer for a crop like sweet cherry (Eeraerts et al., 2020b) that requires cross-pollination to set fruit. Many solitary bees have a flight range below 150 m (Hofmann et al., 2020), reducing the effect of competing co-flowering crops in drawing them away from a target crop compared, for instance, to honey bees (Bänsch et al., 2020; Osterman et al., 2021b). A small flight range, on the other hand, suggests that a local-scale distribution of nesting materials within an orchard is necessary to ensure an overall sufficient pollination service across an orchard by mason bees (Bosch et al., 2021). Optimal distirubution patterns have not been tested for sweet cherry orchards yet. In addition, the presence of non-*Apis* bees can alter the foraging behaviour of honey bees by causing them to switch trees more frequently within an orchard, making them more efficient pollinators and again leading to higher yields (Greenleaf and Kremen, 2006; Brittain et al., 2013; Pitts-Singer et al., 2018; Eeraerts et al., 2020a).

Osmia cornuta and *O. bicornis* have been promoted in European orchards for more than three decades (Krunic et al., 1991; Osterman et al., 2021a) and are nowadays traded by several companies in Europe. Though the role of *Osmia* spp. populations for fruit set have been assessed in several crops (Sheffield, 2014; Pitts-Singer et al., 2018; Boyle and Pitts-Singer, 2019; Ryder et al., 2019), their effect on pollination services in sweet cherry orchards is little understood. In many studies, the effect of mason bees and/or honey bees are investigated separately but not their interaction (e.g. Bosch et al., 2021), while they have been shown to synergistically increase yield (Brittain et al., 2013). Also, guides for mason bee management are rare. In particular, few studies have investigated optimal on-farm distances between orchard trees and mason bee nesting sites for fruit set (Bosch et al., 2021).

In this study, we aimed to test (1) whether mason bee and honey bee populations can be enhanced through the provision of nesting material and employing hives, respectively, by assessing their abundance in 17 commercial sweet cherry orchards in Germany varying in intensity of habitat enhancement. We furthermore tested whether *Osmia* spp. and honey bees synergistically increase sweet cherry fruit set by (2) assessing the relationship between the number of mason bees and honey bees in relation to fruit set across orchards. In a subset of 5 orchards, we investigated (3) whether fruit set varied within an orchard with respect to distance to mason bee nesting material. On the basis of our results, we give recommendations for farmers on their pollination management to ensure stable fruit set in sweet cherry orchards.

2. Methods

2.1. Study sites

Fieldwork was carried out in spring 2020 in orchards within the federal states Saxony-Anhalt and Thuringia, Germany (Fig. 1). Both federal states are dominated by agricultural land use (>60%). We selected 17 sites, of which two are experimental orchards and 15 are commercial mixed fruit orchards (for details, see Supplementary Table A.01). The size of the orchard devoted to cherry cultivation ranged between 0.2 ha and 36 ha (6.6 ± 8.6; mean ± SD). Distances between field sites were >2 km (47.9 ± 28.9 km; mean ± SD) to ensure spatial independence.

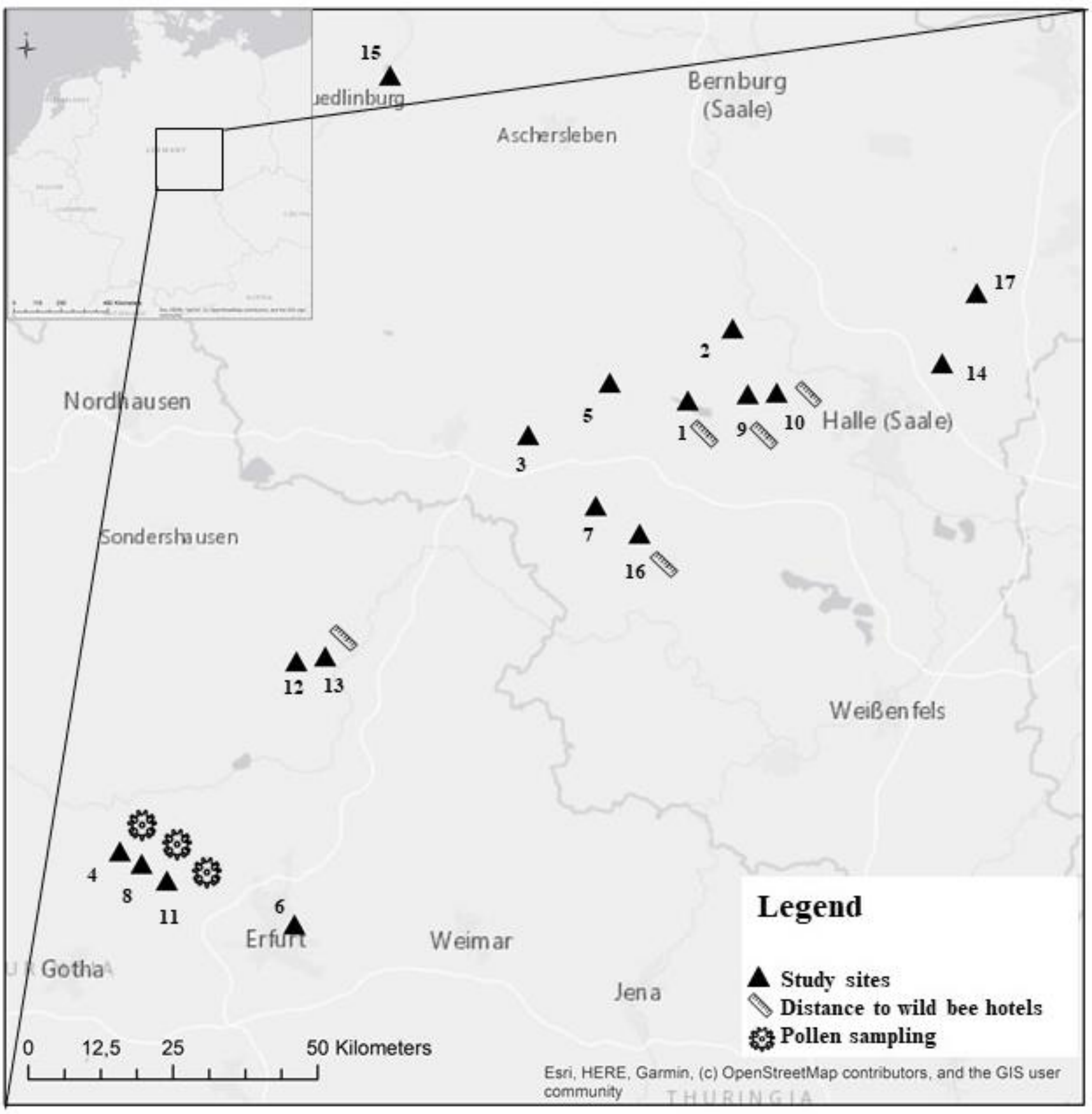

Fig. 1: Study sites in Central Germany. In 2020, bee abundance and fruit set were measured in 17 sweet cherry orchards (black triangles) with varying bee management. In a subset of 5 sites (yardsticks), we measured fruit set with respect to distance to mason bee nesting material. In a subset of 3 sites (pollen grain), trap nests for mason bees were installed and the pollen identity of the provisioned nests was examined.

Pollination management consisted of providing honey bee hives and nesting material for mason bees. Commercial bumble bee nests were not used by cherry farmers in this study. To investigate the effect of bee management on bee abundances and subsequently on fruit set, we selected sites varying in their bee management. Mason bee management ranged from zero (i.e. no nesting material provided) to 8.6 boxes of nesting material provided per ha. On-farm pollinator management was decided prior to the study by the farmer and therefore the size of the boxes varied across sites. To make them comparable, we set the standard size of a nesting material box to be 100 x 54 cm containing approximately 500 tubes each of a length of 13-16 cm and a diameter of 4-10 mm (see Supplementary Fig. 01). The number of honey bee colonies per site (Supplementary Table A.01) varied from zero to 20 hives per ha.

2.2. Flower visitor observations

We quantified the abundance of insect flower visitors during the peak bloom of sweet cherry (16.04.2020 – 23.04.2020) at each site during one day. For each site, two transect walks of 90 minutes each were performed alongside cherry trees on a sunny day, one in the morning and one in the afternoon of the same day. Trees were >50 m distant from the edge of the orchard and included trees used for a pollination experiment (described below). Ambient (shade) temperatures during the transect walks were recorded with a digital thermometer; they ranged from 9°C to 22°C. Flower visitors that touched the reproductive parts of the flower were counted and identified into morphological groups: honey bees, bumble bees, mason bees, other wild bees, butterflies, flies, beetles, and ants.

2.3.Verification of mason bees as cherry flower visitors

To confirm that promoted mason bee populations are flower visitors of cherries, we identified the source of the pollen with which females provisioned their nests. To do so, we distributed 30 cardboard nesting tubes (15 of 7 mm diameter and 15 of 9 mm) per site at three sites (Fig. 1; sites 4, 8, and 11) before cherry bloom (end of February/beginning of March). During full cherry bloom (22.04.2020), the tubes were collected, cut open and the pollen provisions of the larvae were extracted. Per site, we created a pooled pollen sample; pollen identification of each pool was kindly performed by the Hohen Neuendorf Länderinstitut für Bienenkunde (https://www2.hu-berlin.de/bienenkunde/). A solution was made of 1 volume of pollen and 4 volumes of water. Drops of this solution were applied to a microscope slide, dried, and then fixed with glycerol gelatin (Kearns and Inouye, 1993). Under a microscope, all pollen grains were identified and quantified by counting 500 grains following the DIN-Norm 10760.

2.4. Pollination service provisioning in cherry orchards

In order to quantify pollination, we studied one of the most common sweet cherry cultivars, "Regina", which was present in all 17 study sites. This cultivar is self-sterile (S-alleles: S_1S_3) and requires cross-pollination for successful fruit development (Lech et al., 2008; Holzschuh et al., 2012). We chose at least one row of Regina trees in each orchard, which was planted either next to a cross-compatible pollinizer cultivar or which was interspersed with a pollinizer variety in the same row. Pollinizer cultivars varied across sites (Supplementary Table 01).

To quantify pollination service provision across sites, we selected 20 trees in each orchard that were at least 50 m from the orchard edge. On each tree, we applied three flower treatments: insect exclusion treatment (‘bagged’: B), hand pollination treatment (‘hand’: H), and open insect pollination treatment (‘open’: O). For each treatment, we chose a flower bundle, which we marked with coloured ribbons, cord and barrier tape to later locate the treatments. In some cases, several flower bundles were used for one treatment if one flower bundle contained less than three flowers. During full bloom and on the same day as observations of flower visitors, we counted all open and receptive sweet cherry flowers per bundle and removed over-flowered or still closed flowers. The insect exclusion treatment (B) had been bagged in fine netting (1 mm PVC mesh) prior to cherry bloom (6.04.2020 – 12.04.2020) to prevent insect pollination and remained bagged throughout cherry bloom; it enabled us to disentangle the contribution of wind pollination to fruit set. Flower bundles of treatment H were manually pollinated with pollen from at least two flowers of an adjacent pollinizer (see Supplementary Table 01 for pollinizer variety per site) as a measure of maximal fruit set. Treatment O remained unmanipulated as a measure of current pollination service provision.

Fruit set was counted three times, once in May as the initial fruit set (ca. four weeks after flowering), once in June after the so-called June fall (ca. eight weeks after flowering), and once prior to harvest, approximately at the beginning of July (ca. twelve weeks after the experimental manipulations). We divided the number of developed fruits per bundle by the number of flowers per bundle for each fruit count period (i.e., May, June, July) to give the percentage fruit set per treatment. In addition, we recorded the weight of each cherry fruit during the final fruit set count in July.

To investigate if pollination services provided by mason bees differed within sites, we measured the distance of individual trees to nesting material at five sites. At other sites, the distance between trees and nesting boxes was either invariant or no nesting material was provided. Honey bee management at those five sites was comparable, with 1.6 to 5.0 hives per ha.

2.5. Statistical analysis

To assess the effect of nesting material density and honey bee hive density on the abundance of mason bees and honey bees, respectively, as flower visitors of sweet cherry, we used generalised linear mixed models (GLMMs) with Poisson error structure. In both models, we included ambient temperature as an additional predictor variable to test its impact on insect abundance. Location (orchard) was included as a random factor. We compared linear models with non-linear models reaching an asymptote ($y \sim \log(x+1)$) by using the Akaike information criterion corrected for small sample size (AICc) as we expected a saturation effect of pollinator management on flower-visitor abundance. The best fit model was chosen by $\Delta AIC > 2$ with the *AIC* function in the *stats* package (version 3.6.2).

Initial fruit set (after four weeks) and final fruit set (twelve weeks) were correlated (Spearman rank correlation: $R = 0.29$, $P < 0.001$) as well as fruit set in June (eight weeks) and final fruit set ($R = 0.95$, $P < 0.001$). Therefore, we used only fruit set after twelve weeks in the subsequent analysis. Effects of treatment (hand pollination, insect pollination, and wild pollination) on the final fruit set were compared with a linear mixed effect model (LMM), with pollination treatment as predictor and location (orchard) as random factor (R package *lme4*; Bates et al., 2017). We also compared differences in fruit weight between treatments using an LMM, again with orchard as a random factor. To test for differences between treatment groups a Tukey *post hoc* comparison was used (R package *multcomp*; Hothorn et al., 2008).

We wanted to test if open fruit set (treatment O) was affected by bee abundances. As *Osmia* abundance correlated with the abundance of all non-*Apis* bees (Kendall rank correlation: $R = 0.52$, $P < 0.001$) in our study, we used *Osmia* abundance in the subsequent analysis. To investigate whether Osmia and honey bees synergistically improve sweet cherry fruit set, we included *Osmia* abundance x honey bee abundance as fixed factors in an LMM with orchard as a random factor. We also used an LMM with orchard included as a random factor to test the effect of distances between nesting material and orchard trees on fruit set (treatment O) at 5 sites.

3. Results

3.1. Effect of bee management on bee abundance in sweet cherry orchards

A total of 10,021 flower visits were counted on sweet cherry blossoms, of which honey bees (*Apis mellifera*) represented 70.2%, mason bees 15.6%, bumble bees 3.1%, other bees 6.7%, and the other visitors 4.4%. The relative abundance of mason bees per site and transect walk ranged from 0% to 94.1% whilst relative honey bee abundance ranged from 0 to 97.1%. Fourteen of 17 farmers (82%) used honey bee hives, which ranged in density from 1.3 to 17.0

hives per hectare (Supplementary Table 01). Thirteen of 17 farmers (76%) installed nesting material, mainly for mason bees, in their orchards. Nesting material density ranged from 0.1 to 8.6 boxes per hectare (Supplementary Table 01).

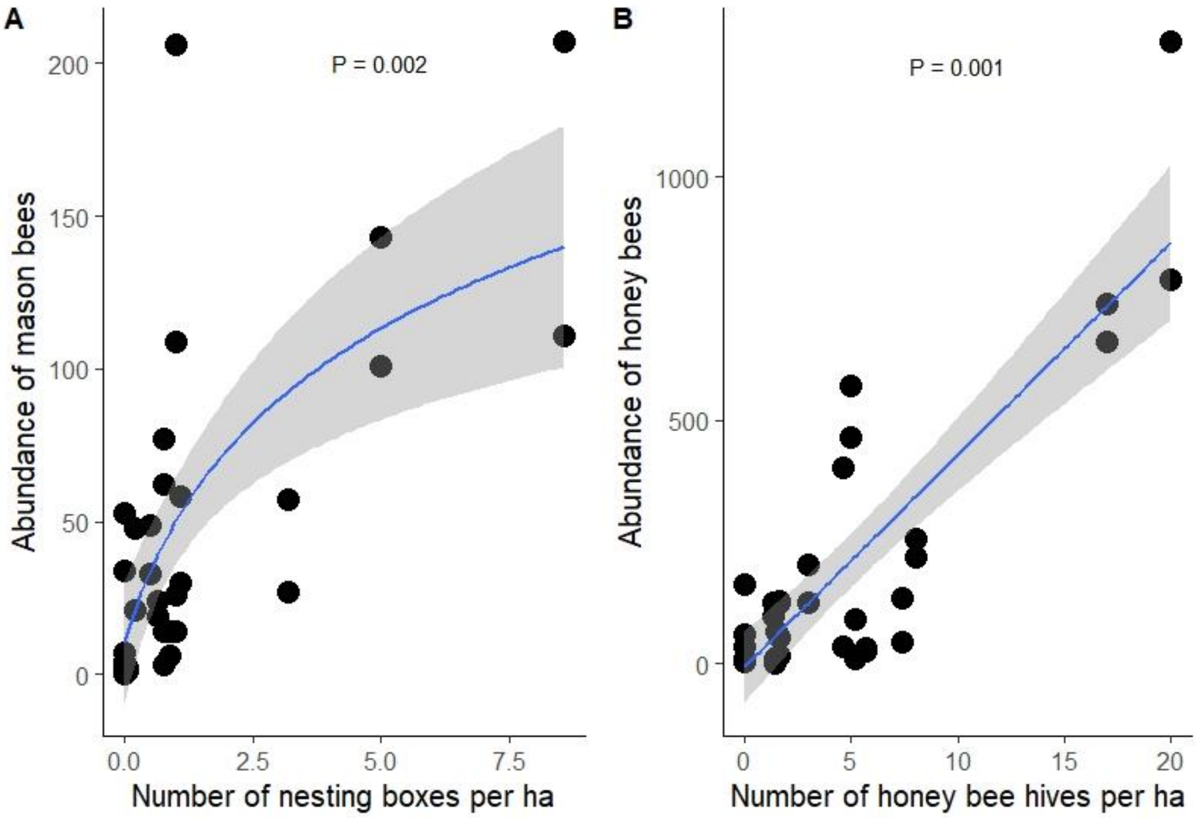

Fig. 2: Number of mason bees (A) and honey bees (B) observed during transect walks in relation to the amount of nesting material or the number of honey bee hives per ha, respectively. Shown in blue are the best fit lines (GLMM) and in grey the 95% confidence intervals.

Pollinator management had a clear effect on flower visitor abundance. With an increasing number of nesting material provided, the number of observed mason bees increased, reaching an asymptote (Fig. 2A; GLMM; $Z_{32} = 3.079$, $P = 0.002$) as the non-linear model provided the best fit (smallest value of AICc, see Supplementary Table 02). Temperature did not affect the abundance of mason bees (GLMM; $Z_{32} = -0.012$, $P = 0.464$). The abundance of honey bees increased with the number of honey bee hives per ha (linear model; Fig. 2B; GLMM; $Z_{32} = 3.275$, $P = 0.001$, see Supplementary Table 02) and with increasing ambient temperature (GLMM; $Z_{32} = 20.016$, $P < 0.001$). Mason bees in the trap nests collected mainly *Prunus* pollen, most likely from cherry trees during full bloom (Supplementary Fig. 02).

3.2. Sweet cherry fruit set and the effect of bee abundance

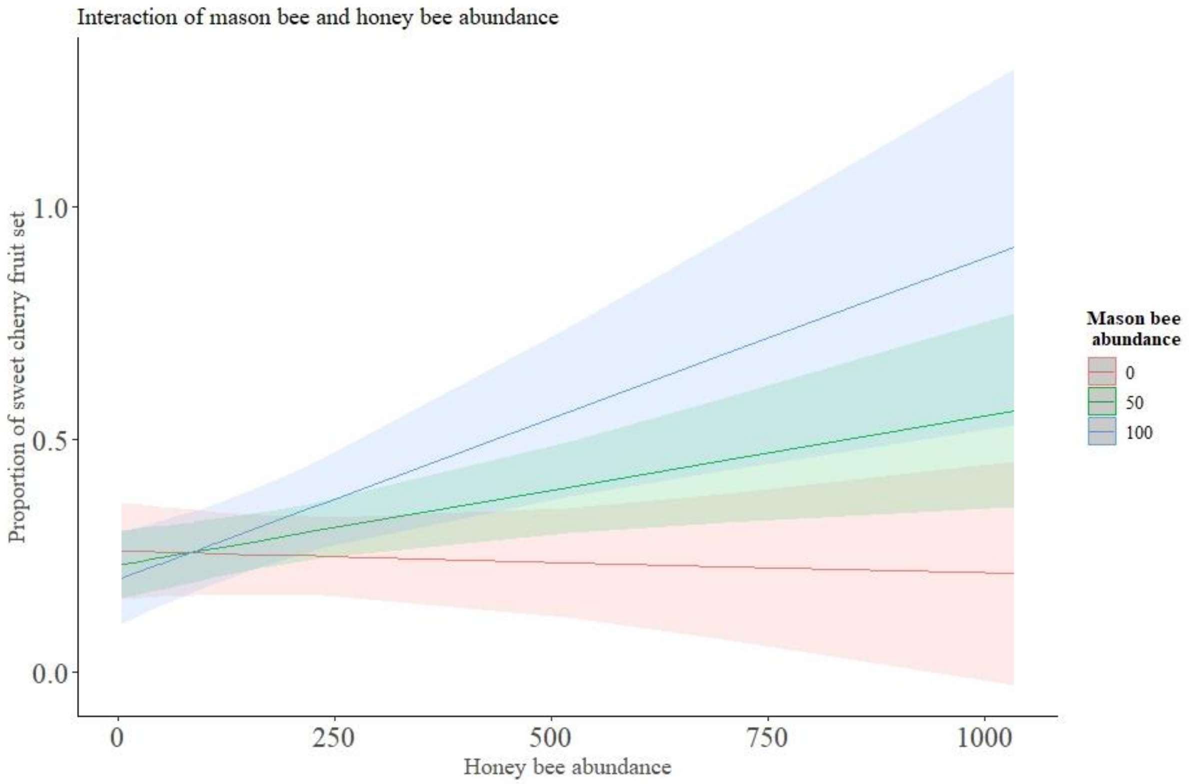

Fig. 3: Predicted interaction effect of mason bee and honey bee abundances on the proportion of open sweet cherry flowers that set fruit (treatment O), estimated from a linear mixed-effect model with orchard as a random factor. The shaded area represents 95% confidence intervals. Effects of increasing honey bee abundance are plotted for different mason bee abundances: no mason bees present (red line), 50 mason bees per transect walk (green line), and 100 mason bees per transect walk (blue line).

Final fruit set of bagged flowers (closed, treatment B) varied between 0% and 6% (mean: 2%, see Supplementary Fig. 03). These data demonstrating the need for sweet cherry flowers to be pollinated by insects to successfully set fruit. The average fruit set of sweet cherries at harvest (treatment O) varied between 9% and 69% (mean: 28%) across orchards. Hand pollination (treatment H) varied between 7% and 68%, though was generally higher than treatment O (mean: 39%). Pollination treatments were significantly different at harvest (Tukey post-hoc, $P < 0.001$), reinforcing the strong positive impact of insect pollination on fruit set (closed vs. insect pollination) and highlighting pollination limitation in our study orchards (insect pollination vs. hand pollination). Fruit weight (g) per harvested fruit did not differ between treatments (Tukey post-hoc, $P > 0.426$; Supplementary Fig. 04).

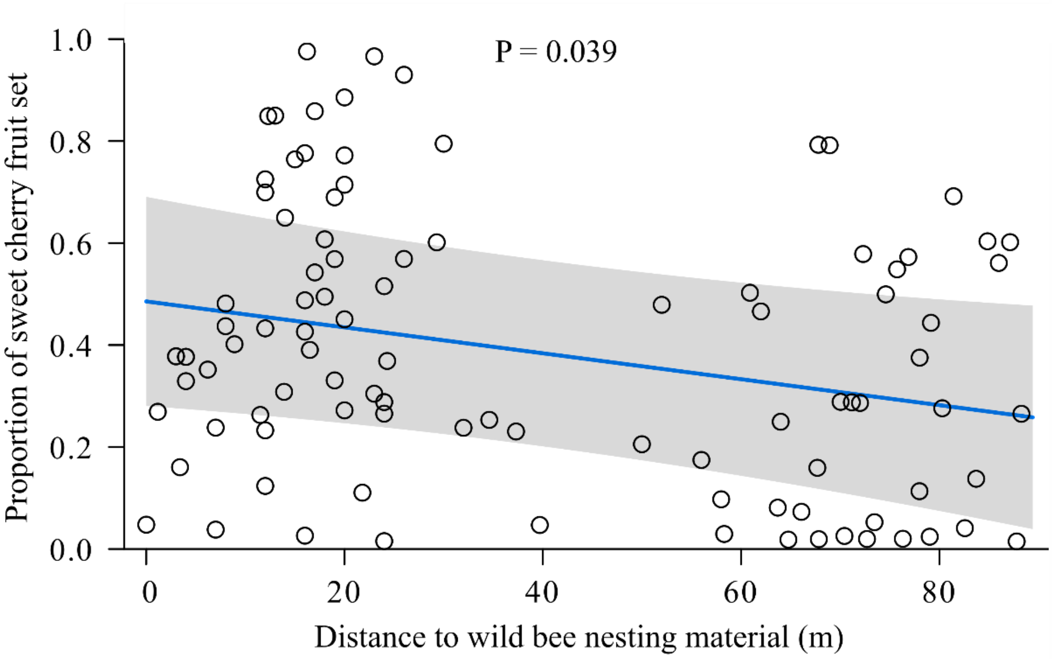

Fig. 4: Proportion of final open fruit set at increasing distance from mason bee nesting material. Each dot represents open sweet cherry fruit set (treatment O) from one tree. The plotted blue line represents the predicted relationship and the shaded areas represent 95% confidence intervals.

4. Discussion

We found that the abundance of flower-visiting mason bees and honey bees can be enhanced by providing nesting material and employing honey bee hives, respectively. The relationship between nesting material and mason bee abundance was, however, not linear but asymptoted. Mason bees interactively with honey bees enhanced sweet cherry fruit set, a crop that is highly dependent on insect pollination. By enhancing honey bees or mason bees alone without the other species also being abundant, fruit set remained low. Also, in a subset of sites, we found that fruit set decreased with increasing distance to nesting material, with little predicted effect of mason bees on cherry fruit set at distances greater than 100-150 m.

4.1. Enhanced bee abundance through bee management

Kornmilch (2010) estimated that 400 female mason bees per hectare are necessary for full fruit set in orchards. This estimation was not specifically calculated for sweet cherry (Kornmilch, 2010). Here, we can not make specific recommendations on the number of female mason bees needed, but we speculate that, for the pollination of sweet cherry, one of the first crops to bloom in spring, farmers might need greater numbers of individuals. We demonstrated that, by providing nesting material, farmers can enhance mason bee abundance on sweet cherry blossoms. As the strongest increase in flower-visiting mason bees can be observed up to 2 nesting boxes per ha (see Fig. 2) we recommend farmers to install 2 nesting boxes per ha, each containing approximately 500 nesting tubes. This on-farm measure increases mason bee abundances in sweet cherry orchards efficient while keeping costs associated with the provision of nesting material low. One reason why the relationship between nesting material and mason bee abundances reached an asymptote might be an increasing parasitism rate with increasing density of mason bees (Groulx and Forrest, 2018). By providing an excess of nesting material, the parasitism rate may increase and therefore the numbers of foraging bees may be reduced. Alternatively, at 5 or more nest boxes per ha, pollination by mason bees may be saturated.

Cocoons of mason bees do not have to be purchased and imported to an orchard as previous studies have shown that local *Osmia* populations increase yearly between 1.3 and 2.8 in nesting material in the beginning (Steffan-Dewenter and Schiele, 2008; Gruber et al., 2011; Bosch et al., 2021). Promoting local mason bee populations without the need to purchase commercially reared cocoons is, therefore, possible and should be preferred, as the import and trade of bees can have negative impacts on wild population (Pirk et al., 2017; Aizen et al., 2020; Osterman et al., 2021a). To later avoid high parasitism rates, renewal of the nesting material is suggested (Kornmilch, 2010).

The preference of *Osmia* bees for fruit trees (Torchio, 1976; Vicens and Bosch, 2000b) is in line with our results of mason bees collecting mainly *Prunus* pollen during cherry full bloom. Also, stable visitation rates by *O. cornuta* throughout the day compared to honey bees, with a peak in the afternoon (Vicens and Bosch, 2000a), support our findings of only honey bees, but not mason bees decreasing in numbers with decreasing temperature. During inclement weather conditions, mason bees can be reliant pollinators of sweet cherry flowers (Vicens and Bosch, 2000a), as these fly throughout the day even during colder temperatures. This in combination with the higher efficiency of mason bees as cherry pollinators compared to bumble bees and honey bees (Eeraerts et al., 2020b) could them an optimal bee to be promoted for pollination services. The fact that mason bee abundance reached its maximum at 150 bees per transect walk, while up to 1000 honey bees were observed during transect walks, illustrates the limitations of mason bee management. Honey bee abundance in contrast showed a linear relationship with the number of hives employed (Fig. 2). The more honey bee hives were provided, the more honey bees were observed during the transect walks. Relying only on mason bees by providing nesting material for those, might not be sufficient, therefore, despite its high efficiency (Eeraerts et al., 2020b).

4.2. The effect of bee abundance on sweet cherry fruit set

We found that mason bees interactively with honey bees increased fruit set of sweet cherry. When mason bee abundance was low, fruit set did not increase with increasing honey bee abundance. A positive relationship was only seen when mason bee abundance increased as well. Also, when mason bee abundance has high but honey bee abundance low, fruit set was also low. Only by increasing both honey bees and mason bees, fruit set increased. Synergistic effects on fruit set between species have been demonstrated in other studies as well (Brittain et al., 2013; Fründ et al., 2013). For instance, almond nut set was synergistically enhanced with *Osmia* and honey bees in experimental cages (Brittain et al., 2013), and higher bee diversity resulted in higher seed production of plants, with the strongest difference comparing one species to <1 species (Fründ et al., 2013). Honey bees have been found to have an increased visitation rate, higher probability of row changes, and single visit efficiency with increasing non-*Apis* bees in several crops (Greenleaf and Kremen, 2006; Brittain et al., 2013; Eeraerts et al., 2020a), which might explain the synergistic effect on fruit set also in our study system. Wild bees, in our case mason bees, could facilitate pollination services by honey bees, especially those crops depending on cross-pollination.

In crops not dependent on cross-pollination this effect might not be as pronounced. Recently, a study in an orchard in the UK showed no effect of enhanced *Osmia* populations on sweet cherry fruit set (Ryder et al., 2019). The study was undertaken in the self-fertile variety “Stelle”, for which cross-pollination might not be as important as for a self-sterile variety, which was used in this study. Also, the study was conducted in polytunnels, with very few other flower visitors present than mason bees (Ryder et al., 2019), which excludes interaction effects among flower visitors and therefore only tested the effect of mason bees alone on fruit set. Even though mason bees have been shown to be effective pollinators of sweet cherry (Eeraerts et al., 2020b) and other fruit trees (e.g. Monzón et al., 2004), honey bees were still often the predominant flower visitor. Indeed, in our study sites honey bees made up 70% of all flower visitors and mason bee abundance seems to reach a saturation point, at which additional nesting material will not increase mason bee abundance further. Relying only on promoted mason bee populations might therefore not result in sufficient yield.

To increase cherry pollination, we recommend therefore a combination of employing honey bees for pollination services as well as habitat enhancement measures for wild bees. However, honey bee hive densities should be moderate to avoid deleterious effects on wild bee populations (Herbertsson et al., 2016; Lindström et al., 2016). We argue that crop pollination alone by honey bees also might bear risks and result in limited fruit set, as honey bees do not fly as frequently during inclement weather conditions and honey bee abundance alone did not positively affect sweet cherry fruit set. Future studies should investigate optimal management practices (e.g. honey bee hive density) applied to local conditions (i.e. density of wild bees), crop types, and varieties and disseminate them to farmers to ensure stable fruit and seed set.

Also, when using bees other than honey bees for pollination management, on-farm practices have to be adapted, especially in mass-flowering crops. For instance, a stingless bee species was found to only forage within 100 m of its colony in orchards while possible flight ranges were reported to be much larger (Evans et al., 2021). In an almond orchard, most *Osmia* bees were recorded within 30 m of their nest and fruit set also decreased with distance to the nest (Bosch et al., 2021). In a pear orchard, 78% of the mason bees were recorded within 50m of the nesting material (Monzón et al., 2004). While we did not record mason bee abundance with increasing distance to the nesting material, we did record fruit set on trees at varying distances to the nesting material. We found that fruit set decreased with distance to nesting material (Fig. 4), suggesting reduced effect of mason bees on sweet cherry fruit set further than 100 m away from nesting boxes. We, therefore, recommend to install nesting material every 100 m, resulting in two nesting boxes per ha to ensure sufficient orchard-wide pollination services.

4.3. Risks associated with managing pollinators

Despite the benefits of managing pollinators for crop yields, risks associated with their management should be taken into consideration (Russo et al., 2021). However, the promotion of local wild bee populations is most likely not harmful and should be preferred over the rearing and trade of managed species, even of native solitary bees, as local genetically adapted populations could be swamped by managed bees (Russo et al., 2021). Nevertheless, habitat enhancement (e.g. increase the quality and quantity of floral resources, protect and restore habitats) for native pollinators in and around crop fields should be given priority to enhance the diversity of pollinators (Osterman et al., 2021a).

5. Conclusions

Our study demonstrates that the presence of nesting material can enhance mason bees as flower visitors in cherry orchards, but might be limited. Fruit set of sweet cherry, a highly pollinator-dependent crop, was synergistically increased by honey bee and mason bee abundances. As other studies have highlighted the facilitative component of non-*Apis* bees on the performance of honey bees, we can encourage farmers to implement measures to protect diverse wild pollinator communities in orchards. Combining several measures to ensure pollination services represents a resilient way to ensure adequate crop pollination.

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Chapter III. Global trends in the number and diversity of managed pollinators

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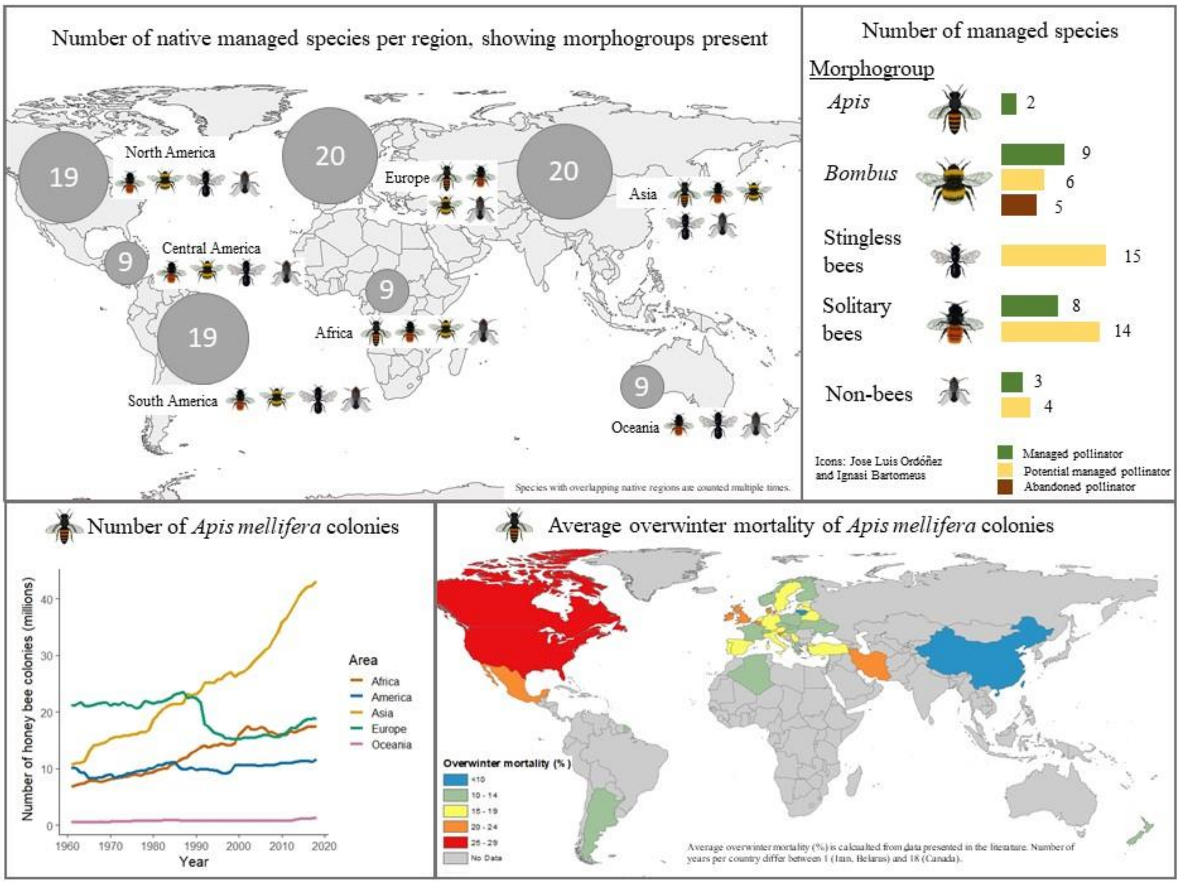
Graphical abstract



Highlights

- Diversity of managed pollinators has increased over time, totaling 66 species
- Native species and their traits might drive the trend in diversification
- Globally, the number of managed honey bee colonies has risen by 85% since 1961
- High colony mortality of *Apis mellifera* is reported, especially in North America
- Managed pollinators may negatively affect native, non-managed pollinators

Abstract

Cultivation of pollinator-dependent crops has expanded globally, increasing our reliance on insect pollination. This essential ecosystem service is provided by a wide range of managed and wild pollinators whose abundance and diversity are thought to be in decline, threatening sustainable food production. The Western honey bee (*Apis mellifera*) is amongst the best-monitored insects but the state of other managed pollinators is less well known. Here, we review the status and trends of all managed pollinators based on publicly accessible databases and the published literature. We found that, on a global scale, the number of managed *A. mellifera* colonies has increased by 85% since 1961, driven mainly by Asia. This contrasts with high reported colony overwinter mortality, especially in North America (average 26% since 2007) and Europe (average 16% since 2007). Increasing agricultural dependency on pollinators as well as threats associated with managing non-native pollinators have likely spurred interest in the management of alternative species for pollination, including bumble bees, stingless bees, solitary bees, and flies that have higher efficiency in pollinating specific crops. We identify 66 insect species that have been, or are considered to have the potential to be, managed for crop pollination, including seven bumble bee species and subspecies currently commercially produced mainly for the pollination of greenhouse-grown tomatoes and two species that are trap-nested in New Zealand. Other managed pollinators currently in use include eight solitary bee species (mainly for pollination services in orchards or alfalfa fields) and three fly species (mainly used in enclosures and for seed production). Additional species in each taxonomic category are under consideration for pollinator management. Examples include 15 stingless bee species that are able to buzz-pollinate, will fly in enclosures, and some of which have a history of management for honey production; their use for pollination is not yet established. To ensure sustainable, integrated pollination management in agricultural landscapes, the risks, as well as the benefits of novel managed pollinator species must be considered. We, therefore, urge the prioritization of biodiversity-friendly measures maintaining native pollinator species diversity to provide ecosystem resilience to future environmental changes.

Keywords: *Apis*, *Bombus*, crop pollination, Meliponini, risk, overwinter mortality

1. Introduction

For most Angiosperm plant species, reproduction depends on pollination provided by a wide range of animal species, including insects, birds, and mammals (Ollerton et al., 2011). Through their contributions to global food security as well as farmer and beekeeper livelihoods and maintenance of wild plant biodiversity, pollinating insects are closely tied to human well-being (Potts et al., 2010, 2016; Hill et al., 2019), facilitating the yield of at least 87 out of the world's 107 leading crops (Klein et al., 2007).

Globally, the total agricultural area has expanded by around 41% from 1961 to 2016, with the area cultivated for pollinator-dependent crops having increased disproportionately (137%), making agriculture more pollinator-dependent than ever (33% of the agricultural area occupied by pollinator-dependent crops; Aizen et al., 2019). This has, however, been accompanied by a trend towards agricultural monocultures rather than diversification (Aizen et al., 2019), which could further lead to pollination deficits through habitat loss for wild pollinators. Regions projected to suffer from a mismatch of pollination demand and supply provided by wild insects include Europe and the United States (Schulp et al., 2014; Koh et al., 2016). Moreover, the dependency of agriculture on pollination is especially high in South America and parts of Southeast Asia (Aizen et al., 2019), where pollination supply has not been evaluated.

Another trend in agriculture, although not as well documented, is the increase in cultivated area under permanent covers, such as greenhouses, tunnels, and row covers. While official data reporting the area under covered environments are rare (e.g., FAO, 2020), Cuesta Roble (2020) estimated that in 1995 around 500,000 ha of crops were cultivated under permanent cover, which increased to 5,630,000 ha by 2019. Crops under cover are partly protected from extreme weather conditions, pathogens and pests, and can allow variety-specific seed production (Cuesta Roble, 2020). However, pollination services by insects are limited in enclosures without active pollinator management (Kendall et al., 2021). A particular challenge is that covers can negatively impact the health and foraging activity of managed honey bees placed in such conditions (Evans et al., 2019; Kendall et al., 2021).

In open fields, wild insects make an important contribution to crop pollination worldwide (Garibaldi et al., 2013, 2014; Rader et al., 2016, 2020). However, there have been ongoing reports of declines in the abundance of wild bees (Biesmeijer et al., 2006; Goulson et al., 2010; Dupont et al., 2011) and other wild insects (Powney et al., 2019; Seibold et al., 2019) as well as declines in insect diversity and biomass (Biesmeijer et al., 2006; Bommarco et al., 2012; Seibold et al., 2019; van Klink et al., 2020; Zattara and Aizen, 2021), representing a threat to the sustainable supply of pollination. By increasing landscape complexity (e.g., presence of wildflower strips, the cover of semi-natural habitat, distance to the nearest semi-natural habitat) and wildlife-friendly farming, the abundance, and diversity of pollinators can be enhanced, leading to higher crop yields (e.g., Holzschuh et al., 2012; Blaauw & Isaacs, 2014; Pywell et al., 2015). Another option to ensure pollination provision, though potentially less desirable, is managing formerly wild pollinator species through *in situ* promotion or active domestication (IPBES, 2016). However, pollinator domestication and associated trade pose novel threats, such as the promotion of insects that become invasive, with associated negative impacts on biodiversity and sustainable provision of pollination services (Aizen et al., 2020; Ghisbain et al., 2021; Russo et al. 2021).

One approach to ensuring sufficient pollination services is through hand pollination, which has been practiced at least since 800 BC, with an Assyrian-dynasty relief showing hand pollination of a date palm tree using a branch holding male flowers (Free, 1982). *Vanilla* is routinely pollinated by hand following the discovery of the method in the 1830s (Arditti et al., 2009). Griggs and Vansell (1949) first mentioned the use of honey bee-collected pollen for artificial pollination of deciduous fruit trees in the first half of the 20th Century. To date, hand pollination is known to have been employed for 20 different crops (Wurz et al., 2021). Artificial pollination with blowers and vibrating devices was an established method for the pollination of tomatoes grown under cover that, because it was labour-intensive and expensive, has nowadays largely been replaced by managed bumble bees (Velthuis and van Doorn, 2006). Nevertheless, artificial pollination remains a topical issue, for example through its accomplishment by mini-drones (Potts et al., 2018). However, by far the greatest attention has been paid to managing or otherwise enhancing the number of bees and other insects as pollen vectors.

For many years, the Western honey bee, *Apis mellifera*, has been the most widely used of managed pollinators (McGregor, 1976; Kevan et al., 1990). However, in recent decades, public and scientific attention has been drawn to abnormally high honey bee colony (particularly overwinter) mortality rates in Europe and the United States of America (vanEngelsdorp et al., 2008; Potts et al., 2016). Many stressors that negatively affect honey bee colonies have been hypothesised: lack of food (floral resources; Neumann and Carreck, 2010), climate change (Le Conte and Navajas, 2008), poor beekeeping practices (Neumann and Blacquière, 2017), chronic exposure to pesticides (Sánchez-Bayo et al., 2016; Battisti et al., 2021) and, most importantly, diseases and pests such as the exotic ectoparasitic mite, *Varroa destructor*, along with the viruses it transmits (Mondet et al., 2014; Brown et al., 2016). The dependence of pollination on a single, managed species, *A. mellifera*, is therefore of rising concern for food security (Winfree, 2008), especially in times of changes in the human diet, a growing world population, and higher per capita consumption (Godfray et al., 2010).

Humans have a long history of managing bees for honey extraction, with perhaps the oldest association being with *A. mellifera*. Managed bees can be circumscribed as those that are provided with artificial nests (Kritsky, 2010). Under this definition, the oldest evidence of managed honey bees dates back to 2450 BCE in Egypt, where stone reliefs show beekeepers working with honey bee hives (Crane, 1999). Apiculture (the management of honey bees) developed independently in many parts of the world (Kritsky, 2017). In Asia, the cavity-nesting Eastern honey bee (*Apis cerana*) seems to have been first managed much later, with the first evidence of beekeeping with *A. cerana* dating to 158-166 CE in China (Kritsky, 2017) and 300 BCE in Afghanistan and Pakistan. In Mesoamerica, the Maya developed a beekeeping culture around the stingless bee *Melipona beecheii*, the first evidence for which dates between 300 BCE and 250 CE (Chase and Chase, 2005). Nowadays, a wide range of pollinator species is managed, including honey bees (*Apis* spp.), several bumble bees (*Bombus* spp.), stingless bees (Meliponini), solitary bees of the genera *Megachile* and *Osmia*, blow flies (Calliphoridae), and hover flies (Syrphidae). This increase in managed pollinator diversity reflects a shift in attention from managed honey bees to alternative pollinator species, driven not only by academic researchers but also by commercial and public interest (IPBES, 2016).

Here, we present the current status and trends of managed bee species, both regionally and worldwide, and examine changes in their numbers and diversity over time. We also highlight several risks that have arisen from managing pollinators. We hypothesise that (1) the use of managed pollinators has increased as the dependence of agriculture on pollination has risen and that (2) the diversity of manageable pollinators is increasing because of greater awareness of the potential negative effects of non-native species along with trends in agriculture (e.g., crops under permanent cover). We furthermore predict that (3) countries or regions with higher rates of *A. mellifera* colony overwinter mortality managed a wider range of alternative pollinators.

2. Materials and Methods

2.1 Number of managed pollinators

We performed a literature search using Web of Knowledge/Web of Science (ISI Thompson-Reuters, webofknowledge.com) and Google Scholar to identify the earliest-dated scientific record of a managed pollinator species (see Supplementary Table 01) in February 2020. We used search terms relevant for the species, for example for the Western honey bee: ("honey bee" OR "honeybee" OR "*Apis mellifera*") AND ("managed pollinator" OR "pollinator" OR ("managed" AND "pollination")). Search terms for each species can be found in Supplementary Table 01 under *species* and *common name/synonym*. Additionally, we used expert knowledge to seek out further publications not found in the above search strategy. We categorized every identified manageable pollinator as (i) current managed pollinator, (ii) potential managed pollinator, or (iii) abandoned managed pollinator. The categorization was based on expert knowledge. We categorized species as potential managed pollinators if we found experimental evidence in the published literature that management is possible but not yet established in practice. Species were categorized as abandoned in the case of bumble bees when we could not find a company any longer producing the species. We furthermore categorized pollinator species into their native geographical regions based on distribution data from Discover Life (https://www.discoverlife.org/) and expert knowledge.

Also using Web of Knowledge/Web of Science (ISI Thompson-Reuters, webofknowledge.com) we performed a literature search with the terms (manage* AND pollinat*) and extracted the number of publications per year to 2019 to address trends in all managed pollinators over time.

2.2 Trends in honey bee hives, honey production and price

The Food and Agricultural Organization of the United Nations (FAO) gathers annual information on crops, livestock, and their products at global, regional, and country levels, and from which we extracted data on the number of honey bee hives, globally and regionally, from 1961 to 2018 as well as the global production of natural (raw) honey in tonnes (FAO, 2020). We calculated the amount of honey harvested per hive (colony) by dividing the total production of honey by the total number of honey bee hives, assuming that honey was derived predominantly from honey bees as only *Apis* honey meets many of the international and regional standards for trading as honey (Vit et al., 2013). Also, we collected the producer price for natural honey in the United States of America from 1992 to 2017 in USD (FAO, 2020).

2.3 Mortality rates of *A. mellifera* colonies

We performed a systematic search of the literature using Web of Knowledge/Web of Science (ISI Thompson-Reuters, webofknowledge.com) and Google Scholar to identify studies providing data on annual and/or overwinter mortality of colonies of the Western honey bee. We used the search terms: ("*Apis mellifera*" OR "honeybee" OR "honey bee") AND ("annual mortality" OR "winter mortality" OR "wintering losses" OR "overwinter mortality" OR "CCD" OR "colony collapse disorder") AND ("survey" OR "question*"). Also, we used expert knowledge to unearth further publications not found in the above search strategy. The PRISMA flow diagram in Supplementary Figure 01 illustrates the detailed selection process, i.e., the number of studies identified and accepted. We only included papers presenting data on beekeeper-reported colony mortality surveyed across entire countries. Data were sorted by geographical region, country and year (see Supplementary Table 02), resulting in 55 studies. Most studies (n = 46; 83%) reported only overwinter mortalities while few (n = 9, 16%) reported annual mortalities; of these, one reported only annual mortality and eight both annual and overwinter mortality (Supplementary Table 02). We, therefore, focused on overwinter mortality in our data analysis described below.

To investigate whether overwinter mortality of honey bee hives differed between years and regions, we used a linear model (LM) in R (R Core Team, 2016) with region and year as fixed factors. The proportions of overwinter mortalities were square-root-transformed prior to analysis to fulfill assumptions of normality. A Tukey post-hoc comparison was used to investigate differences between regions using the R package *multcomp* (Hothorn et al., 2008). Model assumptions were verified by visual assessment using the plot(lm) function in R.

3. Results

Our survey identified a total of 66 insect species formerly or currently managed, or under consideration for management, to pollinate crops (see Supplementary Table 01). Two *Apis* species, nine *Bombus* taxa, eight solitary bee species, and three non-bees are currently managed for the pollination of crops (Fig. 1A). Many other species have been mentioned to have the potential to be managed, including six bumble bee, 15 stingless bee, 14 solitary bee, and four non-bee species (Fig. 1A). Five bumble bee species were managed in the past but are no longer commercially produced (Fig. 1A). We also find that most manageable pollinators are native to Europe (n = 20), Asia (n = 20), North America (n = 19), and South America (n = 19), while for Oceania, Africa and Central America we only recorded nine managed species per region (Fig. 1B). Native species in Africa, Asia, Europe, and North America have for many decades been considered to be suitable managed pollinators (Supplementary Fig. 02). In contrast, native species in Central America, Oceania, and South America have been considered or used only more recently for their pollination services (Supplementary Fig. 02). While *A. mellifera* and solitary bee management have a long history, managing stingless bees or non-bee pollinators is rather recent (see Fig. 2A; Supplementary Fig. 03). Also, the number of publications on managed pollinators and managing pollination services has risen rapidly in the last two decades, reflecting the growing interest in alternative pollinators (see Fig. 2B).

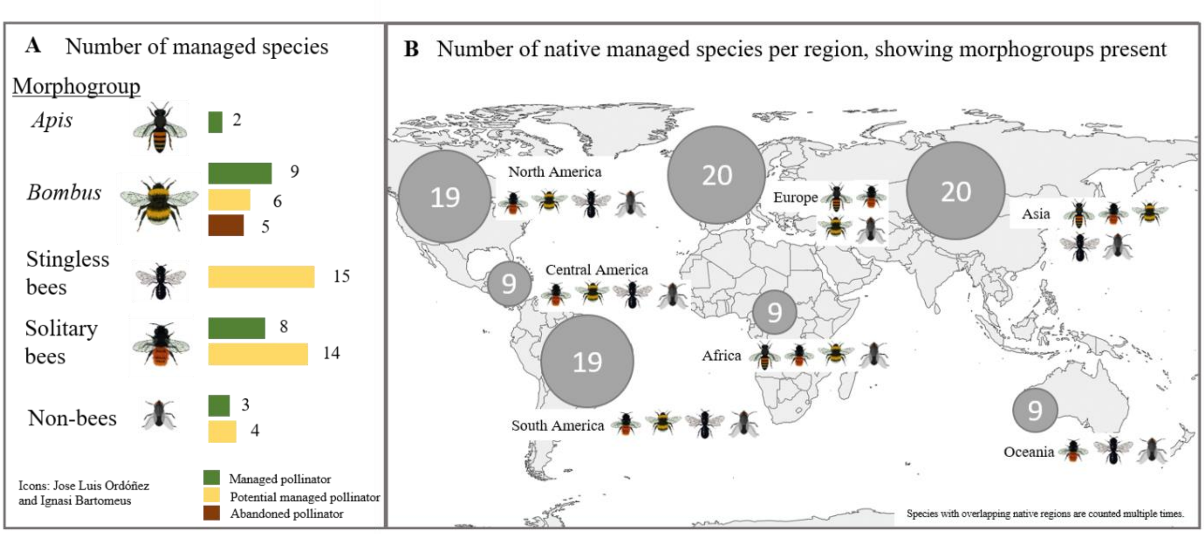


Figure 1 | Number of managed pollinator species (A) per morphogroup divided into the current management status and (B) native per geographical region. Icons under the geographical region represent morphogroups in that region. Species with overlapping native regions are counted multiple times.

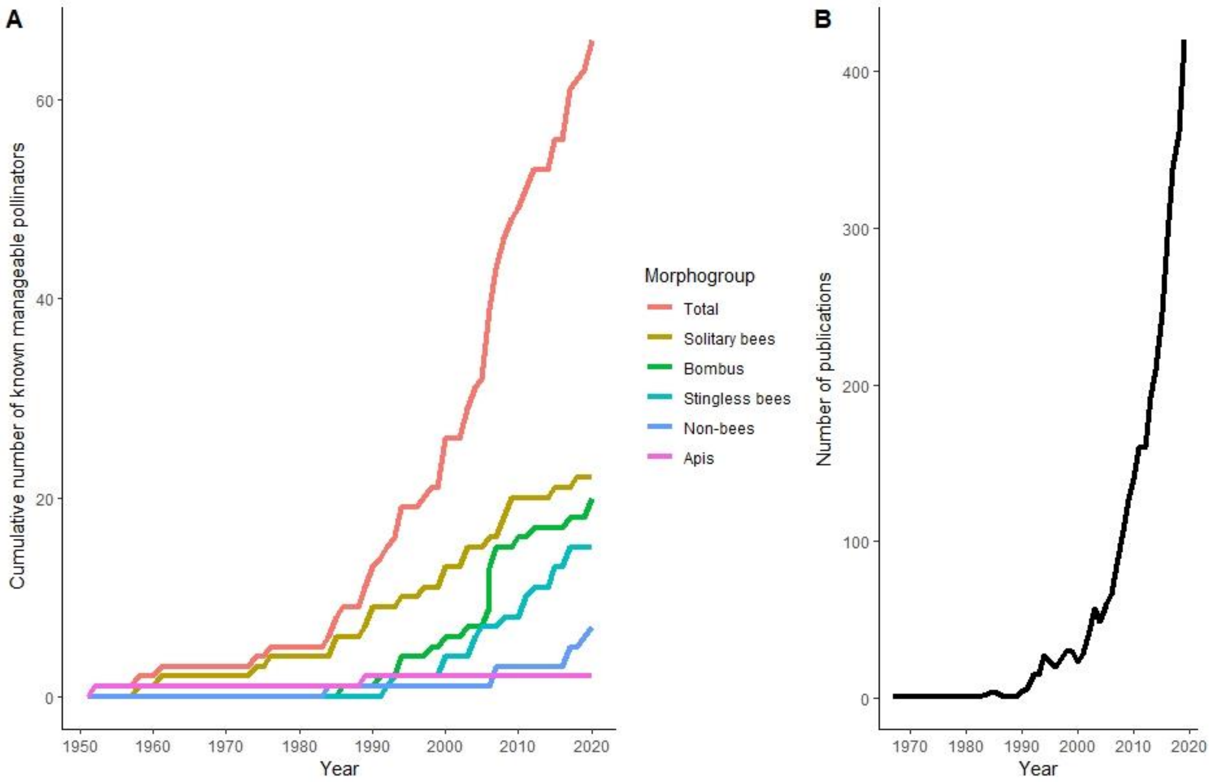


Figure 2 | (A) the cumulative number of known pollinator species in total and divided into morphogroups and **(B)** the **increase in the number of publications on managed pollinators per year** (using the search term manage* AND pollinat*)**.**

3.1 Honey bees

Of the eight widely recognized species of *Apis* (honey bees), only two are managed to any extent, with *Apis mellifera* of primary importance worldwide, and *A. cerana* much less frequently used in its native South and East Asia (Smith 1991; Engel 1999). Over the last 60 years, the number of honey bee colonies has steadily increased (Fig. 3A), with a global stock of more than 92 million colonies in 2018, mostly driven by East Asia (Fig. 3B). This represents an increase of more than 85% in the global number of managed honey bee hives. Europe experienced losses around 1990 but its numbers of managed colonies have increased from around 16 million in 2010 to almost 19 million colonies in 2018. They have not, though, returned to the pre-1990 high of ca. 22 million colonies (see Fig. 3B).

The FAO database reports the number of beehives per country but does not distinguish between different honey bee (*Apis*) species. Data are likely dominated by *A. mellifera*, making it problematic to quantify changes in the number of Eastern honey bee hives (*Apis cerana*). In South Korea, *A. cerana* was widespread in beekeeping operations into the 1980s, but the current trend is toward managing *A. mellifera*, with an associated decline in the number of managed *A. cerana* colonies (Jung and Cho, 2015). It has been estimated that around 2 million *A. cerana* hives exist in China (Chen et al., 2017).

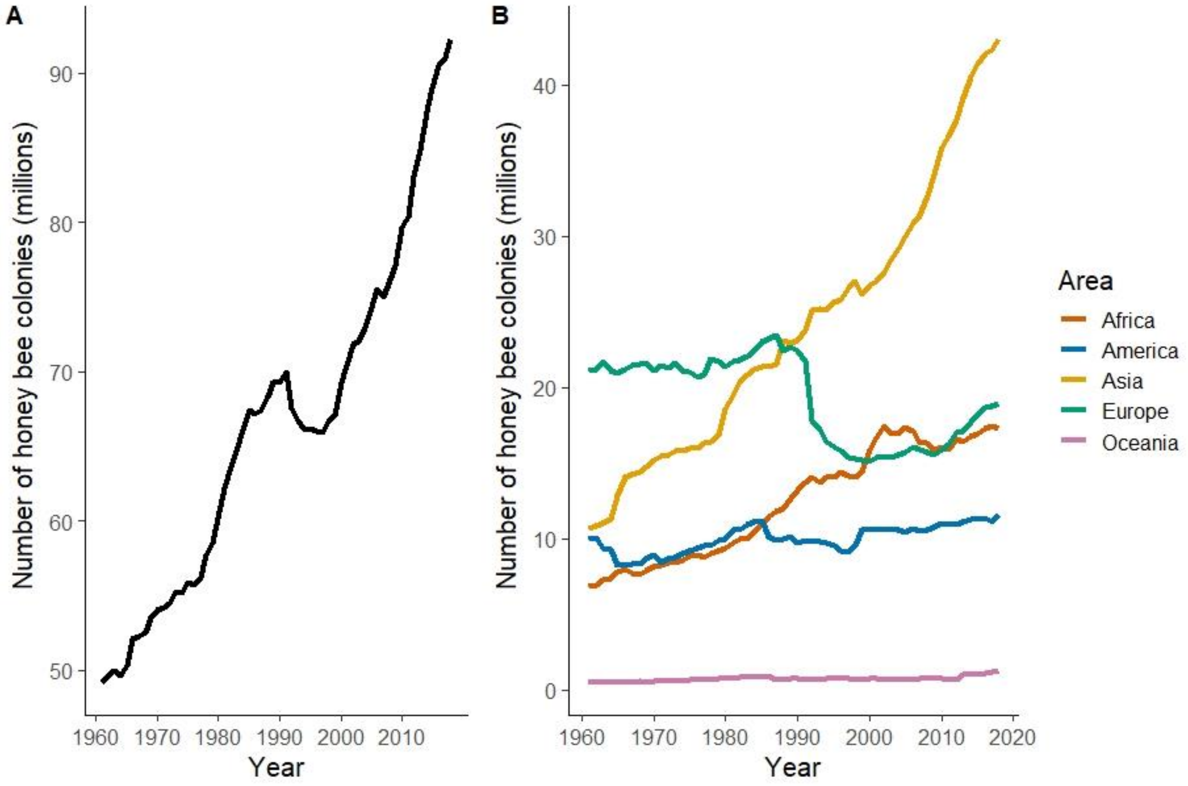


Figure 3 | Numbers of managed honey bee colonies (in millions) **(A) worldwide and (B) divided by geographical region** from 1961 to 2018 (FAO, 2020)

World annual honey production increased from 0.7 million tonnes in 1961 to ca. 1.86 million tonnes in 2018 (see Supplementary Fig. 04A). The average honey yield per colony, likely derived primarily from *A. mellifera*, can vary from year to year, but the overall trend is upwards (see Supplementary Fig. 04B); while less than 15 kg per colony per year was harvested around 1960, more than 20 kg per colony per year was harvested by 2018, an increase of 33% (see Supplementary Fig. 04B). We also report a slight increase in the real (inflation-adjusted) market value for honey (e.g., USA, see Supplementary Fig. 05).

We found 55 studies and reports presenting country-wide annual or overwinter mortalities of *A. mellifera* colonies for which data have been systematically collected since the winter of 2006/07. Before winter 2006/07, up to 30% annual colony losses were reported (see Fig. 4A and 4B, Supplementary Table 02), though this is based on few data points. Thereafter, colony mortality has fluctuated markedly (Fig. 4A and 4B), but there is no linear trend in mortality over time (LM, $t_{266} = -1.168$, $P = 0.244$, Fig. 4A).

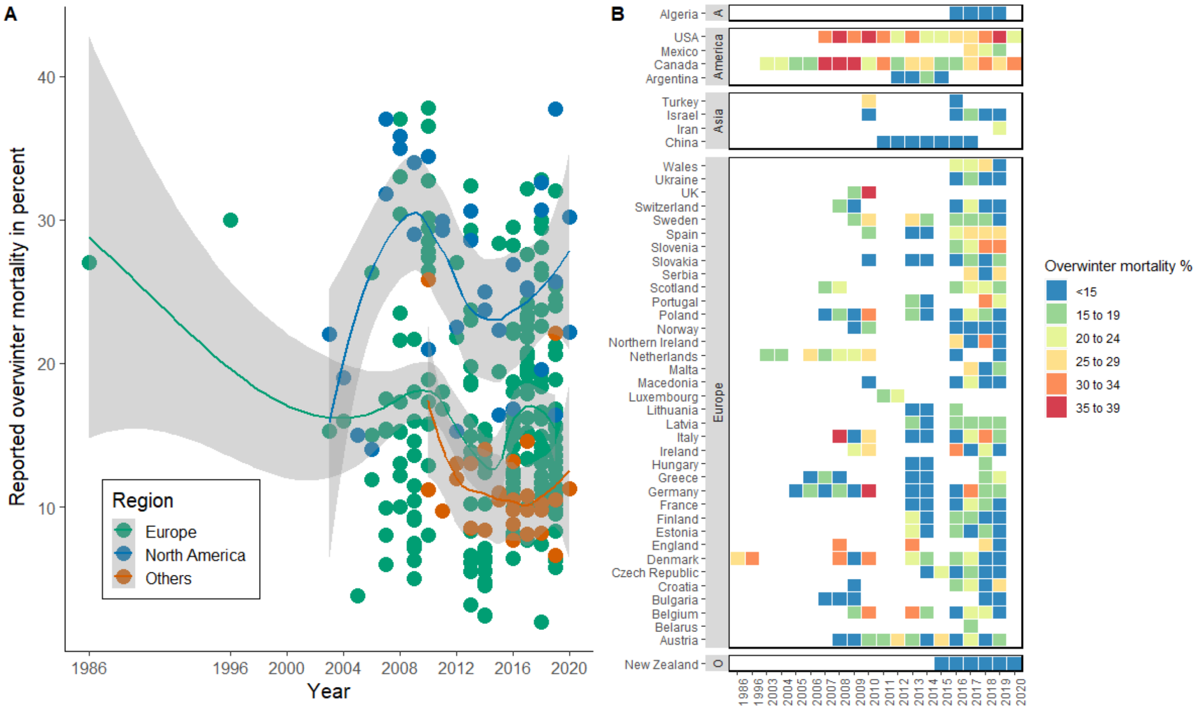


Figure 4 | Overwinter mortality of managed honey bee colonies (A) separated by geographic region over time and (B) by country and year. The category 'Others' includes Africa, East Asia, West Asia, Oceania and South America. Shaded areas represent 95% confidence intervals around locally weighted loess smoothing regression lines. The heat map illustrates overwinter mortality (%) per year and country in six colour categories. Countries are grouped by continents: Africa (A), America, Asia, Europe and Oceania (O). Data and corresponding sources are presented in Supplementary Table 02.

There are, however, some general patterns that can be discerned from the data. North American beekeepers have experienced higher overwinter mortalities of 26% (±7% S.D.) than beekeepers in Europe (16% ± 8% S.D.), who themselves experienced higher losses than other regions (11% ±4% S.D.; post-hoc analysis, $P < 0.005$; Fig. 4A and Fig. 5). Fluctuations within regions can be large; within Europe, several countries reported annual overwinter losses above 30% in one or more years, for example during winter 2007/08 or winter 2009/10 (Fig. 4B). In the USA in recent years, annual losses have exceeded 50% (i.e. 2017/18; 2018/19; 2019/20, Supplementary Table 02). While Europe and North America are well represented in the literature, there are few documented studies on annual colony mortality in Central America, Africa, Asia, Oceania, and South America (Requier et al., 2018; Fig. 4B and Fig. 5; Supplementary Table 02). The first survey of colony losses of managed *A. cerana* in China revealed low overwinter mortality (average 12.8%; Chen et al., 2017) but slightly higher compared to *A. mellifera* (average 9.6 %) in China between 2011 and 2014.

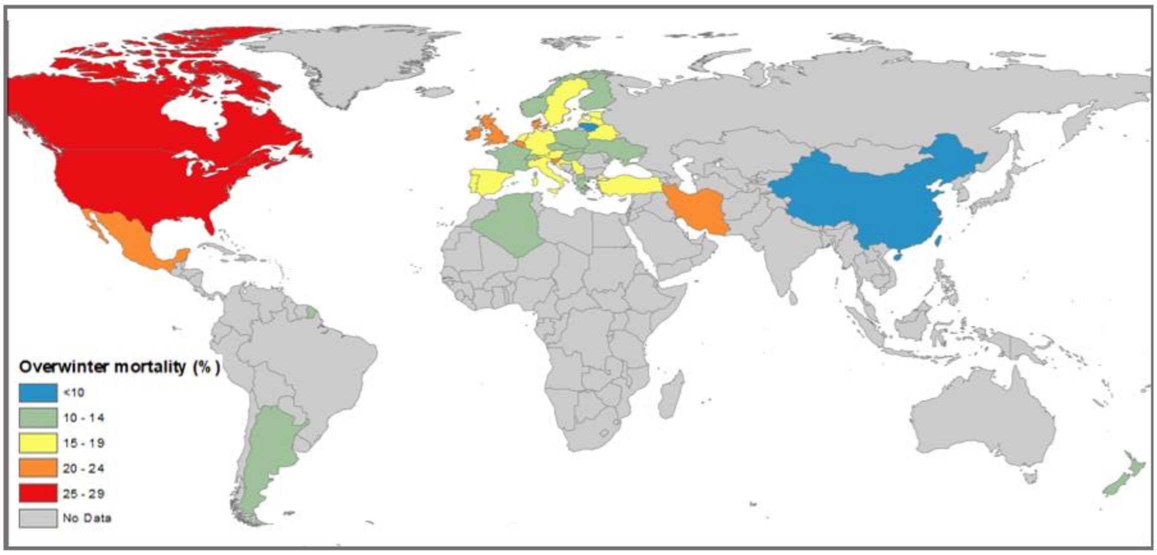


Figure 5 | Average overwinter mortality per country. Grey represents no data available. Number of years per country differ between 1 (Iran, Belgium) and 18 (Canada). Data and corresponding sources are presented in Supplementary Table 02.

3.2 Bumble bees (*Bombus* spp.)

Currently, seven different species or subspecies of *Bombus* are reared (Supplementary Table 03) and two additional species are trap-nested in New Zealand (Donovan, 2007) for pollination. We also found six additional bumble bee species under consideration for management as pollinators and five species that have already been abandoned as managed pollinators (Supplementary Table 01, Fig. 1A).

After the methods for commercial rearing of one bumble bee species, *Bombus terrestris*, were established in the 1980s in Europe, the number of managed colonies of this species traded annually had risen to one million by 2006 (Velthuis and van Doorn, 2006). The current number of *Bombus* colonies traded annually is not publicly known because information is withheld for commercial reasons, but likely exceeds 2 million colonies (IPBES, 2016).

3.3 Stingless bees

The potential of managing stingless bees for pollination services has been evaluated in several studies, particularly in Brazil (Supplementary Table 01), but their pollination management is not yet an established practice. Here, we report 15 species that have been or are under consideration as managed pollinators (Fig. 1A), mostly for crop pollination (of, e.g., strawberry, cucumber, tomatoes, habanero, and sweet pepper) in enclosures (Supplementary Table 01).

3.4 Solitary bees

Eight solitary bees, in particular leafcutter and mason bee species (family Megachilidae, genera *Megachile*, and *Osmia* respectively) but also the alkali bee (*Nomia melanderi*, family Halictidae), are currently managed for crop pollination (Fig. 1A). In addition, 14 other species are under consideration as managed pollinators (Supplementary Table 01, Fig. 1A). Leafcutter and mason bee species can be encouraged to nest in artificial media (e.g., drinking straws, bamboo canes, drilled wood blocks, and polystyrene boards; IPBES, 2016) while the ground-nesting alkali bee can be encouraged to nest in bee beds created by farmers adjacent to cropping fields (Johansen and Mayer, 1982). These latter measures allow the numbers of alkali bees to accumulate over successive years, enhancing the pollination of nearby crops in a very simple manner (Free, 1993; Delaplane and Mayer, 2000). However, management of solitary bees can also include the potentially more destructive commercial harvest, trade, and release beyond their native range (Richards, 1984; Bosch and Kemp, 2001).

Official figures on the size of the managed solitary bee industry (number of bees produced) are lacking, but there are estimates for several species (IPBES, 2016). Around 800 million alfalfa leafcutter bees (*Megachile rotundata*) are traded commercially per year in North America and an additional 1.6 million are promoted in and around alfalfa fields in the USA, making this species the most important managed solitary bee (Peterson et al., 1992; Reisen et al., 2009). *Osmia cornifrons* has been successfully managed since the 1940s in Japan, where it is native and employed in 70% of Japan’s apple production area (Maeta, 1990). Populations of this species are also managed for orchard pollination in China and Korea (Xu et al. 1995, Lee et al. 2008) but the extent of its use is unknown. In 2002, trade of *Osmia bicornis* (=*rufa*) in Europe, *O. cornuta* in central and southern Europe, and *O. lignaria* in the US and Canada was estimated at over one million cocoons (individuals) per species per year for the pollination of orchard crops (Bosch and Kemp, 2002). Current numbers might be higher as a single company in France traded one million cocoons in 2020 (pers. comm. P. Ouvrard). In Korea, an estimate of 0.5

million *Osmia* spp. individuals (mostly *O. cornifrons* and *Osmia pedicornis*) were used to pollinate crops in 2007 (Yoon and Park, 2009).

3.5 Managing insects other than bees for pollination of crops

Currently, three fly species are available commercially for pollination (Fig. 1A): *Lucilia sericata* (common greenbottle fly; produced by, e.g., Koppert), *Eristalinus aeneus* (hover fly; produced by Polyfly), and *Eristalis tenax* (hover fly; produced by Polyfly). The extent of their use is not known as such commercially sensitive information is withheld and does not appear in public databases. In addition, we identify four other fly species under consideration as potential managed pollinators (see Supplementary Table 01; Fig. 1A). These flies have proven to be effective pollinators of crops grown in enclosures (cages or glasshouses) to promote cross-pollination for seed or fruit: the blow flies *Calliphora vomitoria* for onion grown for seed (Currah and Ockendon, 1984), *Calliphora vicina* for hybrid carrot seed production (Free, 1993; Howlett, 2012), *Calliphora albifrontalis* for the pollination of blueberries (Cook et al. 2020b), and the housefly *Musca domestica* for *Allium ampeloprasum* pollination (Clement et al., 2007).

4. Discussion

We clearly demonstrate an increase over the past seven decades in the number of insect species, particularly bees, which are managed as pollinators, as we expected. For the most numerous commercial insect pollinator, the Western honey bee (*A. mellifera*), the number of colonies worldwide has also increased over the past seven decades despite high overwinter colony losses in Northern temperate regions of the world.

Though our data do not address the cause or causes for the increase in the number of managed insect pollinator individuals or species, we hypothesise that the greater reliance of agriculture on insect pollinator-dependent crops (Aizen et al. 2009; 2019), the rise in crop cultivation under permanent cover (Cuesta Roble, 2020), and the rise in awareness of the negative effects of non-native pollinators on local species (Aizen et al., 2020) may all have been important in increasing the demand for managed pollinators, as outlined in our first two hypotheses. For those bee species that produce a surplus of stored honey or other products, increasing market prices might also have led to greater uptake of managed species. High overwinter mortality of *A. mellifera* might have a minor influence, as two-thirds of the species have been mentioned before 2007, when honey bee mortality became widely publicized (Oldroyd, 2007), and regions with higher honey bee overwinter mortality rates such as North America do not have particularly high numbers of native or alternative managed pollinator species.

4.1 Honey bees

Two honey bee species are used for the pollination of crops, the Western honey bee (*A. mellifera*), which is the most prominent pollinator worldwide (IPBES, 2016), and the Eastern honey bee, *A. cerana*, which is native to Asia, ranging from Afghanistan to Japan and south to most parts of Indonesia (Radloff et al., 2010). Both species have a long history of beekeeping management, mostly for honey production (IPBES, 2016). Data collected from the FAO on the number of honey bee hives per year and country are mostly dominated by *A. mellifera* and therefore disentangling the contribution of *A. cerana* is difficult. However, the introduction of *A. mellifera* to all Asian countries in recent decades (Requier et al., 2019) might have negatively affected the number of managed *A. cerana* (Theisen-Jones and Bienefeld, 2016). Colonies of *A. mellifera* are larger and produce more honey than *A. cerana* (Theisen-Jones and Bienefeld, 2016), leading beekeepers to convert from the management of the latter to the former. Nevertheless, *A. cerana* may show useful management traits such as disease resistance or tolerance, making it better adapted to management in tropical Asian countries (Lin et al., 2016; Theisen-Jones and Bienefeld, 2016). Furthermore, *A. cerana* has been shown to outperform *A. mellifera* in the provision of pollination services, e.g. pears in China (Gemeda et al., 2017), an argument for the maintenance of managed *A. cerana* where it is native.

We confirm the ongoing rise in the number of honey bee hives worldwide, with a total increase of more than 85% from 1960 to 2018; this dynamic supports our expectations as the dependency of agriculture on pollination has increased globally and, with it, potentially the demand for pollination services (Aizen and Harder, 2009b). This seems at odds with reports of high rates of colony mortality (e.g., Bruckner et al., 2019). An interesting question, therefore, concerns world honey bee health, for which data on trends in colony numbers are unreliable for many reasons (IPBES, 2016). First, colonies can be divided or reunited during the season (Root et al., 2006), leading to inaccuracy in the estimation of the number of colonies. Second, beekeepers can capture a passing honey bee swarm, increasing their number, or a colony may abscond, leading to colony loss (Root et al., 2006). Third, in Africa and South, Central and southern North America, large numbers of wild or feral honey bee colonies contribute to the population of *A. mellifera* and likely actively contribute to crop pollination (Vogel et al., 2021), though are not registered in databases. Fourth, many colonies are likely not registered, especially in small-scale apiaries, leading to inaccuracy in national estimates (IPBES, 2016).

In Europe, where *A. mellifera* is managed, feral honey bees are scarce (Jaffe et al., 2010). The number of registered honey bee colonies is therefore a product of the number of beekeepers. For example, the loss of *A. mellifera* colonies in Europe around 1990 has been attributed to societal changes (e.g., the collapse of socialist states, increasing wealth; see Moritz et al., 2010; Smith et al., 2013; van Engelsdorp and Meixner, 2010). As a consequence of great uncertainties in the total number of colonies at any one point in time, estimates of overwinter losses of honey bee hives might be a better indicator of honey bee health (IPBES, 2016).

Since monitoring by the science network COLOSS began in 2008, data have been collected on overwinter colony losses in a standardized way, although mostly for Europe. Both the United States of America and Canada have also introduced national programs that report their annual honey bee wintering losses. Data from Central America, Asia, Africa, Oceania, and South America are still scarce. For instance, cases of high colony losses have been reported in South America but, due to the lack of monitoring programs, a general overview is lacking (Requier et al., 2018). This could have negative repercussions for this geographical region in which agriculture is highly pollinator-dependent (Aizen et al., 2019), limiting our ability to predict a pollination shortfall. In Africa, the density of feral honey bees is higher than in Europe (Jaffe et al., 2010). Therefore, colony mortality rates are hard to determine because many colonies go unrecorded and unobserved.

Interrogating the existing data on annual losses suggests some alarming trends; for example, in the USA, honey bee colony losses have exceeded 50% each year for the last three years (i.e., 2017/18; 2018/19; 2019/20; see Supplementary Table 02). There is obviously a need for ongoing documentation of colony losses to help understand their causes. Reported overwinter mortalities vary among geographical regions of the world, and might be a result of differences in beekeeping practices, weather conditions, the prevalence of pathogenic organisms, intensification of agriculture, inadequate nutrition, or the introduction of invasive species (Neov et al., 2019; 2021); these multifactorial drivers deserve to be further studied to understand better the threats to honey bee colony health. That novel pollinator species have been developed across the world and not predominantly in regions experiencing high honey bee overwinter colony mortality (e.g. North America; see Fig. 4 and Fig. 5) suggests that honey bee mortality *per se* does not spur interest in alternative pollinators, arguing against our third hypothesis. Alternatively, if honey bee mortality does promote research on alternative pollinators, then its impact is not limited to the country or region experiencing high colony mortality; global communication and awareness of the need for pollinators may be very effective.

Apis mellifera colony losses stand in contrast to the increasing global number of honey bee hives. However, colony losses might not have a direct effect on the standing number of colonies in a country because beekeepers may compensate for losses, as outlined above. Moreover, the price farmers have to pay for pollination services might well be affected by high annual rates of colony mortality, with an increase in price spurring an increase in the supply of colonies. In Central Europe (Germany), where average overwinter mortality is below 20%, farmers pay around US$35 per colony for pollination services (informal pers. comm. with farmers). In contrast, in the United States, where the average overwinter mortality is above 25%, farmers pay between US$ 74.3 and US$ 143.2 per honey bee colony for pollination services (USDA National Agricultural Statistics, 2017). In 2017, the summed US farm expenses for pollination services provided by honey bees has been estimated at more than US$ 300 million (USDA National Agricultural Statistics, 2017).

The overall pattern of increasing numbers of honey bee colonies worldwide may be either a consequence of an increasing market value of honey (see Supplementary Fig. 05 and Aizen and Harder, 2009a) or increasing demand for honey bee colonies as pollination ‘units’. In a growers’ survey in Europe, one-third of farmers owned managed honey bee colonies and almost half either owned or hired at least one managed pollinator species, including honey bees (Breeze et al., 2019). Similarly in Korea, honey bees have been used in 48% of cases by farmers to pollinate crops (Yoon and Park, 2009). In 2017, in the USA more than 2.6 million colonies were used to pollinate crops, particularly almonds grown in California (USDA National Agricultural Statistics, 2017). With the increased planting of pollinator-dependent crops at a rate greater than the rise in the global stock of domesticated honey bees (Aizen and Harder, 2009b), increasing demand for honey bees in the coming years is to be expected.

Interestingly, we found that honey production per colony has increased by 33% over the past seven decades. The growing production of honey might be a result of the increase in the human population and per capita demand for honey (Aizen and Harder, 2009b). An increase in mass-flowering crops and intensification in beekeeping (Aizen et al., 2019) could potentially also explain this consistent increase in yield per colony. Data collected from the FAO on the honey harvested per year and country do not distinguish its biological origin but will be dominated by *A. mellifera*. Honey harvested from other honey bee or stingless bee species likely represents a marginal proportion of the total world honey yield.

4.2 Bumble bees

The rising number of managed bumble bee species and number of colonies might be driven by a trend towards more cultivated area under permanent cover (Cuesta Roble, 2020), as honey bees do not perform well in these environments. Moreover, honey bees are unable to buzz pollinate (Buchmann, 1983) and, therefore, are unlikely to provide an adequate pollination service to buzz-pollinated crops like tomato that are regularly grown under cover. Estimates of two million *Bombus* spp. colonies traded annually across the world, presented in the IPBES report (2016), might be an underestimation as data on the current number of traded colonies are not available. Most likely, bumble bees are the second most common managed pollinators (after the Western honey bee) used for pollinating approximately 240 crops worldwide (IPBES, 2016), particularly those grown under enclosure (e.g., in glasshouses), but increasingly also for semi-enclosed or open field pollination (Murray et al., 2013). For example, tomatoes are cultivated mostly in enclosed greenhouses, a crop that is now primarily pollinated by bumble bees (*Bombus* spp.) (Morandin et al., 2001). In Europe, tomatoes were planted on around 0.5 million ha in 2017 (FAOSTAT, 2017). If farmers use recommended rates of 10 to 15 bumble bee colonies per hectare (van Ravestijn and van der Sande, 1991), this would suggest that at least 5 million *Bombus* colonies are needed for the pollination of tomatoes grown in greenhouses in Europe alone. This number of colonies is likely an underestimate, given that *Bombus* spp. colony survival time is only around 4 to 6 weeks whereas glasshouse-grown tomato plants survive for several months. Also, bumble bees have been reared not only for agricultural purposes but also as part of conservation strategies. For example, *Bombus subterraneus*, which became extinct in Great Britain in the 20th Century, has been reared in New Zealand for reintroduction to Great Britain, which ironically was the source of New Zealand's *B. subterraneus* founder population in the 19th Century (Howlett et al., 2009).

4.3. Stingless bees

There are many reasons why stingless bees are considered suitable as managed pollinators in the tropics, where they are native. First of all, some species have been traditionally managed for centuries in clay or wooden pots and harvested for honey (Free, 1982; Crane, 1983, 1999;

Cortopassi-Laurino et al., 2006; Vit et al., 2013). One species in particular, *Melipona beecheii*, has been managed by the Maya of the Yucatan Peninsula for the past two millennia, if not longer (Quezada-Euán et al., 2001). Rearing techniques for their management might therefore be adapted from indigenous knowledge.

Stingless bees are social; a colony comprises 100s to 10000s of workers (Roubik, 1989), providing many potential pollinators compared to bumble bees (whose colonies comprise 50-500 workers) or solitary bees. Moreover, stingless bees may be more suited for management in the tropics. For instance, although the Africanized honey bee dominates in the Neotropics, it is not suitable for management of crops grown under permanent cover (e.g. greenhouses) as it exhibits extreme defensive behaviour (Danka and Rinderer, 1986). In addition, when relocated (e.g., to a greenhouse), an Africanized honey bee colony frequently absconds (Danka et al., 1987), making beekeeping problematic. In contrast, stingless bees are considered efficient pollinators that are able to buzz pollinate and likely contribute greatly to the pollination of many crops, especially in the Neotropics (Heard, 1999; Slaa et al., 2006) and especially for crops such as tomatoes and eggplants that rely on buzz pollination (Abak et al., 2000; Velthuis and Van Doorn, 2006). Though bumble bees are efficient buzz pollinators, they are not native to all parts of the world and are costly to purchase. There are therefore many reasons why stingless bees should be considered for management as pollinators where they are native and widespread. Their use would also reduce the risks and known negative impacts on native fauna, including on native bumble bee species, through the introduction of exotic bumble bee species (Aizen et al., 2018, 2020).

4.4 Solitary bees

Solitary bees have long been managed as they are efficient pollinators, partly for crops that honey bees pollinate poorly (IPBES, 2016). The best-known case of a managed solitary bee is the alfalfa leafcutter bee, *Megachile rotundata*, managed for the pollination of alfalfa (*Medicago sativa*), a Eurasian crop introduced to North America as an important fodder plant for cattle but for which honey bees provide inadequate pollination (Free, 1993). *Megachile rotundata* was likely unintentionally introduced from its native range in Europe and Asia to East Coast North America in the 1930s, from where it spread naturally to alfalfa seed-producing regions of Central-Western USA and proved to be an excellent alfalfa pollinator. Through detailed research on its biology, facilitated by its gregarious nesting in artificial domiciles, a viable alfalfa leafcutter bee industry became established in the USA and Canada (Bohart, 1952;

Stephen, 1962, 1961; Stubbs and Drummond, 2001; Pitts-Singer and Cane, 2011). Apart from *M. rotundata*, farmers can manage their land surrounding alfalfa fields by creating bee beds for the ground-nesting alkali bee *N. melanderi* (Halictidae) in the USA and for *Rhophitoides canus* (Halictidae) in Eastern Europe (Ptacek, 1989; Bosch, 2005), both of which are efficient alfalfa pollinators. Both species have not been commercialized to any extent (IPBES, 2016).

Other solitary species such as carpenter bees (genus *Xylocopa*) have been experimentally managed as pollinators of crops such as passion fruit (*Passiflora edulis*) (Junqueira et al., 2012, 2013) and tomatoes (Hogendoorn et al., 2000). For example, in Australia, honey bees and bumble bees are not native whereas *Amegilla chlorocyanea,* the blue banded bee, is a very efficient native pollinator of tomatoes grown in glasshouses (Hogendoorn et al., 2006). These are good cases for how a diverse range of native pollinators can be used to enhance crop pollination services whilst reducing the risks to native fauna inherent to the introduction of a new species through, for example, competitive displacement or pathogen spillover (Aizen et al., 2020, LeCroy et al., 2020; Russo et al., 2021).

Other examples of solitary bees used for pollination services include mason bees (*Osmia* spp.) that are mostly used to pollinate early-flowering fruit trees (Supplementary Table 01), where they increase fruit yields in apples, sweet cherries, and pears (Torchio 1985, Monzón et al. 2004, Bosch et al. 2006). For strawberry pollination, *O. cornuta* was shown to have a positive impact on fruit quality under experimental conditions (Herrmann et al., 2019) and the active management of *O. lignaria* in strawberry fields enhances fruit quality (Horth and Campbell, 2018).

Wild populations of solitary bees can be enhanced by active landscape and field management, particularly by creating nesting habitats and providing floral resources (habitat improvement for pollinators or ‘ecological intensification’). This is a sound alternative that should always be preferred, in terms of both conservation and economic perspectives, to the trading of pollinators. Trading in pollinators can lead to the introduction of new species that especially bear risks through the competitive displacement of native fauna and pathogen spillover (Aizen et al., 2020, LeCroy et al., 2020; Russo et al., 2021). Also, the yield of pollinator-dependent crops tends to increase with the abundance and diversity of wild pollinators (Garibaldi et al., 2013).

4.5 Managing insects other than bees for pollination of crops

Managing non-bees as pollinators has great potential (Kevan et al., 1990; Howlett, 2012; Howlett and Gee, 2019; Cook et al., 2020a) as these insects play a significant role in global crop production (Rader et al., 2016, 2020). The potential of hover flies to pollinate crops was shown by Garratt *et al*. (2016), although they were less effective than honey bees, bumble bees, or solitary bees. Eight percent of global food crops reliant on pollinators are favoured by non-bees and another 77% are visited both by bees and non-bees (Rader et al., 2020). Oil palm (*Elaeis guineensis* Jacq) is an example of a crop completely reliant on non-bee pollinators. To improve the yield of oil palm where it is non-native, manual pollination was undertaken until the weevil *Elaeidobius kamerunicus* was discovered in oil palm's native West Africa as the main pollinator and introduced into the non-native growing areas of oil palm (Syed et al., 1982). Since then, the oil palm pollination strategy has relied on the feral populations of *E. kamerunicus*. But its fluctuating populations have led to concerns, raising the issue of more active management of the weevil to sustain yield by, for example, by manipulating male palm inflorescence density (Li et al., 2019).

Despite their contribution to pollination services, the management of non-bee pollinators currently occurs on a far smaller scale than that of their bee counterparts. But it might have great potential, for example for pollination of crops grown under cover.

4.6 Risks associated with pollinator management

An important risk associated with pollinator management is the introduction for crop pollination of an alien pollinator species that subsequently becomes invasive (Ghisbain et al., 2021; Russo et al., 2021). The mechanisms by which introduced (but also native) managed pollinators and their trade can affect native species and ecosystems include (a) exploitative or interference competition for flower resources and nesting sites (Hansen et al., 2002; Inoue et al., 2008; Howlett and Donovan, 2010; Morales et al., 2013; Hudewenz and Klein, 2015; Lindström et al., 2016; Torné-Noguera et al., 2016; Ropars et al., 2019), (b) inadequate pollination of native flora, leading to changes in the reproduction of native plants (Gross and MacKay, 1998; Dohzono et al., 2008; Valido et al., 2019), (c) undesirable pollination of exotic flora (Barthell et al., 2001; Stout et al., 2002; Morales et al., 2014), (d) transmission of parasites or pathogens to wild or native populations, including the co-introduction of natural enemies (Colla et al., 2006; Morales et al., 2013; Murray et al., 2013; Fürst et al., 2014; Schmid-Hempel et al., 2014), and (e) genetic introgression or reproductive disturbance of native pollinator species (Tsuchida et al., 2010; Kraus et al., 2011). Managed pollinators can even have a negative impact on wild plant reproduction and crop yields when they become superabundant (Aizen et al., 2020; Russo et al., 2021). For instance, high visitation rates of the invasive *B. terrestris* to commercial raspberry in Patagonia resulted in a negative impact on fruit set (reviewed in Aizen et al., 2020). Risk assessments should therefore be implemented before introducing a non-native pollinator species, especially since managed species may have a marked negative effect on native pollinators (Russo et al., 2021).

On the other hand, there has been an increase in the number of manageable pollinator species over time, which highlights the potential or perceived need for additional suitable pollinator species. These could be chosen according to their traits, e.g. their ability to buzz-pollinate in the case of tomato pollination, or ability to nest in the vicinity of a field-grown crop. For successful trait-matching, crop-pollinator networks could be used to identify common flower visitors of that crop, paired with quantification of pollinator efficiency of the species itself or related species with similar traits (e.g., short-tongued vs. long-tongued bumble bees). Such trait matching could pinpoint native species that can be prioritized for investigation and assessed for risks they might pose to other native pollinators and their ecosystems if the managed species becomes invasive.

Given the potential risks associated with pollinator management, and that a combination of species provides better pollination assurance than a single species (e.g., Garibaldi et al., 2013), it is logically more sustainable to enhance and/or manage multiple native pollinator species, e.g., through the creation of habitat for native pollinators in or around crop fields. Habitat enhancement to benefit pollinator abundance and diversity in agricultural landscapes aims to protect and restore favorable habitats, increase the quality and quantity of floral resources, reduce intensive mechanical practices, reduce chemical inputs, and provide nest sites for pollinators (reviewed in Garibaldi et al., 2017; Kleijn et al., 2019). Furthermore, by coupling knowledge of the most efficient pollinators of specific crops with knowledge of their lifecycle requirements, habitat can be specifically designed to support targeted bee and non-bee pollinators for improved pollination (Howlett et al., 2021). Using these approaches, native wild pollinator populations can be enhanced and promoted, resulting in increased pollination of adjacent crops (Blaauw and Isaacs, 2014; Forbes and Northfield, 2017).

4.7 Knowledge gaps and future research

We found the majority of reports on *A. mellifera* mortality from North America and Europe and limited information for Africa, Asia, South America and Oceania. Further surveys in understudied regions and a continuation of the monitoring in well-studied regions as well as investigation of the causes of mortality can help to achieve better understanding of honey bee health across the world. While the number of *A. mellifera* hives is reported worldwide, we lack data for other managed pollinators on the extent of their use so as to identify trends over time. The health of other pollinators and their responses to threats (diseases, pesticides, nutritional deficiencies and climate change) can differ from honey bees, which emphasizes the need to monitor several pollinator species (Wood et al., 2020). Furthermore, while there is increasing research on manageable pollinators and their effects on crops, there is limited information on the pollination management practices of farmers (Breeze et al., 2019) and their willingness to include new species into their pollination management, information which could be important to understand practicable species for farmers. Also, most manageable pollinator species are native to North America, Europe, and Asia. Only recently have a greater number of native species been considered in South America, despite the high dependence on pollinators by agriculture in that geographical region (Aizen et al., 2019). Few species from Central America, Africa, and Oceania are known as manageable pollinators. Previous practices that introduced non-native species to those regions could be avoided in the future if more native pollinators were investigated as manageable species.

5. Conclusions

The number of insect species managed for pollination, especially bees, has increased markedly over recent decades, paralleled by a growing number of honey bee colonies and commercially-reared bumble bee colonies. Currently, 66 species are known as manageable pollinator species globally. While some taxonomic groups (e.g., solitary bees) and species native to geographical regions (e.g., North America) have long been used as managed pollinators, others have only been considered rather recently (e.g., stingless bees and species from South America). The rise in consumer demand for pollination-dependent fruits, nuts, and seeds is likely driving the increasing dependence of agriculture on pollinator-dependent crops and the trend towards crops cultivated under permanent cover. At the same time, there is growing awareness and recognition of the negative effects of non-native species on local pollinators. Only a few bee species are commonly used in pollination, which represents a challenge for food security and farmer livelihoods. For instance, we demonstrate high mortalities of *A. mellifera* colonies, the most widely used managed pollinator, especially in North America. This highlights the need to preserve wild pollinators, e.g., through pollinator-sympathetic land management, as well as to consider a more diverse set of managed pollinator species. Though the management and deployment of novel pollinator species are not without risks, particularly if employed in locations where a pollinator is non-native, crop-specific and sustainable management of a diversity of new pollinator species may contribute to safeguarding future crop yields and food security.

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Chapter IV: On-farm experiences shape farmer knowledge, perceptions of pollinators and management practices

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Abstract

Mitigating pollinator declines in agriculturally dominated landscapes to safeguard pollination services requires the involvement of farmers and their willingness to adopt pollinator-friendly management. However, farmer knowledge, perceptions, and actions to support on-farm pollinators and their alignment with science-based knowledge and recommendations are rarely evaluated. To close this knowledge gap, we interviewed 560 farmers from 11 countries around the world, cultivating at least one of four widely grown pollinator-dependent crops (apple, avocado, kiwifruit, oilseed rape). We particularly focused on non-bee crop pollinators which despite being important pollinators of many crops, receive less research attention than bees. We found that farmers perceived bees to be more important pollinators than other flower visiting insects. However, around 75% of the farmers acknowledged that non-bees contributed to the pollination of their crops, seeing them as additional pollinators rather than substitutes for bees. Despite farmers rating their own observations as being most important in how they perceived the contribution of different crop pollinator taxa, their perception aligned closely with results from available scientific studies across crops and countries. Farmer perceptions were also linked with their pollinator management practices, e.g. farmers who used managed bees for crop pollination services (more than half the farmers) rated these managed bees particularly important. Interestingly, their willingness to establish wildflower strips or manage hedgerows to enhance pollinator visitation was linked to their ecological knowledge of non-bees as well as to government subsidies. Farmers adapted practices to enhance pollination services depending on the crop, which indicates an understanding of differences in the pollination ecology of crops. Almost half of the farmers had changed on-farm pollination management in the past 10 years and farm practices differed greatly between countries. This suggests integrated crop pollination measures are being adapted by farmers to reach best pollinator management practices. Our findings highlight the importance of studying local knowledge as a key to co-design locally-adapted measures to facilitate pollinator-integrated food production as ecological intensification tools.

Keywords: Conservation, Crop pollination, Ecological intensification, Farmer knowledge, Local knowledge, Survey

Introduction

With 38% of the land surface currently under agricultural land use (FAO, 2021), farmers` decision-making and the practices they subsequently implement are crucial for crop yields as well as impacting biodiversity. Ongoing world population growth and changes in human diet preferences (Godfray et al., 2010) further result in increasing land area used for agriculture (Aizen et al., 2019) as well as landscape simplification through agricultural intensification (Kehoe et al., 2017). Approximately 75% of globally important crops depend on animal pollination (Klein et al., 2007), especially crops that provide essential human nutrients (Eilers et al., 2011). Furthermore, the area of land cultivated with pollinator-dependent crops is increasing disproportionately to other crops (Aizen et al., 2019) and the availability of honey bees as managed pollinators (Aizen and Harder, 2009). Although yield stability benefits from diverse pollinator communities (including bee and non-bee) (Hoehn et al., 2008; Garibaldi et al., 2013; Mallinger and Gratton, 2015; Rader et al., 2016; Senapathi et al., 2021), agricultural expansion and intensification remain major drivers of biodiversity loss (Kehoe et al., 2017), decreasing the stability of yield in pollinator-dependent crops (Deguines et al., 2014). Therefore, there is an urgent need for farmers to safeguard pollinators and their diversity to ensure sufficient pollination and secure global food production.

Ecological intensification has been proposed as a more nature-based solution to safeguard food production, while at the same time not harming or even potentially enhancing biodiversity (Bommarco et al., 2013; Kleijn et al., 2019). For example, flower strips have been shown to enhance pollinator communities over time, leading to enhanced crop pollination services and yields in adjacent crops that surpass implementation costs (Blaauw and Isaacs, 2014). Several governmental programs encourage farmers to incorporate biodiversity-friendly measures through subsidies, especially in North America and Europe (Garibaldi et al., 2019; Pe’er et al., 2020). Nevertheless, farmers can be reluctant to implement ecology-based measures, even when evidence supports the benefits they can deliver (Kleijn et al., 2019). Perceptions of agricultural biodiversity and ecosystem services differ substantially between farmers and scientists, suggesting a communication gap (Maas et al., 2021), which might affect the uptake of ecological measures (Knapp et al., 2021).

Effectively employing ecological intensification is knowledge-intensive, context-dependent, and continually being refined as new evidence emerges (Gemmill-Herren et al., 2021). Some aspects of nature`s contribution to agricultural production have only recently been addressed by scientists, for example the contribution of non-bees (i.e. flies, butterflies, beetles, moths, birds) to crop pollination (Rader et al., 2016). Yet it is clear, the contribution of different insect groups to pollination varies with the crop system studied (Rader et al., 2016, 2020) and the geographic region (Brown and Cunningham, 2019; Dymond et al., 2021). In addition, there is often a lack of evidence (Albrecht et al., 2020) or no scientific consensus of optimal practices to boost pollination services (Rollin and Garibaldi, 2019) or recommendations might be context dependent. For example, honey bee colony density recommendations are highly variable even within the same crop (Delaplane and Mayer, 2000; Rollin and Garibaldi, 2019) and fixed hive stocking rates do not guarantee consistent pollinator visitation rates (Howlett and Lankin, 2015; Osterman et al., 2021). In addition, benefits of measures to enhance biodiversity might take several years to be effective (Blaauw and Isaacs, 2014). This uncertainty makes the communication of scientific findings between researchers and farmers and recommendations for best practice problematic.

Farmer perception of pollinators in general, and especially of non-bees, are rarely studied (Garbach and Morgan, 2017; Breeze et al., 2019; Rawluk and Saunders, 2019; Hevia et al., 2021). Yet, local and indigenous knowledge can provide some solutions to the current challenge of pollinator decline, however, there is no integration and analysis of this knowledge for its practical use (IPBES, 2016). Understanding indigenous and local knowledge is crucial because it can provide complementary perspectives and extend our understanding of the spatial and temporal dynamics of biodiversity, provide vital information on the use of locally adapted crop varieties and support practices that are tailored to local visions and needs (Sutherland et al., 2013). The few studies addressing farmer knowledge reveal that local understanding about pollinators and pollination can vary enormously between regions, countries, and crops (Kasina et al., 2009; Frimpong-Anin et al., 2013; Hanes et al., 2015; Smith et al., 2017; Breeze et al., 2019; Elisante et al., 2019; Hevia et al., 2021). While some of these differences arise from variations in information sources or education, it may also derive from personal experiences, which would vary between crops, regions and farming approaches, but this has been little studied. In addition, little is known about how farmer perceptions and knowledge influence their decision-making, and to what extent governmental subsidies can enhance the uptake of environmentally friendly measures (Kleijn et al., 2019).

We interviewed 560 farmers cultivating one of four pollinator-dependent crops (apple, avocado, kiwifruit, and oilseed rape) in 11 countries on four continents, using quantitative surveys. The overall intention was to study farmers as potential local knowledge holders with the aim of:
(1) exploring how farmers perceive the relative importance of different pollinator groups and determine how this changes across geographical regions, and crops;
(2) investigating the source of farmer knowledge, with a focus on non-bees and determine the knowledge gaps farmers perceive should be filled by scientists;
(3) assessing the extent that farmer decision-making, e.g. on-farm pollination management, can be linked to their perception of pollinators, economic incentives, or scientific recommendations.

Methods

Data collection and design of the survey

We surveyed farmers growing at least one of four cultivated crops in countries across both northern and southern hemispheres: apple (*Malus domestica*), oilseed rape (*Brassica napus* L. or OSR), avocado (*Persea americana*), or kiwifruit (*Actinidia deliciosa*). These represent economically valuable crops for which the role of non-bee insects is either well established or not well known (Rader et al., 2016). Detailed information on their pollination requirements can be found in the Supplementary Material. Data were collected from 11 countries across four continents (United Kingdom (UK), Australia, Mexico, New Zealand (NZ), Guatemala, Israel, Germany, Belgium, Poland, Spain, and Slovenia; Table S1 and Fig. 1). The original English version of the survey can be found in the Supplementary Material or online (https://www.surveymonkey.com/r/3QLPZBS). A detailed description of the survey design and the collection process can be found in the Supplementary Methods. In total, we collected 560 fully complete and usable surveys (mean 33 questionnaires ± 12 SD per country and crop; see Table S1). The survey included 13 questions regarding: (i). general farm characteristics and management (e.g. size, crops cultivated, organic or non-organic farming; question 1-4 in the questionnaire); (ii). farmer perceptions of the importance of pollinators in relation to their cultivated crops, with a particular focus on non-bee insects and their pollination services (questions 5, 6, 7, 12); (iii). source of farmer knowledge in regard to non-bees (questions 8, 13); and, (iv). general pollinator management practices in the past, their current practices, and those anticipated in the future (questions 9, 10, 11). The survey data was collected following the German Rat for Sozial- und Wirtschaftsdaten (2017). Every participant was informed that the interviews are voluntarily, will be anonymised and that the interviews can be withdrawn at any time. The survey included a written consent for the collection and processing of the personal survey data (see Supplementary Material).

Farmer perceptions on the importance of bee and non-bee pollinators to their crops production

To determine whether farmers vary in their perception of the importance of different pollinator groups (aim 1, question 5 of the questionnaire), we asked farmers to evaluate the importance of pollinators on a Likert-type scale (Likert, 1932): not at all important pollinator (0), minor pollinator (1), somewhat important pollinator (2) or very important pollinator (3). Farmers rated pollinators separately for 7 different functional groups (i.e. honey bees, bumble bees, other (wild) bees, flies, beetles, moths/butterflies, and others). We then analysed differences in the scores for pollinators using a cumulative linked mixed model (CLMM) in R (R Core Team, 2019), which can be used to analyse ordinal data (function `clmm`, package ordinal`; (Christensen, 2018)). Preliminary analyses revealed a significant two-way interaction between pollinator type and crop cultivated, meaning that the perceived importance of pollinators varied depending on the crop. Therefore, separate analyses were performed for each crop type. Farmer’s identity was included as a random factor to account for non-independence of the scoring. Separate CLMMs for each crop included pollinator type, country, and their interaction (pollinator type*country), as well as production form (i.e. organic vs. non-organic) as fixed factors.

To further investigate farmers’ understanding of the role of non-bees as pollinators, we asked why they perceived non-bees to be effective crop pollinators (aim 1, question 6). Answers were: i. they are more reliable pollinators than bees, ii. they visit my crop when bees are not active, iii. they provide additional pollination above what bees can do and iv. other reasons (open question). We analysed whether farmer responses (reason picked yes or no) differed between the question categories, crop type, country, and production form, by using a generalized linear mixed model (GLMM) with farmer identity as random factor and assuming binomial error distribution.

Farmers were further asked the extent to which non-bees contributed to their crop yield (in percentage, question 7). We analysed differences in the responses with crop type, country, and management type as fixed factors, using a GLM with a Tweedie distribution to account for the zero-inflation of the data using the R package “statmode” (Giner and Smyth, 2016). Additionally, farmers were asked if they think non-bee pollinators could play a more important role in the pollination of their crop in the future (question 12). To investigate differences between countries, crops cultivated and production form, we used a GLM with binomial error distribution.

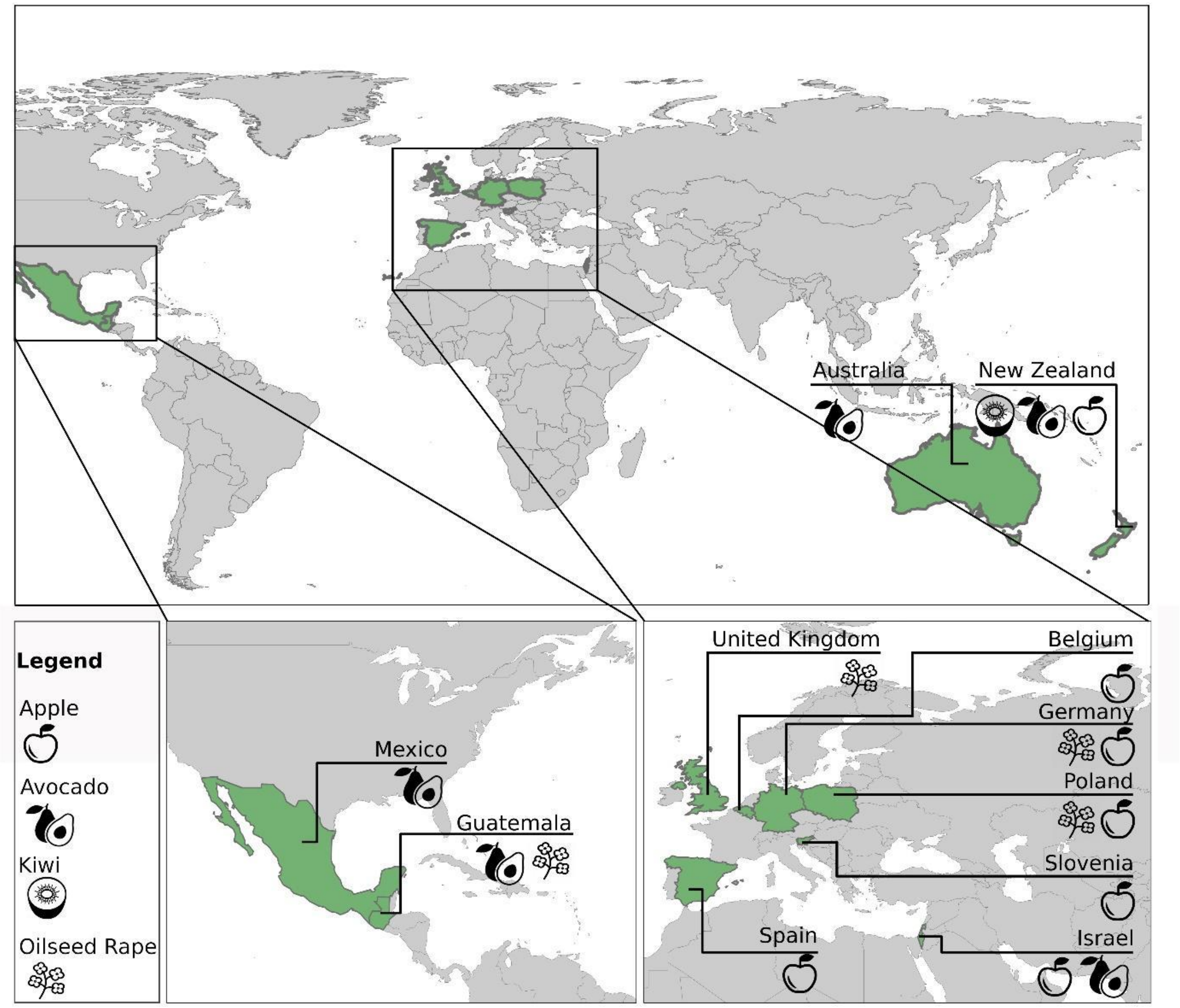

Fig. 1. World map, highlighting the 11 countries (in green) in which farmers were interviewed alongside information on crops grown.

Origin of farmer knowledge and knowledge gaps that should be filled by scientists

To understand how farmers became aware of non-bees as pollinators (aim 2), we asked farmers to state their information sources (question 8). Answers were: i. *I have seen them*, ii. *other farmers*, iii. *farm advisor or agronomist*, iv. *farmer workshop*, v. *through farmer resource (magazine, pamphlet)*, vi. *other media (e.g. radio, tv, internet)*, vii. *scientists (publication, discussion)* and an open option to allow additional answers. Multiple answers were possible. For statistical analyses, we excluded data from Germany and Slovenia as the option “scientists” was not included in those questionnaires. We then tested differences in information source picked (yes/no) between information source, crop type, country, and production form in the remaining dataset by using a GLMM with farmer identity as a random effect and a binomial error distribution.

Farmer perceptions of pollinator importance could be related to on-farm experiences, i.e. by observing the abundance of different flower-visitors per crop and country. Therefore, we performed a literature search for studies which had recorded flower visitor abundance (for details see Supplementary Methods and Table S2). We used a cumulative linked model (CLM) to investigate if the median score of a pollinator per country and crop (i.e. based on Likert evaluations of the importance of each taxa: see above) could be explained by the observed relative abundance derived from scientific studies. Pollinator type and relative abundances were fixed factors.

Knowledge gaps perceived by farmers: Farmers were asked which information and in which format further knowledge of non-bees as pollinators should be disseminated (question 13). For the statistical analysis, we excluded data from Israel as a translation error of the question occurred. We first investigated if farmers desired more information, and then categorised their responses.

Linking farmers` management practices with their perception of pollinators and external incentives

To understand whether farmer knowledge influences their decision-making (aim 3), we asked farmers to outline their practices to promote pollinators or enhance pollination services (see questions 9 and 10 in the questionnaire). These included direct management of pollinators (e.g. honey bee hives) and intensity (e.g hives per hectare) for four pollinator groups (honey bees, bumble bees, other bees, and non-bees). In a separate analysis, for all four managed pollinator types (i.e. providing honey bees hives, bumble bee hives, other bees, and non-bees), we then investigated whether pollinator management (implemented yes/no) is affected by farmer perceptions using GLMs with binomial error distribution, scoring honey bees, bumble bees, other bees, and the median of non-bees, with crop type, country, and production form included as fixed factors. The median of non-bees was used to reflect the overall perception by farmers. We also investigated differences in the number of honey bee hives per ha provided by farmers to their crop, with crop type, country, and production form as fixed factors, using a GLM with a Tweedie distribution.

Habitat enhancement; Farmers were asked whether they promote pollinators or pollination services by i) planting floral strips, ii) managing hedgerows, or iii) other management forms, with the possibility to give free answers, which were categorised post-hoc. We also examined whether external incentives, i.e. subsidies, influenced decision-making regarding hedgerow management or the establishment of wildflower strips. We collected information per country on the existence of governmental economic support for such ecological management interventions. We analysed the three practices (i.e. establishment of floral strips, hedgerow management, and other practices) separately to understand whether farmer perceptions or governmental incentives drive the implementation of pollinator-friendly measures and whether there are differences between crops and production form. In all three cases, we used a GLM with a binomial error structure with implementation (yes/no) as the dependent variable. Farmer perceptions of pollinators were represented by scores given to the importance for honey bees, bumble bees, other bees and the median of non-*Apis* bees. The presence of subsidies was included as a fixed factor for floral strips and hedgerows.

Change in pollination management: Farmers were asked whether their pollination management approach had changed within the last ten years and, if so, in which way (question 11). The given answers were divided into 5 categories post-hoc. The change in pollination management (yes/no) by farmers was investigated by using a GLM with a binomial error distribution in which crop type, country, and farm management type were fixed factors.
All data were analysed in R-3.6.1 for Windows (R Core Team, 2019).

Results

Farmer perceptions of pollinator importance, with a focus on non-bees

Farmers valued pollinator importance differently depending on functional groups. Honey bees were rated as very important (median score 3), bumble bees and other bees as somewhat important (median score 2), and non-bees (flies, butterflies, beetles) as minor pollinators (median score 1). We found that 52% of all farmers rated “other pollinators” with a median of 0 (not at all important) (Fig. 2). For apple, avocado, and OSR farmers, we detected an interaction effect between country and pollinator type (Fig. 2, Table 1), meaning that farmers perceive pollinators differently depending on their location. For example, Australian avocado farmers ranked “other pollinators” relatively higher than farmers from Guatemala, while for bumblebees the reverse was true (Fig. 2). Overall, organic farmers ranked pollinators higher than non-organic farmers (Table 1).

Farmers mainly considered that non-bees contributed additional pollination to their crop (mean ± SE; 74% ± 2) or that they pollinated their crops when bees were not active, *i.e*. different visit time (45% ± 2), while a minority (10% ± 1) rated non-bees as more reliable pollinators than bees and 9% (± 1) indicated they provide additional benefits. The proportion of farmers selecting reasons why non-bees are beneficial differed between the categories described before ($\chi2 = 322.33$, DF = 3, $P < 0.001$), crop cultivated ($\chi2 = 13.67$, DF = 3, $P = 0.004$), countries ($\chi2 = 47.59$, DF = 10, $P < 0.001$), and between production form ($\chi2 = 10.35$, DF = 1, $P = 0.002$, see Fig. 3). For example, in New Zealand only around 30% of the kiwifruit farmers stated that non-bees can provide additional pollination as opposed to around 50% of the apple farmers (Fig. 3). Overall, farmers estimated that non-bees perform 19% of the ecosystem service of pollination. This estimation differed markedly between countries (GLM, $F_{40,\ 2140} = 3.34$, $P < 0.001$), crops ($F_{12,\ 1602} = 2.79$, $P < 0.001$) and also between production form ($F_{4,\ 532} = 2.84$, $P = 0.024$). More farmers (57%) believe that non-bees could play a more important role for crop pollination in the future, then did not (27%). The rest (16%) did not express an opinion or indicated they did not know. These proportions differed between countries ($\chi2 = 52.94$, DF = 10, $P < 0.001$) but not between crops ($\chi2 = 4.96$, DF = 3, $P = 0.175$) nor production form ($\chi2 = 0.83$, DF = 1, $P = 0.364$).

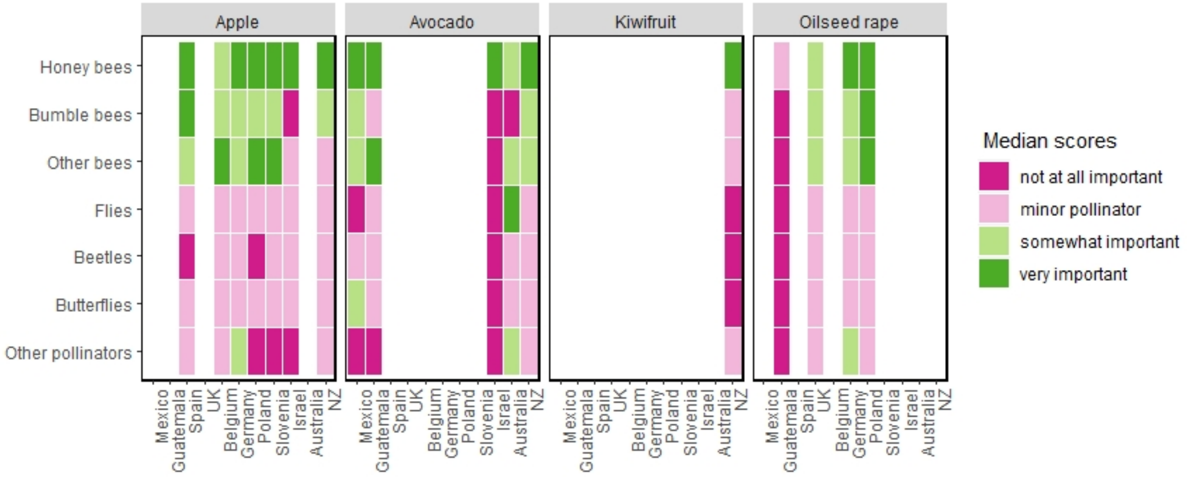

Fig. 2. Importance of pollinator groups across countries. Heat maps illustrating the perceived median importance of pollinators split by the four crops farmers cultivate and by country. Missing data represent options with insufficient scores. Scores of pollinator importance by farmers are following a Likert-type scale: *not at all important pollinator* (0), *minor pollinator* (1), *somewhat important pollinator* (2) or *very important pollinator* (3).

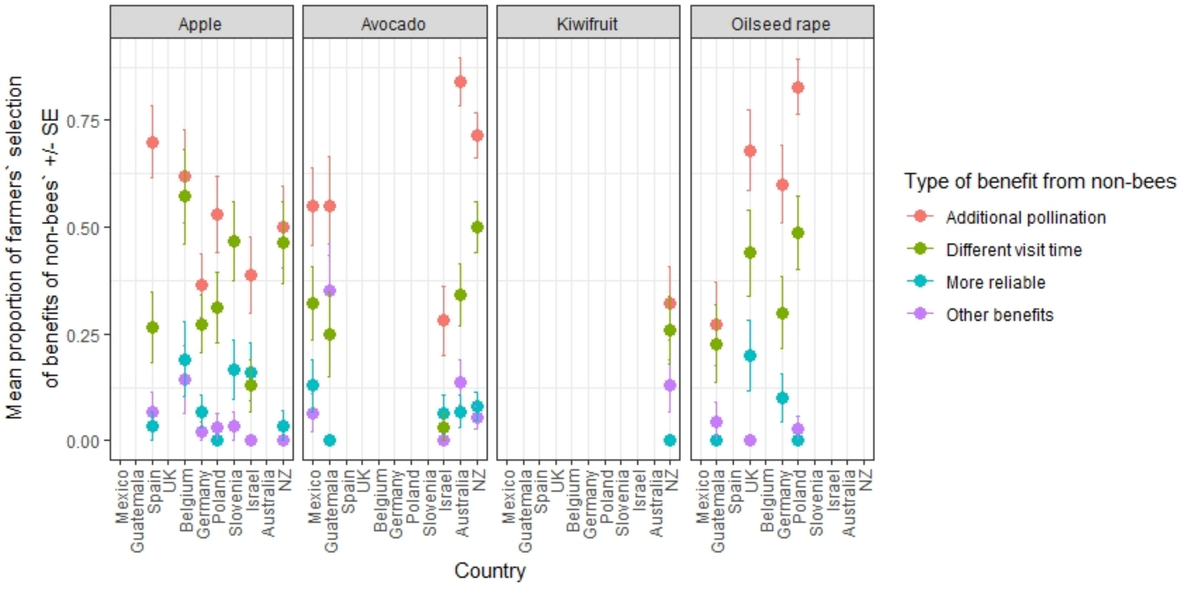

Fig. 3. Mean proportion of farmers selecting the reason for benefits of non-bees for the pollination of their crop for the four crop types and country. Error bars indicate ±1 SE.

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Origin of farmer knowledge and knowledge gaps that should be filled by scientists

Most farmer awareness of non-bees as pollinators was through observing them in the field (57%), 21% through farmer resources (magazines, pamphlets), 19% through workshops, 17% from scientists, 15% from other farmers, 14% from advisors, 9% from other media (e.g. radio, tv, internet) and 6% specified other sources. The proportion of farmers differed between type of information source ($\chi2 = 644.94$, DF = 7, $P < 0.001$), crops ($\chi2 = 49.68$, DF = 3, $P < 0.001$), countries ($\chi2 = 74.82$, DF = 8, $P < 0.001$), as well as between production form ($\chi2 = 6.22$, DF = 1, $P = 0.013$; Fig. 4). Interestingly, farmer scores of pollinator importance were positively related to relative abundance (percentage); as observed per crop and country by researchers (CLM, LRT = 4.917, $P = 0.027$; Fig. 5).

Table 1 | Results of generalized linear mixed-effects models of crop type, pollinator type, their interaction and management on pollinator importance scores

Comparison	***DF***	**LRT**	***P***
Full model			
Pollinator	6	1484.23	**<0.001**
Crop	3	8.25	**0.041**
Organic	1	5.91	**0.015**
Country	10	78.08	**<0.001**
Pollinator x Crop	18	212.93	**<0.001**
Apple			
Pollinator	6	809.73	**<0.001**
Country	6	10.43	0.108
Organic	1	4.37	**0.037**
Pollinator x Country	36	228.21	**<0.001**
Avocado			
Pollinator	6	413.62	**<0.001**
Country	4	30.00	**<0.001**
Organic	1	0.240	0.625
Pollinator x Country	24	304.46	**<0.001**
Kiwifruit*			
Pollinator	6	186.17	**<0.001**
OSR			
Pollinator	6	304.46	**<0.001**
Country	3	53.10	**<0.001**
Organic	1	4.83	**0.028**
Pollinator x Country	18	44.43	**<0.001**

* Kiwifruit farmers were all non-organic and all located in New Zealand

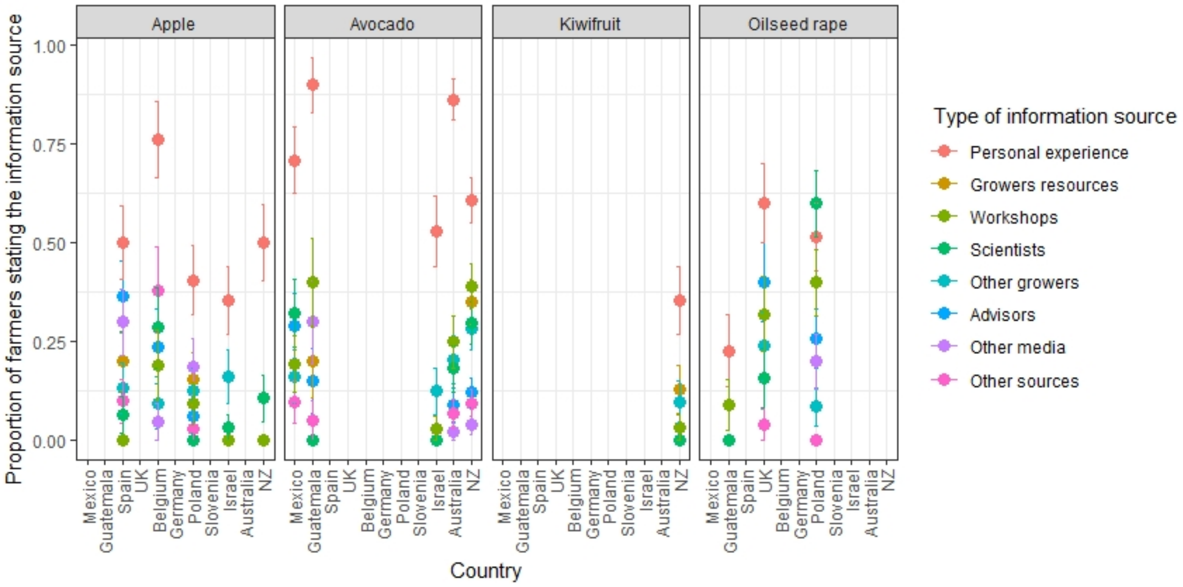

Fig. 4. Mean proportion of farmers stating their information sources for non-bees as pollinators for the four crop types and country. Error bars indicate ±1 SE.

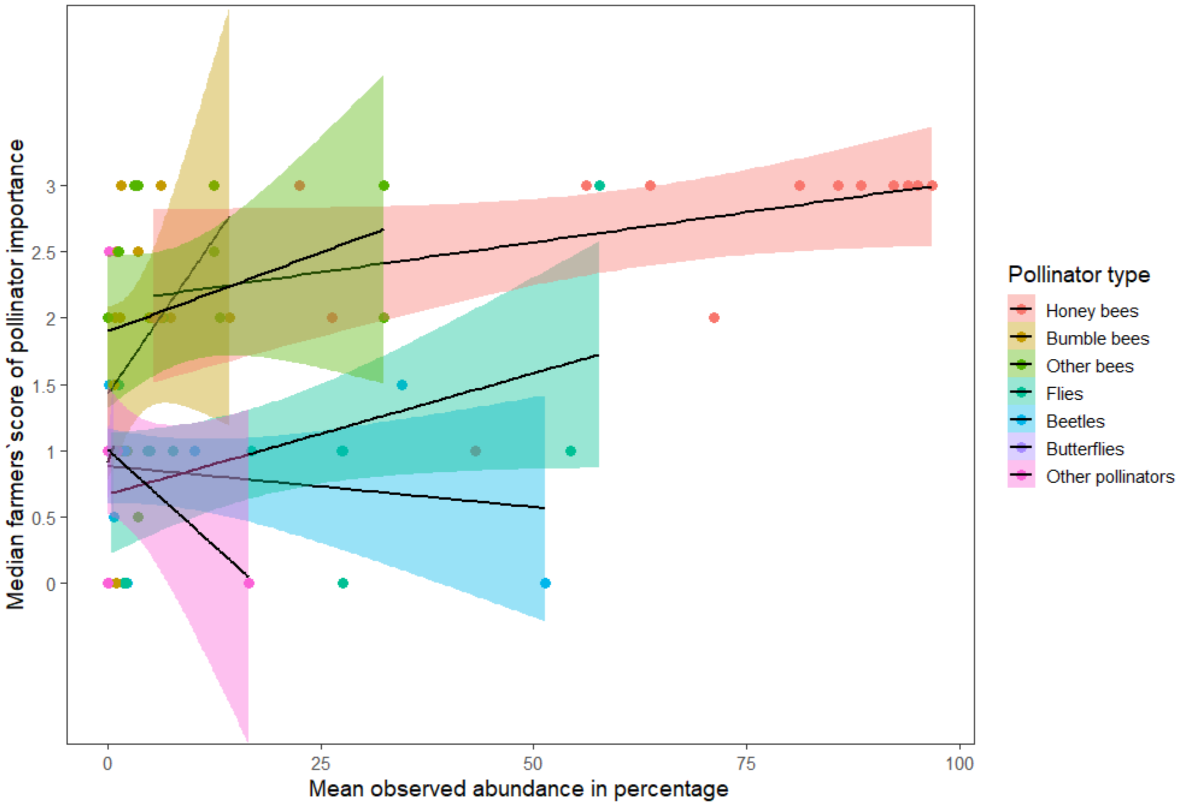

Fig. 5. Linking farmer knowledge with ecological observations. Relationship between the median farmer scores of pollinator importance per crop and country with the mean relative observed abundance in percentage by pollinator type. Plotted lines show the predicted relationships per pollinator type, dots represent means/median per crop and country per pollinator type and shaded areas indicate the 95% confidence intervals of the relationship.

Knowledge gaps perceived by farmers: 62% of farmers stated that they would like to receive more information about non-bees as pollinators. In particular, farmers were interested to know about the importance of non-bees as crop pollinators, their biology, and how to promote them (Fig. S1). Workshops and farmer conferences were mentioned most often as a preferred way to disseminate scientific evidence (Fig. S1).

Linking decision-making with farmer perceptions of pollinators, scientific evidence, and external incentives

We found that 59% of all farmers added managed honey bee hives, 9% bumble bees, and 4% other bees to supplement pollination services. Only 1% of all farmers provided non-bees for pollination services. Those supporting pollination services used one of the four managed pollinator functional groups, but only 3% of the farmers used other pollinators without using honey bees. Overall, 62% of the farmers managed crop pollinators by one or more species and 38% did not.

On-farm management of pollination services was linked to farmer perception of pollinator importance as well as the country (see Table S3). Strong positive links were found between perceived honey bee, bumble bee and other bee importance and their management but no links across taxa (e.g. the use of honey bees was not linked to perceived importance of bumblebees; Table S3). That non-bees were only used by 1% of the farmers (n=6) was slightly surprising, given that some farmers rating them as very important pollinators (i.e. flies (11%, n=63); beetles (7%, n=38); butterflies (8%, n=44)). Interestingly, while the management of bumble bees and other bees are crop dependent, this was not apparent for honey bees indicating that honey bees were ubiquitously implemented across crops (Table S3, Fig. S2). Farmers who provided honey bee hives for pollination services stated also the number of hives per hectare. We compared those with recommendations in studies reviewed by Rollin and Garibaldi (2019), consisting mostly of data from Delaplane and Mayer (2000) (Fig. S3). Only kiwifruit farmers provide a similar number of hives per hectare to those recommended, while farmers cultivating apple, avocado and oilseed rape provide lower numbers than recommended (Fig. S3). We found differences in honey bee hive stocking rate between crops ($\chi 2 = 56.66$, DF = 3, $P < 0.001$), countries ($\chi 2 = 99.66$, DF = 10, $P < 0.001$) and production form ($\chi 2 = 3.68$, DF = 1, $P = 0.049$).

Promoting pollinator services to crops through habitat enhancement was also undertaken by some farmers, with 27% establishing floral strips, 23% managing hedgerows, and 23% stating other forms of management. The establishment of floral strips was positively driven by both availability of subsidies and farmer perceptions of non-bees (Table S4). Hedgerow management was positively influenced by subsidies and differed between crops (Table S4, Fig. S4). For example, no kiwifruit farmer implemented hedgerows while 20% of the OSR famers did so without subsidies and even around 70% when subsidies were present (Fig. S4).

In total, farmers mentioned 24 further habitat enhancement strategies (Fig. S5). The reduction of pesticide use was mentioned most frequently (5%), followed by mixed cropping (3%) and provisioning of nesting habitat (3%). These practices differed strongly between countries (Table S4). For example, farmers from Mexico and Guatemala indicated the use of mixed crops, mainly traditional plants that grow in the Mayan milpa agroecosystem or the use of arboreal plants as hedges that also provide flowers. Interestingly, some farmers, mostly avocado and kiwifruit farmers, actively attract pollinators with scent or sugar syrup. Some also carried out artificial pollination i.e. spraying of pollen for an adequate pollination service (Fig. S5). Moreover, some farmers implemented non-bee-specific measures (e.g. an Australian avocado farmer, stated: “use dead kangaroos for flies”).

Almost half of the farmers (45%) stated that they had changed their pollination management (habitat enhancement and managed pollinators) in the last 10 years, while the rest did not answer this question (19%) or had not changed their pollination management (36%). The proportion of stated changes in pollination management differed between countries ($\chi2 = 76.32$, DF = 10, $P < 0.001$) and crops ($\chi2 = 20.56$, DF = 3, $P < 0.001$) but not between production form ($\chi2 = 0.00$, DF = 1, $P = 0.962$). We identified 29 different types of changes (see Fig. S6) of which the increase in honey bee hive number was mentioned most often (11%), while some farmers stated they no longer used or had reduced the number of honey bees for pollination services (7%).

Discussion

To our knowledge this is the first study to examine farmer knowledge of non-bee pollinators across multiple countries and crops. Although the importance of managed and wild bees as pollinators of most insect-pollinated crops grown across the globe has been widely recognised by scientists (Garibaldi et al., 2013, 2017; Rollin and Garibaldi, 2019) and farmers (Hanes et al., 2015; Garbach and Morgan, 2017; Park et al., 2018; Eeraerts et al., 2020; Maas et al., 2021), the role of non-bee insects has been largely overlooked until recently (Rader et al., 2016, 2020; Hevia et al., 2021; Howlett et al., 2021). The limited research on the effectiveness of non-bee crop pollinators (Rader et al., 2020) and their management on farms (Howlett et al., 2021) has provided an opportunity to assess farmer knowledge about these pollinators in the absence of extensive scientific research and management recommendations. We show that farmers are holders of knowledge mainly obtained through their own experiences. This knowledge largely mirrored scientific research findings (where available), and was nuanced, varying between countries, crops grown and production system (i.e. non-organic vs. organic).

Farmer perceptions of pollinator importance with a focus on non-bees

Farmers generally ranked bees higher than non-bees in their importance as pollinators of their crops, a finding reflected in the scientific literature (Rader et al., 2016, 2020) and recorded from other farmers (Hevia et al., 2021). However, non-bees were recognized by the majority of farmers as probable pollinators providing useful additional and complementary pollination services to that provided by bees rather than potentially replacing them. This is supported by the conclusions of a meta-analysis of global studies conducted by Rader et al. (2016). On average, farmers estimated a contribution of 19% from non-bees to the pollination service provided to their crop. This compares with findings by Rader et al. (2016) that found non-bees contribute 25-50% of the total number of visits to crops and that fruit set increases with non-bee abundance independently of bee visitation rate. Despite limited research compared to bees, many farmers perceived that non-bees play a useful role in crop pollination.

Origin of farmer knowledge and knowledge gaps that should be filled by scientists

In this study, we demonstrate for the first time that farmer knowledge of the perceived importance of pollinators is connected to the relative abundances of pollinators, as reflected in published studies (Table S2). This suggests that farmers observe, recognise and value pollinator taxa based on their abundance as crop flower visitors. A particularly interesting finding of our study is that the extent of knowledge held by farmers on non-bee pollinators was based on their own observations (>50% of farmers) rather than through scientific research findings. To date, scientists have largely focussed on the importance of bees, the management of pollinators (Garibaldi et al., 2017; Rollin and Garibaldi, 2019) and landscape/habitat enhancement strategies to promote wild and managed bees (Garibaldi et al., 2017). As a result, comprehensive management guidelines towards promoting non-bees are largely lacking (Rader et al., 2020; Howlett et al., 2021). We therefore believe that farmer knowledge is an untapped resource that could be harnessed to co-design farmer-scientist research that delivers knowledge and recommendations better suited to farmers across agricultural landscapes.

Linking decision-making with farmer perceptions of pollinators, scientific evidence, and external incentives

Around 60 percent of the interviewed farmers used one or more managed pollinators. Nearly all of these farmers placed honey bees in or near their crops for pollination (59% of farmers) with just 3% using managed non-Apis pollinators (i.e., bumble bees, other bees, non-bees) without managing honey bees at the same time. The global importance of honey bees as a managed pollinator of insect-pollinated crops is well recognised (Garibaldi et al., 2013; Rollin and Garibaldi, 2019), including by farmers (Hanes et al., 2015; Garbach and Morgan, 2017; Park et al., 2018; Eeraerts et al., 2020; Hevia et al., 2021). Farmer perceptions of bees were linked to pollinator management. Farmers providing bees on their farms simultaneously rated those managed pollinator taxa higher than farmers not providing them. At the same time, we found marked differences in bee pollinator management between countries, e.g. differences in the use of honey bee hives as well as their stocking rate was mainly explained by location. Regional differences in pollinator abundances and availability driven by landscape structure or geographical region could be the driver behind the use, or not, of honey bees. For example, in New Zealand, avocado and kiwifruit farmers must rely heavily on managed honey bees as few wild pollinators visit these crops (Howlett et al., 2017; Read et al., 2017). In other countries, wild pollinators visiting these crops can occur in much higher abundance (Miñarro and Twizell, 2015; Dymond et al., 2021). Also, regional differences might occur due to differences in beekeeping costs or differences in pollination requirements of cultivars (Eeraerts et al., 2020). Adapting to local conditions through their own experiences could therefore drive farmers' decision-making rather than science/industry recommendations as those where only mentioned for kiwifruit (only sampled in New Zealand) but not for the three other crops. To avoid pollination deficits or deleterious effects of too-high stocking rates on wild bee populations or crop production (Sáez et al., 2014; Lindström et al., 2016), the effect of pollinator density should be further investigated, especially since many farmers stated they increased stocking rates. Findings should be well communicated between scientists and practitioners (Evans et al., 2021), to develop more dynamic site-specific recommendations that optimise pollination services.

Farmer decision-making might not only be related to their own knowledge and perceptions. While there are many studies on managing bees, farmer uptake of these vary greatly (Stephen, 1961; Crane, 1983; Velthuis and Van Doorn, 2006). For example, in a survey in Belgium most cherry farmers perceived solitary bees as important pollinators but their management or encouragement was very low due to the absence of practical management guidelines (Eeraerts et al., 2020). While the knowledge and perception of farmers was linked in this study with the management of bees, managing non-bees was almost non-existent despite some farmers rating them as very important pollinators. Lack of experience or the uncertainty of their contribution to pollination can be barriers to establishing new pollinator management practises (Hanes et al., 2015; Breeze et al., 2019), and only a few studies investigate the benefit and potential of non-bees as managed pollinators (Howlett and Gee, 2019). We conclude that farmer knowledge can be linked to their decision-making, but only when practices are well established, clear, and easy to implement.

Although our study indicates farmers mostly have a solid understanding of pollinators and their contribution to crops, habitat enhancements might be perceived as an economic risk (Breeze et al., 2019; Kleijn et al., 2019). Also, pollinator-friendly measures targeted at increasing pollinator diversity showed variable effects on crop pollination and yield (Albrecht et al., 2020). We found that around a quarter of the farmers established wildflower strips and a quarter managed hedgerows to support pollinators. The presence of governmental subsidies explained the increasing establishment of floral strips and management of hedgerows; however, bureaucratic procedures can also act as a barrier for the implementation (Eeraerts et al., 2020). Thus, applications for subsidies should be made as easy as possible to encourage implementation (Eeraerts et al., 2020).

Additionally, traditional practices in Mexico (living hedges) and Guatemala (milpa agroecosystem) seem to fulfil similar functions to those provided by hedgerows and floral strips. The existence of this traditional management practises may explain the lack of government subsidies for pollinator management in the region. Living hedges are native plants from each ecological region chosen for their resistance, provision of wood, shade and nectar (Reyes and Rosado, 2000). The milpa agroecosystem is a complex Mayan practice that consists of growing mixed crops within a system of rotation and regeneration that allows heterogeneity of food sources that seems to be favourable to native bee populations (Landaverde-González et al., 2017). Through it, the value of the assessment of traditional farming practices is highlighted, since these can offer valuable contributions to the conservation of pollinator biodiversity and the sustainable use of ecosystems (IPBES, 2016).

In the past 10 years, 45% of interviewed farmers had adapted their pollination management, including beekeeping, encouragement of pollinators, and land management (Fig. S6), suggesting that farmers are trialling a variety of measures to boost on-farm pollinator diversity through their own experiences. Our study highlights the strong potential for delivering future applied outcomes by using local knowledge held by farmers to guide research activities resulting in more resilient on-farm pollination and the willingness of farmers to adopt practices that support crop pollination (McCracken et al., 2015). This provides opportunities to verify the effectiveness of farmer-led strategies, which may then be more easily integrated into broader farm management practices (Kleijn et al., 2019).

Knowledge gaps perceived by farmers: Most (62%) farmers were keen to receive more information on pollination management, particularly from scientists, about non-bee pollinators. Some farmers were also interested to know which flowers apart from their crop can be beneficial for non-bee pollinators. Ecological plant-pollinator network analysis provides a useful tool to communicate those findings to farmers (Howlett et al., 2021). Scientific evidence should be disseminated through direct contact such as farmer conferences and workshops rather than (social) media or magazines if it is to influence farmer decisions. Indeed, social learning can be of great importance to adopt new management techniques (Garbach and Morgan, 2017).

Shortcomings and knowledge gaps

Despite our efforts to reach a broad range of farmers, we acknowledge that our sample might be biased towards famers with better ecological knowledge, as they were more likely to respond to our questionnaire. Furthermore, our sample was also biased towards farmers with pre-established contact with researchers, as we used our existing farmer networks, which could be the reason for a high percentage of farmers stating scientists as an information source of non-bees as pollinators. Nevertheless, the high level of farmer responses *i.e.* the number of questionnaires per country and crop, gave us a substantial insight into differences in farmers` knowledge and their decision making. We made efforts to target a broad range of farmers by approaching them through a wide range of ways e.g. farming press, direct contact, farmer conferences, regular mail, and internet platforms. Also, we argue that better informed farmers can support early stage implementations of new techniques and inform others in farmer networks (Garbach and Morgan, 2017).

Conclusions

Here, we demonstrated that farmer perceptions of pollinators are linked to their on-farm experiences and that these perceptions are closely aligned with the scientific literature. This highlights that local knowledge provides an important and accurate source of information which should be more widely recognized when shaping pollinator management decisions. We also conclude that farmer decision-making is influenced by their beliefs and external incentives. We recommend the dissemination of scientific evidence, especially those of complex coherency, through direct contact, such as farmer conferences and workshops. By using local and indigenous knowledge, ecological measures to increase pollination services can be restructured through cooperation between scientists and farmers.

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General Discussion

The global agricultural landscape has experienced enormous transformations in the past century. In total, the agricultural area has risen by 40.6% since 1961 (Aizen et al., 2019), resulting in the conversion of natural habitats into crop fields. Land-use intensification in croplands is reducing species richness and abundance of pollinators (Millard et al., 2021) and insufficient diversification of crops is threatening the supply of the ecosystem service of pollination (Aizen et al., 2019), as monocultures can be associated with reduced pollination (Eeraerts et al., 2017; Aguilera et al., 2020). Also, crops are more frequently grown under permanent cover (Cuesta Roble, 2020), limiting the pollination services provided by wild bee communities and altering the environmental conditions for managed pollinators (Kendall et al., 2021). An increasingly pollinator-dependent agriculture (Aizen et al., 2019), which experiences these transformations, needs adaptive and innovative pollination management to ensure stable yields for a growing human population; this is a call for the concept of Integrated Crop Pollination (ICP; Isaacs et al., 2017) and might need political measures to promote sustainable farming as well as farmer commitments to implement biodiversity-friendly measures (Mupepele et al., 2021).

In this thesis, I investigated local and landscape-scale effects on pollinators and the ecosystem service of pollination that they provide in agricultural areas. I reviewed the trends and the diversity of managed pollinators to gain inside into management practices as well as opportunities for ICP. To better understand drivers of farmer decision-making, I analysed a global dataset of farmer perceptions in regards to pollinators and their on-farm practices, linking it to pollinator composition, external incentives, and the cultivated crop.

The effect of mass-co-flowering crops on pollinators and pollination

The rapid expansion of pollinator-dependent oilseed crops has been one of the major transformations of European agriculture in the past 60 years (Aizen et al., 2019). In Europe, oilseed crops including oilseed rape (OSR) were grown on 0.3 million ha in 2019, an increase of 470% compared to their cover in 1961 (FAOSTAT, 2021). Mass-flowering crops, like OSR, can to some degree attract pollinators and provide additional resources for pollinators so that the abundance of pollinators within the agricultural landscape increases (Westphal et al., 2003; Holzschuh et al., 2013). However, profuse large fields may over-ride the attraction effect and can instead cause a decrease in pollinator density in those fields (Holzschuh et al., 2011, 2016). To which extent OSR affects other co-flowering crops through either facilitation or competition for pollinators has rarely been investigated (Bänsch et al., 2020).

In this thesis (**Chapter I**), I demonstrated that OSR can change the pollinator community composition in co-flowering apple orchards. Honey bees are drawn away from apple orchards by OSR, probably as a consequence of its higher nectar content per flower (Quinet et al., 2016; Carruthers et al., 2017), in combination with higher flower density in OSR. This result is similar to another study on co-flowering strawberry and OSR, in which honey bee abundance decreased in strawberry fields with increasing OSR flower availability (Bänsch et al., 2020). On the contrary, I found that solitary bees (here: non-*Bombus* wild bees) were facilitated by OSR in the landscape. This contradicts our expectation since Non-*Bombus* wild bees have a shorter foraging range (often below 150 m) compared to bumble bees and honey bees (Greenleaf et al., 2007; Redhead et al., 2016; Hofmann et al., 2020), which would suggest a stable abundance of non-*Bombu*s wild bees with increasing OSR in the landscape.

One reason for this might be a consequence of reduced competition with honey bees for resources in apple orchards as the latter are drawn away by OSR (Hudewenz and Klein, 2015; Lindström et al., 2016; Angelella et al., 2021). Another explanation might be the spillover of non-*Bombus* wild bees from OSR to apple orchards. While being visually attracted to the area by OSR, they might choose to forage in apple orchards as, for instance, mason bees have a strong preference for fruit trees (**Chapter II**). Also, non-*Bombus* wild bees might benefit from the nutritional value of having a diverse set of foraging possibilities. *Osmia bicornis*, for instance, has been found to have a reduced number of offspring in OSR monocultures compared to OSR in connection to diverse flower plantings or grasslands (Holzschuh et al., 2013; Klaus et al., 2021). The implications of co-flowering crops on foraging distribution patterns of flower visitors are taxa dependent and might change with the mix of co-flowering crops. Bänsch *et al*. (2020) showed that bumble bees are attracted from strawberry fields to OSR fields, while here (**Chapter I**), bumble bee abundance remained stable. More studies are needed to shed light on pollinator preferences in different co-flowering crop combinations.

Fruit set and seed set in the study apple orchards remained stable, even with increasing OSR coverage in the landscape and decreasing number of flower-visiting honey bees. I suggest that the increasing number of wild pollinators might have compensated for the loss of honey bees. Indeed, the importance of wild bees in apple orchards has been demonstrated in other studies (Mallinger and Gratton, 2015; Pérez-Méndez et al., 2020). Therefore, the promotion of pollinator-friendly landscapes and on-farm management practices can safeguard the ecosystem service of pollination in an increasingly pollinator-dependent agriculture, in which pollination by honey bees might not be reliable. Even though wild bees might have compensated for the loss of flower-visiting honey bees, these might not be possible when experiencing a parallel loss of pollinator diversity and abundance. As I found that sweet cherry fruit set (Chapter II) enhanced only through interactive effects, landscapes with co-flowering crops are likely to require a higher diversity of pollinator species for efficient pollination services to buffer spatial and temporal changes in pollinator foraging distribution. Future studies investigating the extent to which crops co-flower, compare their attractiveness, and pollinator community composition could help us to further understand how co-flowering crops impact yield and further inform on the importance of diverse pollinator communities and pollinator management in this context. Furthermore, disentangling the causes of the facilitation of wild bees could give a better understanding of landscape-scale drivers on pollinator abundance to enhance crop pollination.

Effect of managing pollinators on crop yield

Farmers can manage pollinators and enhance pollinator habitats in order to improve pollination services in agricultural landscapes (Garibaldi et al., 2017). Here, I demonstrated that (**Chapter II**), by providing nesting material, farmers can enhance mason bee populations foraging in sweet cherry orchards. Furthermore, I investigated the relationship between pollination services in the orchards and two managed bee taxa, *A. mellifera* and *Osmia spp*. I showed that fruit set of sweet cherry did not increase when only the abundance of one managed pollinator species was enhanced. However, on the contrary, increasing the abundance of honey bees and mason bees simultaneously increased the seed set through an interaction effect.

One explanation reason for this result could be that the two pollinator taxa alter the foraging behavior of the other and therefore interactively enhance pollination services. In previous studies on crop pollination, honey bees were shown to have an increased visitation rate, a higher probability of row changes, and a higher single visit efficiency when wild bees were present versus when they were absent (Greenleaf and Kremen, 2006; Brittain et al., 2013; Eeraerts et al., 2020a). Another possible reason could be the difference in functional niche coverage between the two pollinator taxa, such as the difference in temperature dependency (Fründ et al., 2013). This could explain the synergistic effects of species diversity on fruit set I found here (**Chapter II**) and which has been found previously (Brittain et al., 2013; Pérez-Méndez et al., 2020). Therefore, these findings support that bee species diversity is important to maximize fruit and seed set (Klein et al., 2003; Fründ et al., 2013).

Fründ *et al*. (2013) showed that the strongest positive effect on seed set was seen when increasing from one pollinator species to two pollinator species and in apple farms, it was demonstrated that by having two managed pollinator species, yield increased 2.4-fold compared to only having honey bees (Pérez-Méndez et al., 2020). Therefore, even promoting two pollinator species might positively affect fruit set, especially when these two differ in their functional traits (Fründ et al., 2013; Woodcock et al., 2019; Pérez-Méndez et al., 2020), particularly for crops that require cross-pollination. Even though pollinator communities in crops might be dominated by a small subset of dominant species (Kleijn et al., 2015), their contribution to crop pollination might be context-dependent and limited when other species are rare. The translation from species abundance to their importance in crop pollination without measuring fruit and seed set should be done with caution. In future studies, more focus should be on the inter-species interplay and the resulting effects on crop pollination.

In highly intensified agricultural landscapes (such as my study area), in enclosures, or when crops are grown outside of their native range, active pollinator management might be needed as wild pollinators might be rare and consequently, crops could be pollination-limited. I can recommend farmers to not only rely on one single managed species but to promote several pollinator species, also as diverse pollinator communities might buffer spatial and temporal fluctuation better (Senapathi et al., 2021).

Integrated crop pollination by managing pollinator species

Apart from honey bees and mason bees, many other insect species can be managed for the pollination of crops. I found that, to date, 66 species are mentioned in the literature as manageable pollinator species (**Chapter III**), of which 22 are currently in use. A diversification of managed pollinators has been argued as important for food security, since honey bees, the most commonly managed pollinator, has experienced high overwinter mortalities since 2008 (**Chapter III**). However, I found that around half of the species have been recognized as manageable before 2008. Instead, the rapidly changing agricultural landscape, including the increase in the cultivation of crops under permanent cover (Cuesta Roble, 2020), the negative effects of land-use intensification on pollinators (Millard et al., 2021), crops grown outside of their natural range (Khoury et al., 2016), an increase in the pollination-dependency of agriculture (Aizen et al., 2019), and the awareness of risks associated with non-native pollinators (Russo et al., 2021) could have driven the observed increase in the number of manageable pollinator species. For instance, *Bombus terrestris* rearing methods were established in the 1980s as a source of pollinators for the pollination of tomatoes in greenhouses (Velthuis and Van Doorn, 2006), and many other species have been tested and established (**Chapter III**) to replace *B. terrestis* where it is not native. Also, stingless bees are considered as manageable pollinators in the Neotropics and Oceania as they can fly in enclosures and have been managed previously for honey production (**Chapter III**). Establishing new species as managed pollinators requires an understanding of their effectiveness and their ecology, as well as management recommendations. The fact that farmers seem to mainly rely on honey bees as managed pollinators, while alternative species are rarely used (**Chapter IV**), indicates that there might be a gap between science and practice as described in other studies (Kleijn et al., 2019; Maas et al., 2021). This gap hinders the integration of alternative managed pollinators. Since the benefits of pollinators are context-dependent and management can be complex (**Chapter II**) it is important to transfer knowledge between science and practice to ensure stable crop pollination.

Farmer perceptions and their decision-making

In addition to actively managing pollinators, integrating crop pollination into farm management includes the adoption of practices protecting local, wild pollinator communities by reducing the risks of pesticide exposure, enhancing habitat for food and nesting resources as well as improving horticultural practices (Garibaldi et al., 2017; Isaacs et al., 2017). However, biodiversity-friendly measures are rarely implemented in practice, despite scientific evidence supporting their utility (Kleijn et al., 2019). Integrating pollination into farm management needs the willingness and knowledge of farmers, who cultivate and utilize 38% of the global terrestrial surface (FAO, 2021). By performing the first global-wide study on farmer knowledge of pollinators (**Chapter IV**), I demonstrated that farmers seem to become aware of the pollinator communities in their crop mainly through their own observations. Scientific records of relative pollinator abundance are aligned with farmer perceptions of pollinators and are reflected in their pollination management. For instance, farmers were more likely to manage bee species if they perceived them to be important. While observing pollinators on crops and recognizing their abundance might be viable, understanding the effects of biodiversity, crop (**Chapter I**), and species interactions (**Chapter II**), or how abundance relates to yield might be knowledge-intensive and require additional training (Garratt et al., 2019).

Almost half of the interviewed farmers had changed their pollination management in the last 10 years (**Chapter IV**). This illustrates the willingness and awareness of farmers to adapt their on-farm measures to increase pollination services or to promote biodiversity in a changing agricultural landscape. Farmers applied a wide range of measures, often adapted to a crop’s pollination ecology, and frequently going beyond scientific recommendations. For instance, non-bees were promoted by avocado farmers through the application of scent and the provision of dead meat upon which pollinator flies could lay eggs. Although flies are not important pollinators of many crops, this practice aligns well with the crops pollination ecology as blowflies are effective pollinators of avocado (Dymond et al., 2021). Local knowledge can be a powerful tool to conserve and enhance pollinator communities and should be considered in building effective policies that are adapted to the capacities of farmers and local conditions (Gemmill-Herren et al., 2021). Through co-designed experiments and pollination management strategies, locally adapted measures, as promoted by the ICP concept, can be implemented to mitigate the loss of pollinator diversity and abundance to maintain or enhance biodiversity and crop pollination.

Finally, the decision-making of farmers was also affected by agricultural policies. Governmental subsidies to implement biodiversity-friendly measures enhanced their uptake and can be seen as an important tool to stop the decline of biodiversity in the agricultural landscape (Mupepele et al., 2021). That farmers are both willing to change their pollination management and are more prone to use biodiversity-friendly measures as a consequence of subsidies could be of significant importance, since it highlights the responsibility governments and decision-makers have to implement sufficient policies (Garibaldi et al., 2019; Gemmill-Herren et al., 2021). Agricultural practices have indeed been the driver of biodiversity decline in pollinator taxa across the world (Millard et al., 2021). However, my study shows that a foundational pillar to break this trend is already there; the willingness of farmers to implement ecological intensification and biodiversity-friendly measures.

Conclusions

In this thesis, I demonstrated how utilising both wild and managed pollinators as part of ICP could buffer spatial and temporal fluctuations in pollinator abundances. To ensure a stable supply of flower visitors in a crop dependent on cross-pollination, wild, especially diverse pollinator communities might play an important role. Mason bees, can be promoted as alternative managed pollinators. Proving nesting material represents a relatively simple measure for farmers, which enhances wild bee populations. I showed, however, that only synergistically do honey bees and mason bees enhanced the fruit set of sweet cherry, which highlights the need to monitor crop yield as well as pollinator abundances, as the contribution to crop yield of a single species might be context-dependent. Priority should be given to promoting a diverse set of pollinators as part of the ICP. A rising number of insect species are tested as managed pollinators, increasing the options for farmers to enhance crop yields under conditions where pollination services by wild insects are limited. Despite the diversity of manageable pollinators, farmers rely predominantly on a single species, *Apis mellifera*. Further studies should investigate optimal management strategies and how different taxa complement each other in their pollination provision. As the Western honey bee experiences high overwinter mortalities, is not native to all parts of the world, and is not an effective pollinator for all crops and conditions, other measures to enhance pollination services should be supported and well communicated. Promoting a diverse set of pollinators to ensure stable crop yield is often knowledge-intensive, and the pollination management on farms might have to be adapted to changes in agricultural landscapes. Farmers are important knowledge holders, with their perceptions shaped by on-farm experiences. Co-designing measures together with scientists to improve on-farm biodiversity could be the key to resilient and adaptive pollination management. Policies can thereafter be directed and implemented as an important tool to enhance the uptake of biodiversity-friendly measures.

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Appendix

Supplementary Material Chapter I

Apple pollination is ensured by wild bees when honey bees are drawn away from orchards by a mass co-flowering crop, oilseed rape

Supplementary Methods

To determine how well genus-level taxonomic assessment of biodiversity in Sachsen-Anhalt apple orchards reflected species-level assessment, flying insects were collected in four independent apple orchards in Sachsen-Anhalt in 2019. Each orchard was sampled for 3 consecutive days in warm (>18^0C) and sunny (<70% cloud cover) weather using 9 pan traps (3 white, 3 yellow, 3 blue) installed at 9 am and emptied at 4 pm, as described in the main manuscript. In addition, apple flower visitors were collected with a hand net in two transect walks per day, each of 1.5 hours duration, for the same three days and within the same orchard rows used for pan trapping. All bees (total n=3379 individuals) were identified to species either morphologically or through DNA barcoding (see Radzevičiūtė *et al*. (2017) for methods) and then species-diversity plotted against genus-level diversity (Supplementary Information Fig. A.1).

Supplementary Results

Effects of apple orchards on bees in oilseed rape fields

The automated model selection approach to explore the effects of apple orchards and land use on the abundance of honey bees, bumble bees and other wild bees estimated by transect walks in OSR resulted in one best model for each bee group (ΔAICc < 2). The percentage of apple orchards at a 1 km radius and the presence of honey bee hives were both included in the best models for the abundance of honey bees, bumble bees and other wild bees in OSR (Supplementary Table A.5). We found that the number of recorded honey bees in OSR was higher in sites with honey bee hives in apple orchards (GLM; $Z_9 = 3.459$, $P < 0.001$, $R^2_{adj} = 0.26$). The abundance of honey bees in OSR was not affected by the proportion of apple orchard at 1 km radius (GLM; $Z_9 = -0.043$, $P = 0.966$, $R^2_{adj} = 0.26$). Neither the proportion of apple orchards at 1 km radius nor the presence of honey bee hives in apple orchards had a statistically significant effect on the number of OSR flower-visiting bumble bees (GLM; $Z_9 = -0.007$, $P = 0.944$; $Z_9 = -1.068$, $P = 0.286$, $R^2_{adj} = -0.15$). We detected a positive effect of the proportion of apple orchards on wild bee (excluding bumble bees) individuals during transect walks in OSR fields (GLM; $Z_9 = 3.376$, $P < 0.001$, $R^2_{adj} = 0.51$) and the presence of honey bee hives in apple orchards negatively affected the number of wild bees in OSR fields (GLM; $Z_9 = -3.159$, $P = 0.002$, $R^2_{adj} = 0.51$).

The automated model selection approach to explore the effects of land use on the Shannon diversity of bees and bee richness estimated using pan traps in OSR also resulted in one best model for each bee group ($\Delta AICc < 2$). The percentage of apple orchards at a 1 km radius and the presence of honey bee hives in apple orchards were both included in the best models for both Shannon bee diversity and observed bee richness (Supplementary Table A.5).

Supplementary Figures

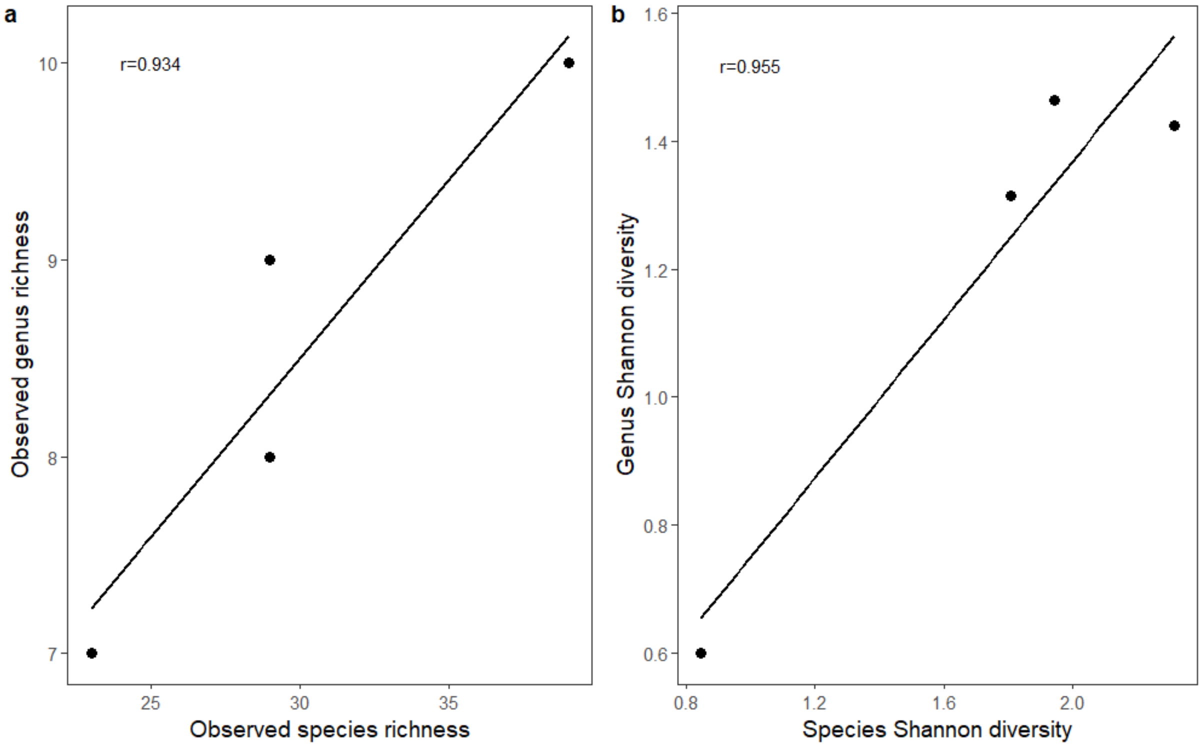


Figure A.1. Relationship between a) observed bee genus richness and observed bee species richness and b) between bee genus Shannon diversity and bee species Shannon diversity of apple flower visitors. Plotted lines show the least squares best fit line and the Pearson correlation coefficient is presented, demonstrating a very high correlation between genus-level and species-level metrics of bee biodiversity.

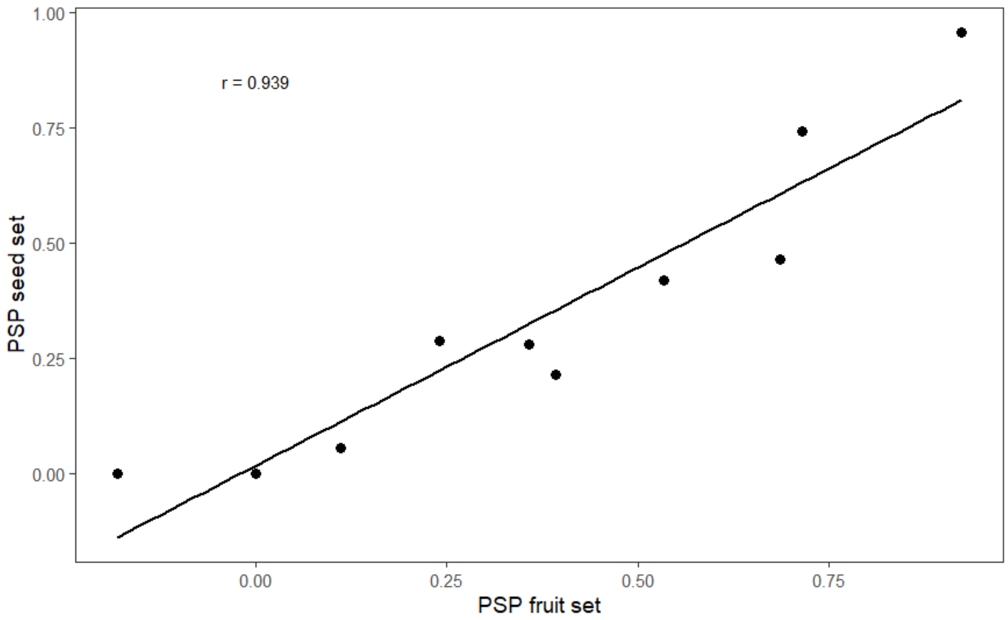


Figure A.2. Relationship between our index of pollination service provision (*PSP*) in apple, calculated as fruit set (x-axis) and seed set (y-axis). Plotted lines show the least squares best fit line and the Pearson correlation coefficient is presented (Pearson r = 0.939, $P < 0.001$).

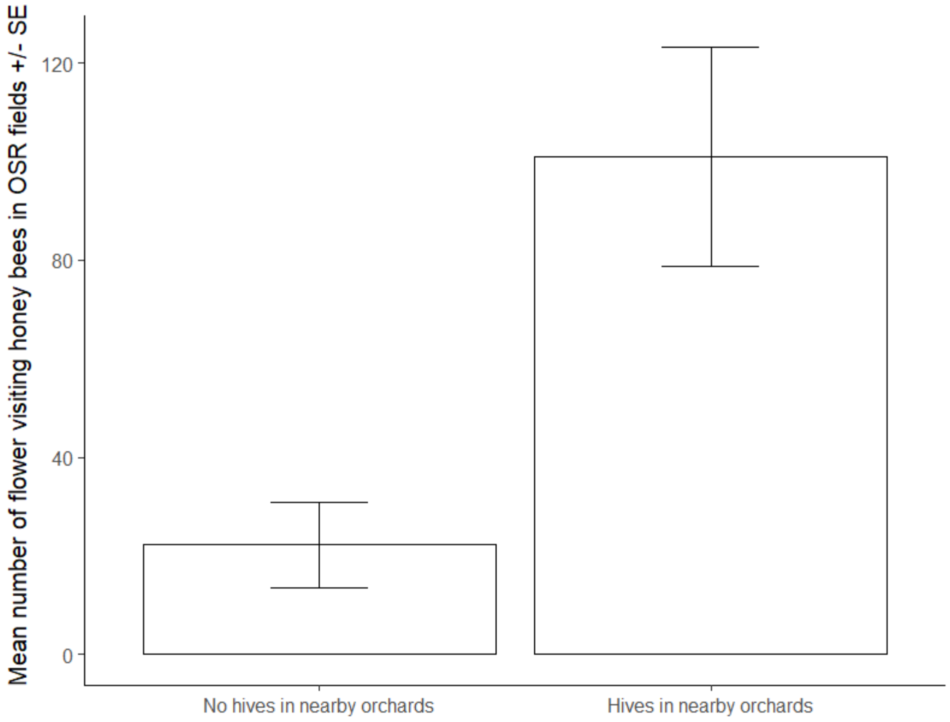


Figure A.3. Honey bee density in oilseed rape fields. Mean number of flower visiting honey bees in OSR fields in relation to presence/absence of honey bee hives in their paired apple orchards (GLM, $t_9 = 3.459$, $P < 0.001$).

Supplementary Tables

Table A.1. Coordinates of field sites used in our study and the proportion of oilseed rape withina 1 km radius around the 12 apple orchards.

Site	Coordinates				Percentage of oilseed rape (radius 1km) around apple orchards	Size of apple orchard (ha)	Percentage of apple orchard (radius 1km) around oilseed rape fields	Size of oilseed rape field (ha)	Date of sampling	Weather*	
	Apple orchards		Oilseed rape fields							Temperature (°C) during midday	Wind speed (m/s)
	Latitude	Longitude	Latitude	Longitude							
Aseleben	51°29'32.6"N	11°38'44.2"E	51°29'43.7"N	11°38'44.8"E	8.7	157.9	35.2	65.6	03.05.2017	13.8	6.7
Eisleben Aue	51°30'39.3"N	11°35'29.2"E	51°30'29.3"N	11°35'30.1"E	14	26.5	5.3	17.2	01.05.2017	15.4	6.8
Eisleben Windmühle	51°30‘09.4“N	11°33‘47.4“E	51°30‘33.4“N	11°32‘42.4“E	0	58	0	71.2	10.05.2017	9	3.5
Gatterstädt	51°24'03.6"N	11°31'19.2"E	51°24'04.9"N	11°30'21.6"E	0	53.2	0	125.9	07.05.2017	15.9	2.9
Goseck	51°11'47.4"N	11°52'30.2"E	51°11'39.1"N	11°52'46.3"E	32.2	50.3	5.8	166.8	30.04.2017	13.6	7.9
Helmsdorf	51°35'36.6"N	11°38'05.9"E	51°35'27.7"N	11°38'17.6"E	17.3	93.9	14.9	33.4	03.05.2017	13.8	6.7
Höhnstedt	51°30'08.9"N	11°45'08.9"E	51°29'42.9"N	11°45'41.4"E	31.2	132.9	18.3	346.5	01.05.2017	15.4	6.8
Naumburg	51°09'54.2"N	11°49'14.4"E	51°29'42.9"N	11°45'41.4"E	21.5	27.4	7.9	13.2	30.04.2017	13.6	7.9
Plößnitz	51°32'22.5"N	12°03'28.0"E	51°32'24.0"N	12°03'22.1"E	7.5	11.6	2.7	9.6	11.05.2017	15.9	3.6
Querfurt	51°22'20.2"N	11°35'13.7"E	51°09'48.8"N	11°49'24.7"E	4.3	28	1.2	257.8	07.05.2017	15.9	2.9
Spören	51°36'29.8"N	12°06'45.5"E	51°35'54.5"N	12°06'54.1"E	0	22.4	0	223.5	11.05.2017	15.9	3.6
Zeitz	51°03'22.9"N	12°09'24.1"E	51°03'11.1"N	12°09'28.8"E	18.6	79.2	13.9	30.4	10.05.2017	13.3	3.5

*Weather data were extracted from the closest Deutscher Wetterdienst station(DWD, 2018a, 2018b)

Table A.2. Total number of flying insects in apple orchards observed in transect walks and caught by pan traps.

	Apple orchards		**Oilseed rape fields**	
	Transect walk	**Pan trap**	**Transect walk**	**Pan trap**
Apis mellifera	1476	9	788	24
Bombus	133	0	77	1
Other wild bees	119	490	154	499
Other Hymenoptera	2	63	0	100
Diptera	84	10511	210	28244
Coleoptera	3	147	2	1348
Homoptera	0	3	0	1
Lepidoptera	1	0	6	0
Neuroptera	0	2	0	2
Thysanoptera	0	10	0	36
Total number	**1818**	**11235**	**1237**	**30255**

Table A.3. Spearman rank correlation coefficients (r_s) of the relationship between the area of oilseed rape in the landscape around 12 apple orchards at increasing area (given as radius in metres) from the orchard border and measures of bee abundance, bee diversity and pollination (PSP, measured as fruit set and as seed set) within the apple orchards; values in bold represent the highest absolute correlation within a row.

Radius	**250m**	**500m**	**750m**	**1000m**	**1500m**	**2000m**
Transect walks (flower visitors)						
Honey bee abundance	-0.553	-0.577	-0.546	**-0.580**	-0.348	-0.073
Bumble bee abundance	**0.322**	0.243	0.155	0.142	0.229	0.200
Other wild bee abundance	0.324	0.456	0.556	**0.570**	0.384	0.162
Pan traps (bee diversity)						
Shannon bee diversity	-0.124	0.022	0.085	**0.090**	0.080	0.025
Bee richness	-0.445	-0.514	-0.504	-0.541	**-0.573**	-0.428
Pollination service provision (*PSP*)						
Fruit set	0.053	-0.012	-0.141	-0.092	-0.092	**-0.154**
Seed set	0.082	0.015	0.016	**0.117**	-0.019	-0.091

Table A.4. Final LM and GLM results of the number and diversity of bees in apple orchards in relation to the area of oilseed rape in the surrounding 1 km radius buffer and the presence/absence of honey bees hives in the orchard. *P* values < 0.05 are highlighted in bold.

Model	**Explanatory variable**	**Estimate**	**Degrees of freedom**	**t/z**	***P***
Transect walk data in apple orchards					
Number of flower-visiting honey bees	Intercept	4.609			
	Percentage of oilseed rape in 1 km buffer	-0.033	9	-3.071	**0.002**
	Presence of honey bee hives in orchard	0.790	9	3.361	**< 0.001**
Number of flower-visiting bumble bees	Intercept	1.840			
	Percentage of oilseed rape in 1 km buffer	0.019	9	0.897	0.370
	Presence of honey bee hives in orchard	0.490	9	1.058	0.290
Number of flower-visiting other wild bees	Intercept	1.957			
	Percentage of oilseed rape in 1 km buffer	0.025	9	2.123	**0.034**
	Presence of honey bee hives in orchard	-0.043	9	-0.165	0.870
Pan trap material collected in apple orchards					
Bee diversity (Shannon)	Intercept	0.565			
	Percentage of oilseed rape in 1 km buffer	0.002	9	0.423	0.682
	Presence of honey bee hives in orchard	0.097	9	0.933	0.375
Observed bee richness	Intercept	4.078			
	Percentage of oilseed rape in 1 km buffer	-0.044	9	-1.968	0.081
	Presence of honey bee hives in orchard	-0.162	9	-0.326	0.752

Table A.5. Final LM and GLM results of the number and diversity of bees in oilseed rape fields in relation to area of apple orchards in the surrounding 1 km radius buffer and the size of the focal oilseed rape field.

Model	**Explanatory variable**	**Estimate**	**Degrees of freedom**	**t/z**	**P**
Transect walk data in oilseed rape fields					
Number of flower visiting honey bees	Intercept	3.109			
	Percentage of orchard in 1 km buffer	-0.001	9	-0.043	0.966
	Presence of honey bee hives in orchard	1.514	9	3.459	**< 0.001**
Number of flower visiting bumble bees	Intercept	2.139			
	Percentage of orchard in 1 km buffer	-0.002	9	-0.071	0.944
	Presence of honey bee hives in orchard	-0.511	9	-1.068	0.286
Number of flower visiting other wild bees	Intercept	2.547			
	Percentage of orchard in 1 km buffer	0.046	9	3.376	**< 0.001**
	Presence of honey bee hives in orchard	-0.929	9	-3.159	**0.002**
Pan trap material collected in oilseed rape fields					
Bee diversity (Shannon)	Intercept	0.689			
	Percentage of orchard in 1 km buffer	0.006	9	1.718	0.120
	Presence of honey bee hives in orchard	0.032	9	0.457	0.659
Observed bee richness	Intercept	2.934			
	Percentage of orchard in 1 km buffer	0.011	9	0.995	0.346
	Presence of honey bee hives in orchard	0.459	9	1.887	0.178

Table A.6. Fruit set; estimates and test statistics of the post hoc comparisons from the LM testing fruit set in relation to experimental manipulation of flowers

Comparison	**Estimate**	**DF**	**Z**	***P***
Bagged vs supplementary	-3.9448	1	-7.551	< 0.001
Open vs supplementary	-1.5932	1	-5.525	< 0.001
Open vs bagged	2.3516	1	4.510	< 0.001

Reference to Supplementary Information:

DWD, 2018a. recent air temperature [WWW Document].

DWD, 2018b. recent wind [WWW Document].

Radzevičiūtė, R., Theodorou, P., Husemann, M., Japoshvili, G., Kirkitadze, G., Zhusupbaeva, A., Paxton, R.J., 2017. Replication of honey bee-associated RNA viruses across multiple bee species in apple orchards of Georgia, Germany and Kyrgyzstan. Journal of Invertebrate Pathology 146, 14-23

Supplementary Material Chapter II

Managed mason bees enhance pollination services in sweet cherry orchards

Supplementary Tables

Table A.1. Description of the study sites

Number	Orchard	Orchard management	Bee management		Latitude	Longitude	Pollinizer variety	Orchard size in ha	Area of cherry cultivation in ha
			Mason bee nesting material/ha	Honey bee hives/ha					
1	Aseleben	Commercial, IPM	0.65	1.61	51.572.140	11.767.439	Rubin	6.22	6.22
2	Beesenstedt	Commercial, IPM	0.06	1.65	51.572.503	11.732.081	Sylvia	18.00	8.50
3	Beyernaumburg	Commercial, IPM	0	0	51.470.662	11.414.594	Henriette	6.00	6.00
4	Döllstädt	Commercial, IPM	0.88	1.48	51.064.875	10.782.511	Rubin	6.75	6.75
5	Eisleben	Commercial, IPM	1.00	5.20	51.507.664	11.565.084	Henriette	3.00	2.50
6	Erfurt	Experimental, IPM	8.57	0	50.992.652	11.052.581	Rubin	1.40	0.84
7	Gatterstädt	Commercial, IPM	0	8.00	51.399.474	11.523.638	Rubin	12.00	2.00
8	Großfahner	Commercial, IPM	1.10	7.38	51.053.088	10.815.892	Rubin	2.71	2.71
9	Höhnstedt	Commercial, IPM	1.00	5.70	51.499.598	11.757.832	Sam	130.00	7.00
10	Johannashall	Commercial, IPM	0.75	3.00	51.572.140	11.767.439	Skeena	4.00	4.00
11	Kleinfahner	Commercial, IPM	0.20	16.95	51.036.593	10.854.890	Rubin	5.12	5.12
12	Kindelbrück 1	Commercial, IPM	0.75	1.40	51.254.971	11.100.536	Sam	20.00	20.00
13	Kindelbrück 2	Commercial, IPM	0.50	4.60	51.248.409	11.057.025	Sam	36.00	36.00
14	Plößnitz	Commercial, Organic	0	20.00	51.539.550	12.060.131	Kordia	15.00	2.00
15	Quedingburg	Experimental, IPM	3.20	1.33	51.813.164	11.199.462	Fertar	7.50	0.16
16	Querfurt	Commercial, IPM	5.00	5.00	51.370.171	11.588.193	Rubin	11.00	2.00
17	Spören	Commercial, IPM	0	0	51.606.711	12.113.216	Canada Giant	7.50	0.50

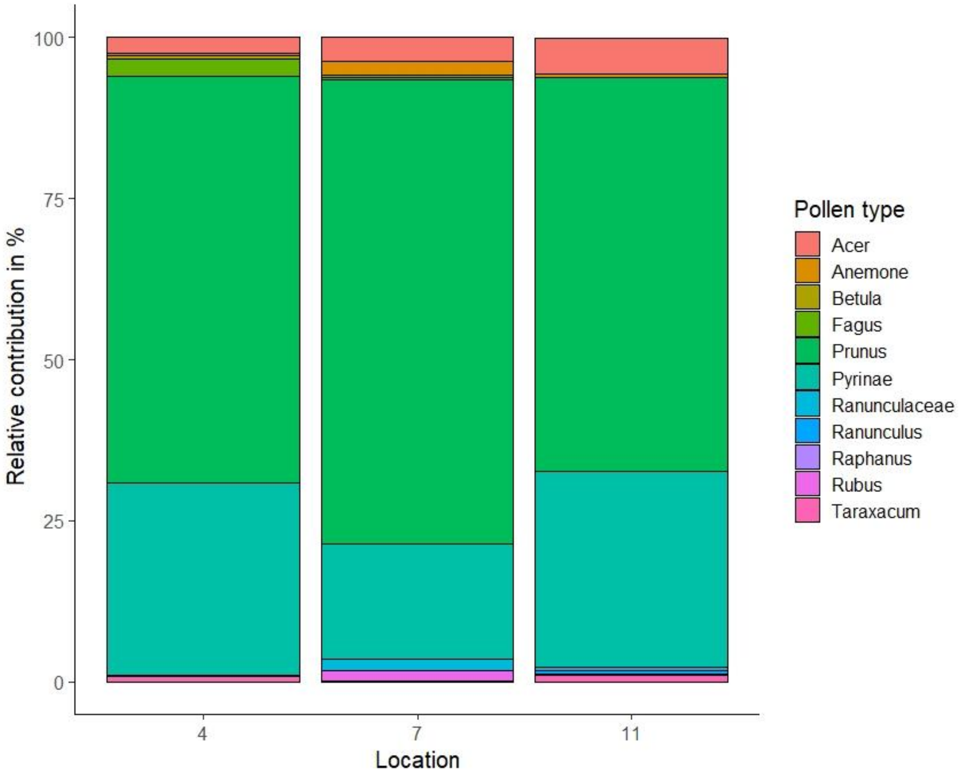
Table A.2. Results of the bee abundance model selection based on AIC criterion

Model		Intercept	Effect measure	Estimate	Z	P*	AIC**
Osmia abundance	Linear model	2.542	Wild bee nesting/ha	0.587	2.478	0.013	333.83
			Temperature	-0.012	-0.723	0.470	
	Log (x+1) model	2.182	Log(wild bee nesting/ha +1)	1.775	3.079	0.002	331.44
			Temperature	-0.012	-0.732	0.464	
Honey bee abundance	Linear model	2.102	Honey bee hives/ha	0.141	3.275	0.001	778.67
			Temperature	0.121	20.016	<0.001	
	Log (x+1) model	1.675	Log(hives/ha +1)	0.790	2.602	0.009	781.21
			Temperature	0.121	20.024	<0.001	

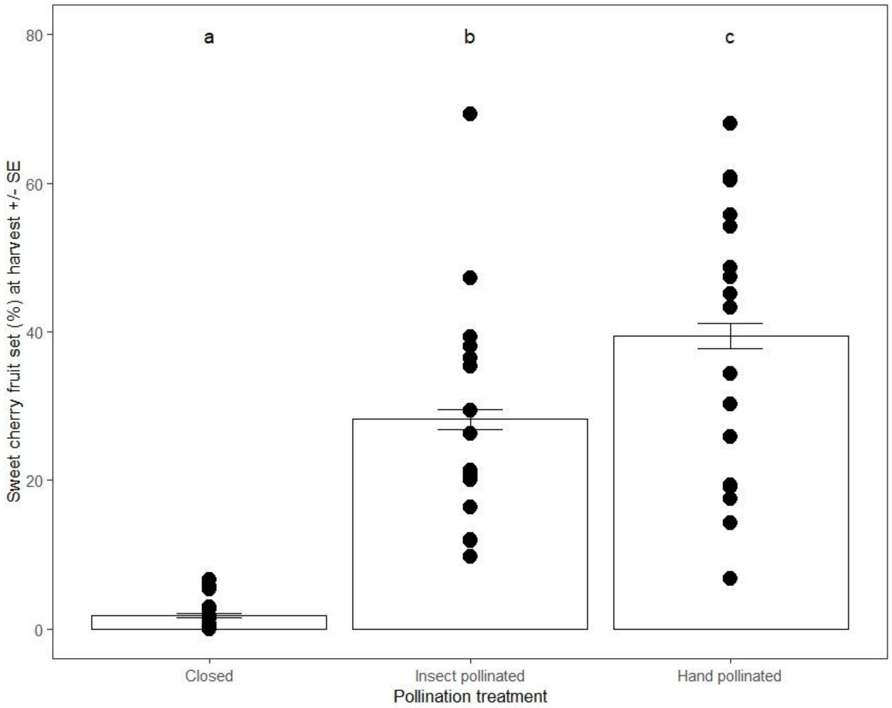
* P values < 0.05 are highlighted in bold.

** Lowest AIC values are highlighted in bold

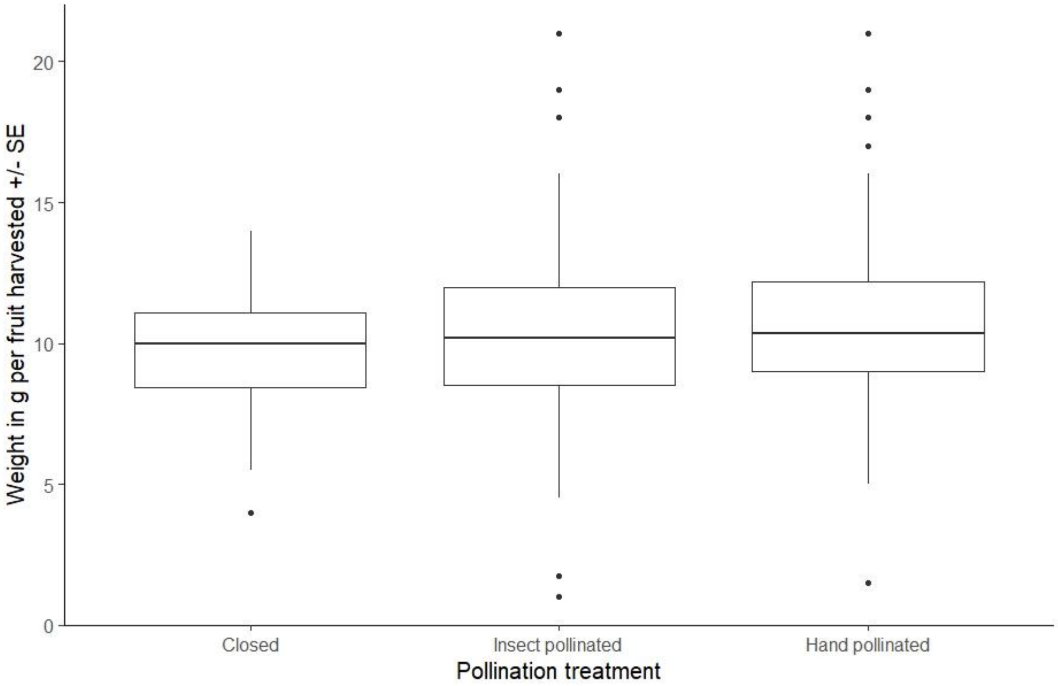
Supplementary Figure A.1: Example of a nesting material used in sweet cherry orchards.



Supplementary Figure A.2: Pollen types identified in trap nests at three locations.



Supplementary Figure A.3: Mean sweet cherry fruit set (%) for experimental pollination treatments ± S.E. Different letters indicate significant differences (P < 0.05). Dots represent fruit set per orchard.

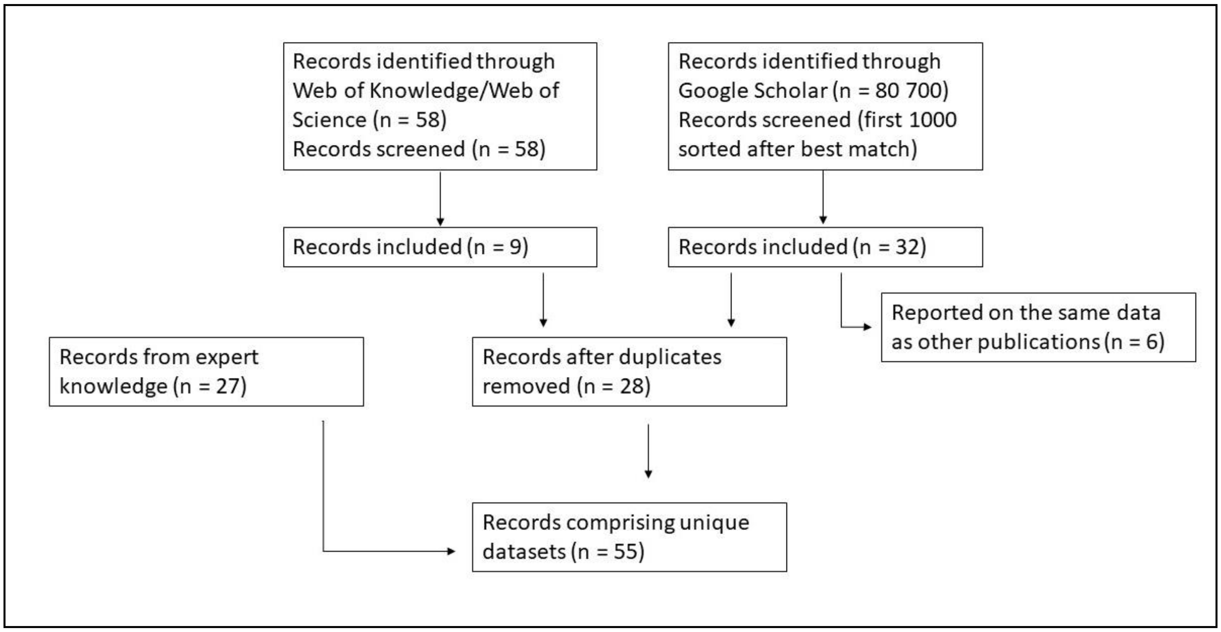


Supplementary Figure A.4: Weight in g per fruit for the pollination treatments. Horizontal line in the box, boxes and whiskers indicate median, 25th–75th percentiles and minimum–maximum, respectively.

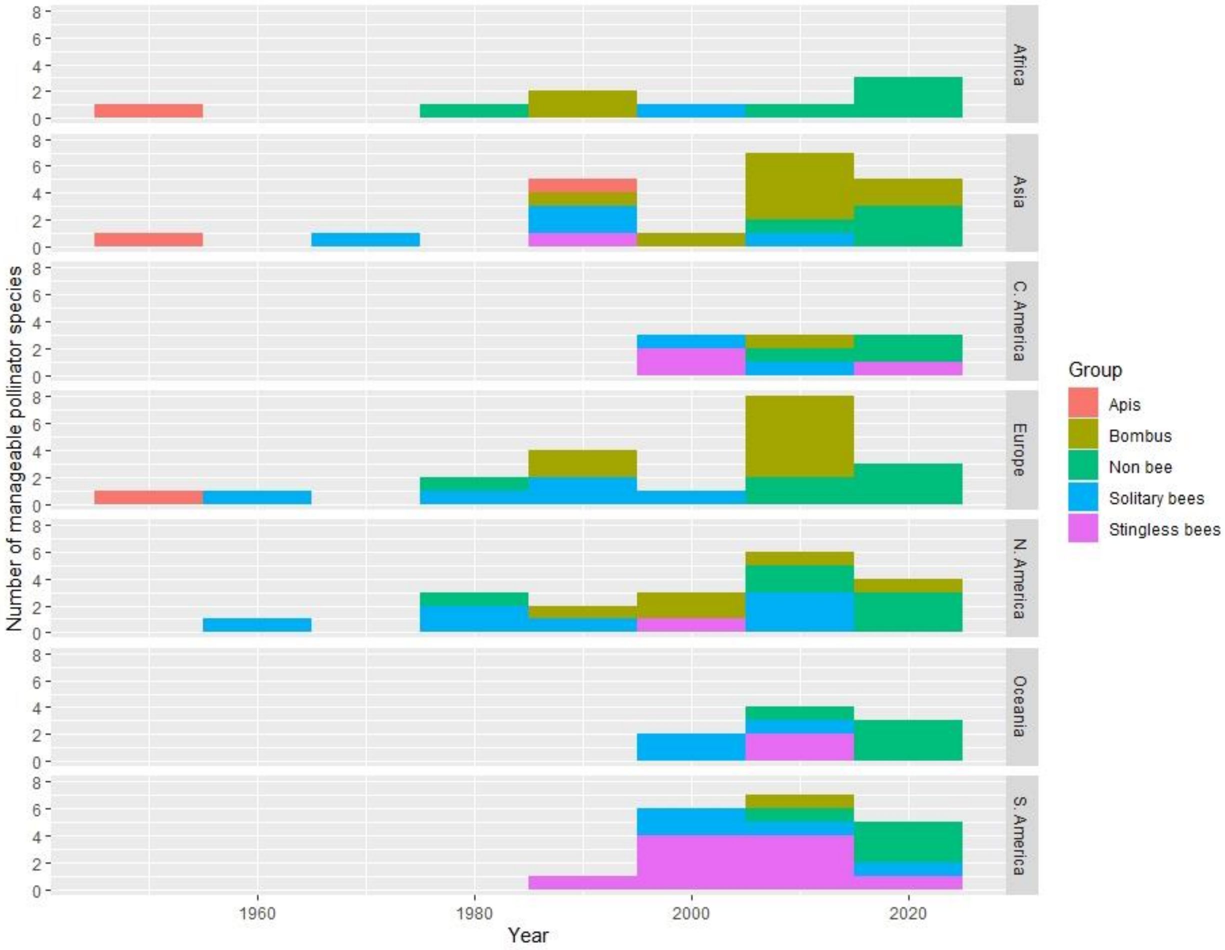
Supplementary Material Chapter III

Global trends in the number and diversity of managed pollinator species

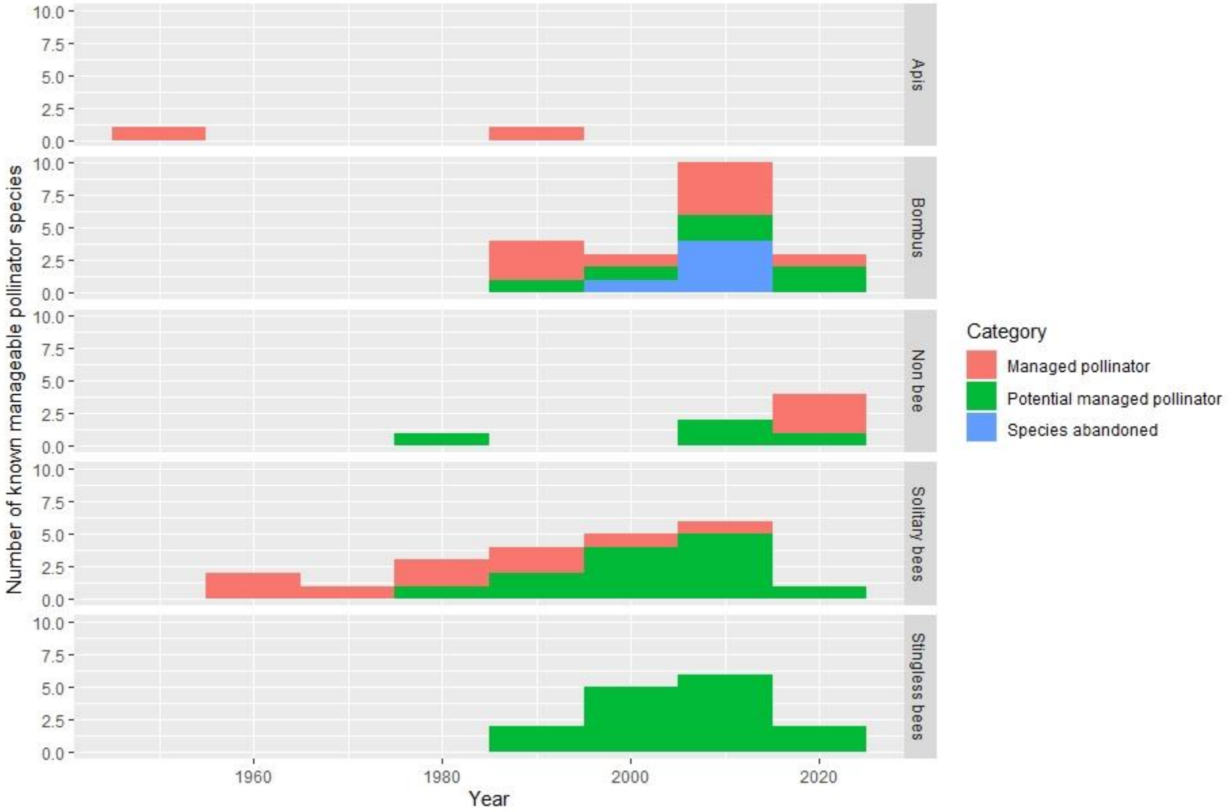
Supplementary Figures



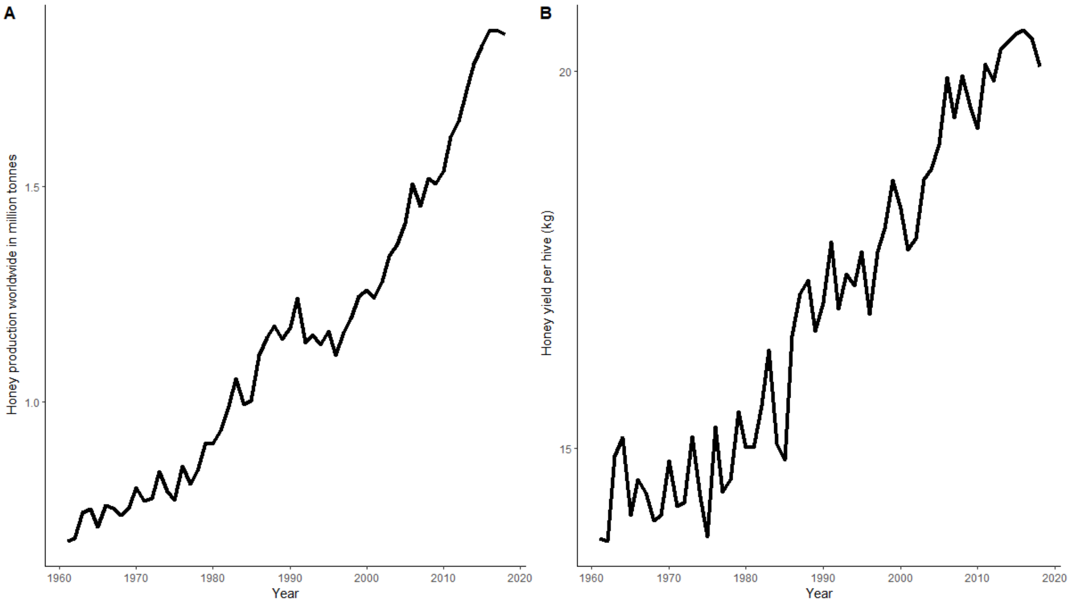
Supplementary Figure 01 | PRISMA flow chart diagram describing the protocol used in the literature search and the number of papers identified by each method as n (in parentheses).



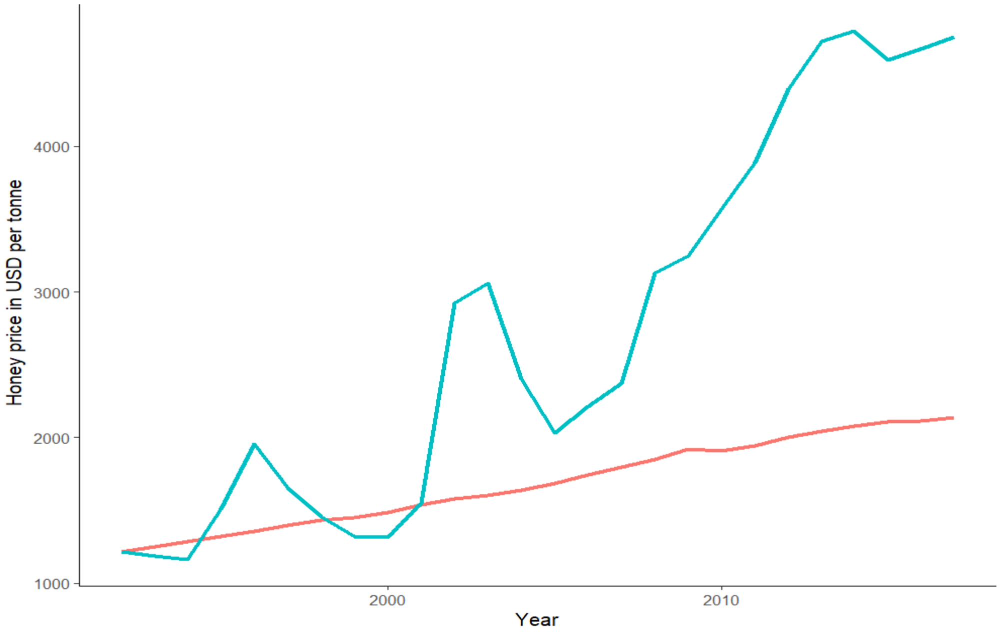
Supplementary Figure 02 | The number of known managed pollinator species as the sum of species per decade in which they were first mentioned, split by their geographical region of origin and by taxonomic group. Species native to more than one region are shown multiple times (e.g. *Apis mellifera*, which is native to Africa, Asia and Europe).



Supplementary Figure 03 | The number of known managed pollinator species as the sum of species per decade in which they were first mentioned, split by taxonomic group and current management category.



Supplementary Figure 04 | Worldwide honey production in millions of tonnes (A) and the average honey yield per hive in kg (B) from 1961 to 2018 (FAO, 2020)**.**



Supplementary Figure 05 | Producer price for natural honey in the United States from 1992 to 2017 in US$ per tonne (blue) and price corrected for the inflation rate (red), with a starting price of 1992.

Supplementary Tables

Supplementary Table 01 | Managed or potentially manageable pollinators, their effect on crop pollination, earliest reference and management practice. Search terms for the earliest references are listed under species and common name/synonym.

Species	Common name/ synonym	Country/ Region	Crops pollinated	Condition tested	Effects on crop pollination	Management	Status	Managed/ considered since	References
Honey bees									
Apis cerana	Eastern honey bee/honeybee, Asiatic honey bee/honeybee	South and East Asia	Cotton (*Gossypium hirsutum*), cucumber (*Cucumis sativus)* For a list of crops visited by *Apis cerana* see Klein et al. (2007).	Greenhouse, Open fields, vinyl house	*Apis cerana* has been shown to outperform *A. mellifera* in pollination of e.g. pears. Quality of cucumbers improved compared to no bees.	Long history of beekeeping for honey extraction.	Managed pollinator	1989	(Bhale and Bhat, 1989; Klein et al., 2007; Bui et al., 2017; Gemeda et al., 2017)
Apis mellifera	Western honey bee/honeybee, European honey bee/honeybee	Origin: Europe, Africa, West Asia, introduced worldwide except Antarctica	Farmers stated to use honey bees for: acacia, almond, apple, apricot, berries, bilberry, blueberry, cannabis, cereals, cherry, chestnut, Chinese wolfberry, citrus, cranberry, cucumber, cucurbita, eucalyptus, field	Greenhouse, Open fields	*Apis mellifera* is less effective for many crops than other flower visitors and slightly less effective than the mean of the community. Its long history of management and the visitation frequency might explain the reason for why *A. mellifera* is the most	Long history of beekeeping mainly for honey extraction, with the earliest evidence of management dating back to 2450 BCE in Egypt.	Managed pollinator	1952	(Woodrow et al., 1952; Crane, 1999; Klein et al., 2007; Breeze et al., 2019, Page et al., 2021)

		bean, fruits, grape, hazelnut, horticultural crops, kiwifruit, lemon, Lucerne, oilseed rape, orange, orchards, paprika, pea, peach, pear, plum, pumpkin, raspberry, red clover, seed plants, strawberry, sunflower, tomato, vegetables, watermelon, wheat, white clover; for more crops visited by *A, mellifera* see Klein et al. (2007)		commonly used pollinator worldwide.				
Bumble bees								
Bombus spp.	Europe	Farmers stated to use bumble bees for: apricot, aubergine, berries, bilberry, blueberry, brassica, cherry, cucumber, kiwifruit, loquat, lucerne, melon, orchards, peach, pear, raspberry, red clover, runner bean, strawberry tomato, vegetables, white clover						(Breeze et al., 2019)
Bombus ardens Smith	Japan	*Corydalis ambigua* (source for the drug tetrahydropalmatine), potentially tomato	Open field	More fruits and seeds than when visited by nectar robbing bumble bees	Rearing attempts but not chosen in the end for commercialization	Species abandoned	2006	(Velthuis and Van Doorn, 2006; Dohzone et al., 2008)

Bombus atratus Franklin	*Bombus pauloensis*	Colombia	Lulo/ Naranjilla *(Solanum quitoense* L.)	Open field	Visits reproductive parts of the flower. Fruit or seed set not assessed.	Commercially available from e.g. Biobest	Managed pollinator	2007	(Almanza, 2007)
Bombus breviceps Smith		China	Black cardamom (*Amomum subulatum*)	Open field	Effective pollinator of black cardamom	High colon foundation rate of field-collected queens (86.5%)	Potential managed pollinator	2020	(Deka et al., 2011; Liang et al., 2020)
Bombus canariensis Smith	*Bombus terrestris canariensis*	Europe	See *B. terrestris*				Managed pollinator	2006	(Velthuis and Van Doorn, 2006)
Bombus diversus Smith		Japan			Assessed for pollination of tomato. A long tongued species that could be suitable for flowers with long corollas, such as red clover	Rearing attempts but not chosen in the end for commercialization	Species abandoned	2006	(Velthuis and Van Doorn, 2006)
Bombus ephippiatus Say		Mexico	Tomato (*Solanum lycopersicum*)	Greenhouse	Seed set and fruit quality were similar to hand pollination and higher than mechanically or not-pollinated flowers	Can be reared in the laboratory	Potential managed pollinator	2012	(Vergara and Fonseca-Buendia, 2012)
Bombus friseanus Skorikov		China			Important pollinator of alpine plants.	High colony foundation rate of field-collected queens (95.5%)	Potential managed pollinator	2020	(Liang et al., 2020)
Bombus hortorum Linnaeus		Europe (origin), New Zealand	Faba bean (*Vicia faba* L.), red clover (*Trifolium pretense*)	Open field	More efficient than *Apis mellifera* or *Bombus terrestris* in faba beans	Trap nested	Managed pollinator	2007	(Donovan, 2007; Marzinzig et al., 2018)

Bombus huntii Greene	Hunt‘s bumblebee/ bumbe bee	Western Canada	Highbush blueberry (*Vaccinium corymbosum*)	Open fields	*B. huntii* collected more blueberry pollen than *B. vosnesenskii* and *Apis mellifera*	Commercially available from Biobest	Managed pollinator	2017	(Bobiwash et al., 2018)
Bombus hypocrita Pérez		Japan	Tomato (*Solanum lycopersicum*)	Greenhouse	Fruit set similar to pollination by *B. ignitus* and *B. terrestris*	Can be reared in the laboratory	Potential managed pollinator	1994	(Ono et al., 1994; Asada and Ono, 1997)
Bombus ignitus Smith		Japan	Tomato (*Solanum lycopersicum*)	Greenhouse	Fruit set similar to pollination by *B. hypocrita* and *B. terrestris*	Commercially available from Biobest	Managed pollinator	1997	Asada and Ono, 1997; 2000)
Bombus impatiens Cresson	Common eastern bumblebee/ bumble bee	USA	Sweet pepper (*Capsicum annum*), habanero pepper (*Capsicum chinense*), Tomato (*Solanum lycopersicum*)	Greenhouse, cages	Sweet pepper fruit quality increased compared to no bees; performed better than mechanical vibration for fruit set and fruit quality in habanero pepper but as good as *Nannotrigona perilampoides*. Fruit set and fruit quality of tomatoes higher than when pollinated by *N. perilampoides* or mechanical vibration.	Commercially available from Biobest, Koppert	Managed pollinator	1994	(Shipp et al., 1994, Palma et al. 2008a, 2008b)
Bombus lucorum Linnaeus	White-tailed bumblebee/ bumble bee	China, Europe				Rearing attempts but not chosen in the end for commercialization	Species abandoned	2006	(Velthuis and Van Doorn, 2006)

Bombus occidentalis Greene	Western bumblebee/ bumble bee	Canada	Tomato (*Solanum lycopersicum*)	Greenhouse	Not assessed	Possible to rear in the laboratory but colony health diminished in greenhouses	Species abandoned	2003	(Whittington and Winston, 2003; 2004)
Bombus patagiatus Nylander		China	Tomato (*Solanum lycopersicum*), pimiento (*Capsicum annum*), Chinese watermelon (*Citrullus lanatus*)	Greenhouse	Not assessed	Possible to rear in the laboratory.	Potential managed pollinator	2010	(Wu et al., 2010)
Bombus ruderatus Fabricius	Ruderal bumblebee/ bumble bee, large garden bumblebee/ bumble bee	New Zealand, Chile (origin Europe and North Africa)	Red clover (*Trifolium pretense*)	Open fields	Higher seed set in red clover fields.	Trap-nested and introduced into Chile	Managed pollinator	1986	(Arretz and Macfarlane, 1986; Donovan 2007)
Bombus terrestris audax Harris	See below	UK	See below	See below	See below	Commercially available.	Managed pollinator	2006	(Velthuis and Van Doorn, 2006)
Bombus terrestris dalmatinus Dalle Torre	Buff-tailed bumblebee/bumble bee, large earth bumblebee/ bumble bee	Netherlands	Tomato (*Solanum lycopersicum*), several buzz-pollinated crops	Greenhouse, Open fields	Effective pollinator of tomatoes. Higher yields than when pollinated by *A. mellifera* or mechanically.	Commercially available. Most commonly used bumble bee with more than one million colonies sold per year in 2006.	Managed pollinator	1991	(Banda and Paxton, 1991; van den Eijnde et al., 1991; Velthuis and Van Doorn, 2006; Cooley and Vallejo-Marín, 2021)
Bombus terrestris sassaricus Tournier	See above	Italy, Sardinia	See above	See above	See above	Not produced any longer.	Species abandoned	2006	(Velthuis and Van Doorn, 2006)

Bombus vosnesenskii Radoszkowski	Yellow-faced bumblebee/ bumble bee, Vosnesensky bumblebee/ bumble bee	Canada, USA	Tomato (*Solanum lycopersicum*)	Greenhouse	Effective pollinator of tomatoes. Fruit size was positively affected by pollination by *B. vosnesenskii*		Potential managed pollinator	1998	(Dogterom et al., 1998)
Stingless bees									
Austroplebeia australis Friese	Bush bee, *Trigona australis*	Australia	Sweet pepper (*Capsicum annum*)	Greenhouse	Potential to increase fruit yield and quality. However, *A. australis* can cause damage to styles.	Used by stingless beekeepers.	Potential managed pollinator	2011	(Greco et al., 2011a)
Melipona beecheii Bennet		Mexico	Achiote (*Bixa orellana*)	Open field	Single visit efficiency higher than Africanized honey bees for fruit set, fruit weight, seed weight and seed number.	Long management practices since the time of the Maya, with the first evidence between 300 BCE and 250 CE.	Potential managed pollinator	2017	(Caro et al., 2017; Chase and Chase, 2005; Vit et al., 2013)
Melipona fasciculata Smith		Brazil	Eggplant (*Solanum melongena*)	Greenhouse	Increased fruit set. Alternative to bumble bees.	Easily maintained in artificial hives.	Potential managed pollinator	2013	(Nunes-Silva et al., 2013; Venturieri et al., 2017)
Melipona favosa Fabricius		Netherlands (origin: Venezuela)	Sweet pepper (*Capsicum annum*)	Greenhouse	Risk: Imported from Venezuela Increased number of fruits per plant compared to no bees.	Kept in traditional hives by stingless beekeepers in Latin America.	Potential managed pollinator	2000	(Meeuwsen, 2000; Vit et al., 2013)

Melipona quadrifasciata Lepeletier	Brazil	Tomato (*Solanum lycopersicum*)	Greenhouse Does not visit tomato flowers in open field conditions.	Similar fruit set to manual pollination and more efficient pollinator than honey bees.	Used for honey production in Brazil and Argentina.	Potential managed pollinator	2005	(Del Sarto et al., 2005; dos Santos et al., 2009; Vit et al., 2013)
	Brazil	Apple	Added colonies under field conditions.	Higher seed and fruit set, when combining stingless bees and honey bees as managed pollinators.	See above.			(Viana et al., 2014; Vit et al., 2013)
Melipona subnitida Ducke	Brazil	Sweet pepper *(Capsicum annuum* L.)	Greenhouse	No significant difference between restricted pollination and pollination by bees.	Used for honey production in Brazil.	Potential managed pollinator	2004	(Cruz et al., 2004; da Silva et al., 2005; Vit et al., 2013)
Nannotrigona perilampoides Cresson	Mexico	Tomatoes (*Solanum lycopersicum*)	Greenhouse	Similar fruit set to mechanical vibration but exotic *Bombus impatiens* was a more efficient pollinator.	Used for honey production in Costa Rica and Mexico.	Potential managed pollinator	2004	(Arce et al., 1994; Cauich et al., 2004; Palma et al., 2008b; Vit et al., 2013)
	Mexico	Habanero pepper (*Capsicum chinense*)	Greenhouse	Similar pollination efficiency to exotic *Bombus impatiens.* An alternative pollinator under tropical conditions.	See above.			(Cauich et al., 2006; Palma et al., 2008a; Vit et al., 2013)

Nannotrigona testaceicornis Lepeletier	Brazil	Cucumber (*Cucumis sativus*)	Greenhouse	Highest yield in greenhouses with stingless bees compared to no pollinators or open fields.	Used for honey production in Colombia and Argentina.	Potential managed pollinator	1992	(dos Santos et al., 2008; Vit et al., 2013)
	Costa Rica	Sage (*Salvia farinacea*)	Netted enclosure	Increased seed yield compared to no bees.	See above.			(Slaa et al., 2000; Vit et al., 2013)
	Japan (origin: Brazil)	Strawberry (*Fragaria* × *ananassa*)	Greenhouse		See above.			(Maeta et al., 1992; Vit et al., 2013)
Plebeia emerina Friese	Brazil	Canola/Oil seed rape (*Brassica napus*)	Open field condition. Added colonies.	Similar pollination efficiency to *A. mellifera*	Easy to manage.	Potential managed pollinator	2015	(Witter et al., 2015)
Plebeia nigriceps Friese	Brazil	Strawberry (*Fragaria* × *ananassa*)	Protected environment	Reduction of misshapen fruit.	Used in Brazil in stingless beekeeping.	Potential managed pollinator	2012	(Witter et al., 2012, 2007)
Scaptotrigona depilis Moure	Brazil	Cucumber (*Cucumis sativus*)	Greenhouse	Highest yield in greenhouses with stingless bees compared to no pollinators or open fields.	Kept in artificial hives by stingless beekeepers, for example in Bolivia.	Potential managed pollinator	2008	(dos Santos et al., 2008; Vit et al., 2013)
Tetragonisca angustula Latreille	Brazil	Strawberry (*Fragaria* × *ananassa*)	Greenhouse	increase in weight and shape compared to self-pollination and open pollination in the field	Used in many countries for honey production.	Potential managed pollinator	2000	(Malagodi-Braga and Peixoto Kleinert, 2004; Vit et al., 2013)

		Costa Rica	Sage (*Salvia farinacea*)	Protected enclosures	Increased seed yield compared to no bees.	See above.			(Slaa et al., 2000; Vit et al., 2013)
Tetragonisca fiebrigi Schwarz		Brazil	Canola/Oil seed rape (*Brassica napus*)	Open field condition. Added colonies.	Effective pollinator but seed mass lower than when pollinated by honey bees	Easy to manage. Used in Argentina in man-made hives.	Potential managed pollinator	2015	(Vit et al., 2013; Witter et al., 2015)
Tetragonula carbonaria Smith	Sugarbag bee, bush bee	Australia	Macadamia (*Macadamia integrifolia*)	Open field condition.	Pollination by only stingless bees as efficient as open pollination.	Used for honey production in Australia.	Potential managed pollinator	2011	(Heard, 1994; Greco et al., 2011b; Vit et al., 2013)
Trigona minangkabau Sakagami and Inoue		Japan (origin: Indonesia)	Strawberry (*Fragaria × ananassa*)	Greenhouse	Risk: Imported from Indonesia Stingless bees could pollinate strawberries as well as honey bees if more bees are introduced.	No traditional use recorded. Kept in greenhouses in Japan.	Potential managed pollinator	1993	(Kakutani et al., 1993)
Solitary bees									
Solitary bees			Farmers have reported using solitary bees for: apple, blueberry, cherry, chokeberry, kiwifruit, Lucerne, oleaginous crops, plum, raspberry, red clover, strawberry, wheat, white clover						(Breeze et al., 2019)
Amegilla chlorocyanea Cockerell	Blue banded bee	Australia	Tomato (*Solanum lycopersicum*)	Greenhouse	Increase in fruit weight by 21% compared to hand pollination.	Breeding programs need to be implemented to use the bee in greenhouses.	Potential managed pollinator	2006	(Hogendoorn et al., 2006)

Anthophora abrupta Say		USA	Visits a broad variety of plants. Therefore, this species could be used for many crops.		Unknown	Provision of nesting material (clay).	Potential managed pollinator	2015	(Graham et al., 2015)
Anthophora plumipes Pallas	Hairy-footed flower bee, shaggy fuzzyfoot, *Anthophora acervorum*	Germany	Cabbage, orchards	Open fields	Good seed set of cabbage; visits apple flowers at lower ambient temperatures than honey bees (pers. obs.).	Provision of nesting material (clay).	Potential managed pollinator	1990	(Thalmann and Dorn, 1990)
Anthophora villosula Smith	former subspecies of *A. plumipes*	Japan (origin), USA	Blueberry, apple, strawberry	Open fields	Superior pollinator of blueberries in Japan. European subspecies of this bee have been managed to increase the pollination of fruit trees and orchards. Potential for strawberry pollination as fruit set and seed increased relative to no pollination.	Provision of nesting material (clay).	Potential managed pollinator	1994	(Adhikari and Miyanaga, 2016; Batra, 1994; Stubbs and Drummond, 1999)
Centris analis Fabricius		Brazil	Acerola (*Malpighia emarginata*)	Open fields	Increased yield in acerola	Sources of floral oil and availability of nesting sites	Potential managed pollinator	2009	(Lourenço et al., 2019; Magalhães and Freitas, 2013; Oliveira and Schlindwein, 2009)

C. tarsata Smith		Brazil	Cashew (*Anacardium occidentale*)	Open fields	More efficient pollinator than *A. mellifera*	Availability of nesting sites	Potential managed pollinator	2018	(Freitas and Paxton, 1998; Oliveira-Rebouças et al., 2018)
Megachile pugnata Say	Sunflower leafcutter bee, *Megachile scobiculata, Megachile bucephala, Megachile disparilis, Megachile lucrosa, Megachile temporalis*	North America	Sunflower	Open fields	Increased sunflower pollination. Active earlier during the day than honeybees or bumblebees.	Provision of nesting boxes	Potential managed pollinator	1985	(Parker and Frohlich, 1985)
M. rotundata Fabricius	Alfalfa leafcutter bee	Europe and Asia (origin) North America, New Zealand, Australia	Alfalfa, lowbush blueberry, carrots, vegetables, canola, melon, sweet clover, cranberry	Open fields	In the USA tripled alfalfa seed production. In New Zealand, bees have been observed foraging on 10 different introduced plant species of the families Asteraceae, Brassicaceae, Crassulaceae and Fabaceae. In Canada, Leafcutter bees saved the alfalfa industry.	Commercially available, provision of nesting material	Managed pollinator	1961	(Stephen, 1961; Pitts-Singer and Cane, 2011; Howlett and Donovan, 2010)
Nomia melanderi Cockerell	Alkali bee	New Zealand and North America (origin)	Red clover, alfalfa	Open fields	Greater seed production in lucerne. Both males and females are superior to	Creation of bee beds	Managed pollinator	1958	(Stephen, 1958; Johansen et al. 1982; Cane, 2008a)

					honeybees in pollinating alfalfa.				
Osmia aglaia Sandhouse	*Osmia laeta*	USA	Raspberry (*Rubus idaeus*), blackberry (*Rubus occidentalis*)	Open fields	Same efficacy as honey bees	Polystyrene foam substrate (with paper straw liners) for nesting	Potential managed pollinator	2008	(Andrikopoulos and Cane, 2018; Cane, 2008b)
O. bicornis Linnaeus	Red mason bee, *Osmia rufa*	Germany, Poland	Oilseed rape, blackcurrant, strawberries, orchards	Open fields, tunnels	They are efficient pollinators of blackcurrant and strawberries, even in tunnels.	Commercially available, provision of nesting material	Managed pollinator	1997	(Fliszkiewicz et al., 2011; Schindler and Peters, 2011; Wilkaniec and Radajewska, 1997)
O. bruneri Cockerell		USA	Raspberry (*Rubus idaeus*)	Open fields	Same efficacy as honey bees	Uses same nesting material as *O. aglaia*	Potential managed pollinator	2008	(Andrikopoulos and Cane, 2018; Cane, 2008b)
O. cornifrons Radoszkowski	Hornfaced bee	Japan (origin), USA, Korea, China	Orchards, especially apple, mustard, blueberries, strawberry, melon, watermelon	Open fields, greenhouses	The hornfaced bee is 80 times more effective than honey bees for pollinating apples. In Japan, hornfaced bees pollinate up to 70 percent of the country's apple crop.	Providing nesting material	Managed pollinator	1974	(Maeta and Kitamura, 1974; Maeta, 1990, Xu et al. 1995; Yoon and Park, 2009)
O. cornuta Latreille	Horned bee	Spain, France and Yugoslavia	Orchards, oilseed rape, blackberry, strawberry	Open fields	Generally increases pollination in apples, pears and almonds. *Osmia* pollinated orchards had enhanced yields	Commercially available, providing nesting material	Managed pollinator	1984	(Asensio, 1984; Bosch 1994; Herrmann et al., 2019; Krunić and

					in favourable years, also safeguards yield in years that would otherwise be devoid of any fruit.				Stanisavljevic, 2006)
O. lignaria Say	Blue orchard bee	North America	Orchards	Open fields	Orchard pollination. They are particularly efficient pollinators of fruit trees, promote cross-pollination and increase yield in cultivars of cherry that require cross-pollination.	Commercially available, providing nesting material	Managed pollinator	1976	(Bosch et al., 2006; Torchio, 1976; Torchio, 1985)
O. pedicornis Cockerell		Korea	Apple orchards	Open fields	Improvement of fruit quality and seed set.	Providing nesting material	Managed pollinator	2009	(Yoon and Park, 2009)
O. ribifloris Michener	Currant mason bee	USA	Highbush blueberry	Open fields	Observed pollen transfer.	Provision of nesting boxes	Potential managed pollinator	1990	(Torchio, 1990)
Rhophitoides canus Eversmann	Grey-haired alfalfa bee	Czech Republic	Alfalfa	Open fields	Stabilization of seed production.	Creation of bee beds	Managed pollinator	1989	(Ptacek, 1989)
Xylocopa aeratus Smith	Golden-green carpenter bee, *Letis aeratus*	Australia	Tomato (*Solanum lycopersicum*)	Greenhouses	Fruits are heavier and contain more seeds than fruits not pollinated by *Xylocopa*	No technique for rearing this species has been developed	Potential managed pollinator	2000	(Hogendoorn et al., 2000)

X. bombylans Fabricius	Peacock carpenter bee	Australia	Tomato (*Solanum lycopersicum*)	Greenhouses	Fruits are heavier and contain more seeds than fruits not pollinated by *Xylocopa*	No technique for rearing this species has been developed	Potential managed pollinator	2000	(Hogendoorn et al., 2000)
X. frontalis Olivier		Brazil	Passionfruit (*Passiflora edulis*)	Open fields	Increased fruit set	Provision of nesting boxes	Potential managed pollinator	2003	(Freitas and Filho, 2003)
X. grisescens Lepeletier		Brazil	Passionfruit (*Passiflora edulis*)	Open fields	Increased fruit set	Provision of nesting boxes	Potential managed pollinator	2003	(Freitas and Filho, 2003)
Flies									
Calliphora albifrontalis Malloch	Western golden-haired blowfly	Australia	Southern highbush blueberry (*Vaccinium corymbosum*)	Glasshouses	Fruit set and fruit quality of blueberries increased compared to no insect present	Adults can be collected using fly traps and then reared in the laboratory.	Potential managed pollinator	2020	(Cook et al., 2020)
C. vicina Robineau-Desvoidy	Blue bottle blowfly	USA	Leek (*Allium ampeloprasum*)	Cages	Seed set increased with fly density	Commercially available in the USA. Can be reared in the laboratory.	Potential managed pollinator	2007	(Clement et al., 2007)
C. vomitoria Linnaeus	Blue bottle fly, orange-bearded blue bottle, bottlebee	UK	Onion (*Allium cepa*)	Cages	Similar crossing and selfing movements to honey bees.	Can be reared from anglers` supplies	Potential managed pollinator	1984	(Currah and Ockendon, 1984)
Eristalinus aeneus Scopoli		Spain	**For seed production:** watermelon, melon, cucumber, onion, garlic, carrot, celery, fennel, broccoli,	Cabins, tunnels and greenhouses	Increase seed set and fruit set	Commerically available	Managed pollinator	2017	(Polyfly, 2017)

			cauliflower, rapeseed, sunflower, chrysanthemum **For greenhouse crops:** watermelon, melon, sweet pepper, eggplant, strawberry, raspberry, blackberry, mango, avocado						
Eristalis tenax Linnaeus	Common drone fly	Spain	See above for *Eristalinus aeneus*	Cabins, tunnels and greenhouses	Increase seed set and fruit set	Commercially available	Managed pollinator	2017	(Polyfly, 2017)
Lucilia sericata Meigen	Common green bottle fly, sheep blow fly, *Phaenicia sericata*	Germany	Strawberry (*Fragaria* x *ananassa*)	Cages	Fruit quality was higher than control treatment. Fruit set was not higher than control cages.	Commercially available from Koppert Biological Systems	Managed pollinator	2019	(Herrmann et al., 2019)
Musca domestica	Housefly	USA	Leek (*Allium ampeloprasum*)	Cages	Seed set increased with fly density	Commercially available in the USA. Can be reared in the laboratory.	Potential managed pollinator	2007	(Clement et al., 2007)

Supplementary Table 02 | Overwinter mortality of honey bee colonies across regions and years, given to the same accuracy as in the original citations. Note that some political regions are separated into their constituent regions for some years (e.g. United Kingdom into England, Northern Ireland, Scotland and Wales).

	Country	Year	Overwinter mortality	Overall mortality	Source
Europe	Austria	2007/08	13%	NA	(Brodschneider et al., 2019)
		2008/09	9.3%	NA	(Brodschneider et al., 2019; van der Zee et al., 2012)
		2009/10	17.3%	NA	(Brodschneider et al., 2019; van der Zee et al., 2012)
		2010/11	18%	NA	(Brodschneider et al., 2019)
		2011/12	27%	NA	(Brodschneider et al., 2019)
		2012/13	18.5%	NA	(Brodschneider et al., 2019)
		2013/14	13%	NA	(Brodschneider et al., 2019)
		2014/15	28.4%	NA	
		2015/16	8.1%	NA	(Brodschneider et al., 2019, 2016)
		2016/17	23.4%	NA	(Brodschneider et al., 2019, 2018)
		2017/18	12.2%	NA	(Gray et al., 2019)
		2018/19	15.7%	NA	(Gray et al., 2020) cf. Oberreiter and Brodschneider, 2020; 15.2%
	Belarus	2016/17	14.7%	NA	(Brodschneider et al., 2018)
	Belgium	2008/09	18.0%	NA	(van der Zee et al., 2012) cf. Nguyen et al., 2010; 19.9%
		2009/10	32.7%	NA	
		2012/13	32.4%	NA	(Laurent et al., 2016)
		2013/14	14.8%	NA	(Laurent et al., 2016)
		2015/16	12.2%	NA	(Brodschneider et al., 2016)
		2016/17	23.4%	NA	(Brodschneider et al., 2018)
		2017/18	19.4%	NA	(Gray et al., 2019)
		2018/19	10.7%	NA	(Gray et al., 2020)
	Bulgaria	2006/07	6%	NA	(Ivanova and Petrov, 2010)
		2007/08	10%	NA	
		2008/09	5%	NA	
		2017/18	2.0%	NA	(Gray et al., 2019)
		2018/19	5.8%	NA	(Gray et al., 2020)
	Croatia	2008/09	13.6%	NA	(Gajger et al., 2010)
		2015/16	16.4%	NA	(Brodschneider et al., 2016)

	2016/17	23.1%	NA	(Brodschneider et al., 2018)
	2017/18	13.0%	NA	(Gray et al., 2019)
	2018/19	24.0%	NA	(Gray et al., 2020)
Czech Republic	2013/14	6.5%	NA	(Brodschneider et al., 2019)
	2014/15	19.4%	NA	
	2015/16	6.4%	NA	(Brodschneider et al., 2019, 2018)
	2016/17	15%	NA	(Brodschneider et al., 2019, 2018)
	2017/18	13.7%	NA	(Gray et al., 2019)
	2018/19	12.7%	NA	(Gray et al., 2020)
Denmark	1985/86	27%	NA	(Vejsnæs et al., 2010)
	1995/96	30%	NA	
	2007/08	33%	NA	
	2008/09	7.5%	NA	(van der Zee et al., 2012)
	2009/10	30.1%	NA	
	2012/13	19.8%	NA	(Laurent et al., 2016)
	2013/14	14.9%	NA	(Laurent et al., 2016)
	2015/16	15.5%	NA	(Brodschneider et al., 2016)
	2016/17	19.3%	NA	(Brodschneider et al., 2018)
	2017/18	13.7%	NA	(Gray et al., 2019)
	2018/19	9.8%	NA	(Gray et al., 2020)
England	2007/08	30.4%	NA	(Aston, 2010)
	2012/13	29.3%	NA	(Laurent et al., 2016)
	2017/18	28.1%	NA	(Gray et al., 2019)
	2018/19	9.5%	NA	(Gray et al., 2020)
Estonia	2012/13	23.0%	NA	(Laurent et al., 2016)
	2013/14	10.2%	NA	(Laurent et al., 2016)
	2015/16	15.5%	NA	(Brodschneider et al., 2016)
	2016/17	13.4%	NA	(Brodschneider et al., 2018)
	2017/18	16.4%	NA	(Gray et al., 2019)
	2018/19	13.2%	NA	(Gray et al., 2020)
Finland	2012/13	23.7%	NA	(Laurent et al., 2016)
	2013/14	12.4%	NA	(Laurent et al., 2016)
	2015/16	15.4%	NA	(Brodschneider et al., 2016)
	2016/17	14.6%	NA	(Brodschneider et al., 2018)
	2017/18	10.7%	NA	(Gray et al., 2019)

	2018/19	6.3%	NA	(Gray et al., 2020)
France	2012/13	13.9%	NA	(Laurent et al., 2016)
	2013/14	13.7%	NA	(Laurent et al., 2016)
	2015/16	13.4%	NA	(Brodschneider et al., 2016)
	2016/17	19.5%	NA	(Brodschneider et al., 2018)
	2017/18	16.1%	NA	(Gray et al., 2019)
	2018/19	10.2%	NA	(Gray et al., 2020)
Germany	2004/05	3.8%	NA	(Genersch et al., 2010)
	2005/06	15.0%	NA	
	2006/07	8.0%	NA	
	2007/08	15.2%	NA	
	2008/09	10.4%	NA	(van der Zee et al., 2012)
	2009/10	37.8%	NA	
	2012/13	13.3%	NA	(Laurent et al., 2016)
	2013/14	6.2%	NA	(Laurent et al., 2016)
	2015/16	11.7%	NA	(Brodschneider et al., 2016)
	2016/17	32.2%	NA	(Brodschneider et al., 2018)
	2017/18	18.9%	NA	(Gray et al., 2019)
	2018/19	14.8%	NA	(Gray et al., 2020)
Greece	2005/06	11.9%	NA	(Hatjina et al., 2010)
	2006/07	15.4%	NA	
	2007/08	12.2%	NA	
	2012/13	6.6%	NA	(Laurent et al., 2016)
	2013/14	5.6%	NA	(Laurent et al., 2016)
	2017/18	18.4%	NA	(Gray et al., 2019)
	2018/19	21.2%	NA	(Gray et al., 2020)
Hungary	2012/13	8.3%	NA	(Laurent et al., 2016)
	2013/14	4.8%	NA	(Laurent et al., 2016)
	2017/18	18.4%	NA	(Gray et al., 2019)
Ireland	2008/09	21.7%	NA	(van der Zee et al., 2012)
	2009/10	26.5%	NA	
	2015/16	29.5%	NA	(Brodschneider et al., 2016)
	2016/17	13.3%	NA	(Brodschneider et al., 2018)
	2017/18	22.6%	NA	(Gray et al., 2019)
	2018/19	10.7%	NA	(Gray et al., 2020)
Italy	2007/08	37%	NA	(Mutinelli et al., 2010)

	2008/09	6.3%	NA	(van der Zee et al., 2012)
	2009/10	27.4%	NA	
	2012/13	5.5%	NA	(Laurent et al., 2016)
	2013/14	4.8%	NA	(Laurent et al., 2016)
	2015/16	12.5%	NA	(Brodschneider et al., 2016)
	2016/17	19.2%	NA	(Brodschneider et al., 2018)
	2017/18	29.4%	NA	(Gray et al., 2019)
	2018/19	16.5%	NA	(Gray et al., 2020)
Latvia	2012/13	18.7%	NA	(Laurent et al., 2016)
	2013/14	7.0%	NA	(Laurent et al., 2016)
	2015/16	15.0%	NA	(Brodschneider et al., 2016)
	2016/17	18.5%	NA	(Brodschneider et al., 2018)
	2017/18	16.6%	NA	(Gray et al., 2019)
	2018/19	14.1%	NA	(Gray et al., 2020)
Lithuania	2012/13	3.2%	NA	(Laurent et al., 2016)
	2013/14	2.4%	NA	(Laurent et al., 2016)
	2015/16	18.7%	NA	(Brodschneider et al., 2016)
Luxembourg	2010/11	16.8%	NA	(Clermont et al., 2014)
	2011/12	21.8%	NA	
Macedonia	2009/10	12.9%	NA	(van der Zee et al., 2012)
	2015/16	8.0%	NA	(Brodschneider et al., 2016)
	2016/17	22.5%	NA	(Brodschneider et al., 2018)
	2017/18	13.2%	NA	(Gray et al., 2019)
	2018/19	13.2%	NA	(Gray et al., 2020)
Malta	2016/17	24.2%	NA	(Brodschneider et al., 2018)
	2017/18	13.2%	NA	(Gray et al., 2019)
	2018/19	16.8%	NA	(Gray et al., 2020)
Netherlands	2002/03	15.31%	NA	(van der Zee, 2010)
	2003/04	16.02%	NA	
	2005/06	26.32%	NA	
	2006/07	15.30%	NA	
	2007/08	23.49%	NA	
	2008/09	21.7%	NA	(van der Zee et al., 2012)
	2009/10	27.8%	NA	
	2015/16	10.8%	NA	(Brodschneider et al., 2016)
	2018/19	12.1%	NA	(Gray et al., 2020)

Northern Ireland	2015/16	28.2%	NA	(Brodschneider et al., 2016)
	2016/17	10.0%	NA	(Brodschneider et al., 2018)
	2017/18	29.9%	NA	(Gray et al., 2019)
	2018/19	11.0%	NA	(Gray et al., 2020)
Norway	2008/09	7.1%	NA	(van der Zee et al., 2012)
	2009/10	15.8%	NA	
	2015/16	12.1%	NA	(Brodschneider et al., 2016)
	2016/17	7.7%	NA	(Brodschneider et al., 2018)
	2017/18	11.7%	NA	(Gray et al., 2019)
	2018/19	8.3%	NA	(Gray et al., 2020)
Poland	2006/07	9.9%	NA	(Topolska et al., 2010)
	2007/08	15.3%	NA	
	2008/09	11.5%	NA	(van der Zee et al., 2012) cf. Topolska et al. 2010; 8.7%
	2009/10	29.4%	NA	
	2012/13	16.0%	NA	(Laurent et al., 2016)
	2013/14	4.5%	NA	(Laurent et al., 2016)
	2015/16	11.3%	NA	(Brodschneider et al., 2016)
	2016/17	21.8%	NA	(Brodschneider et al., 2018)
	2017/18	14.2%	NA	(Gray et al., 2019)
	2018/19	10.7%	NA	(Gray et al., 2020)
Portugal	2012/13	14.9%	NA	(Laurent et al., 2016)
	2013/14	7.1%	NA	(Laurent et al., 2016)
	2017/18	32.8%	NA	(Gray et al., 2019)
	2018/19	20.6%	NA	(Gray et al., 2020)
Scotland	2006/07	17.5%	22.4%	(Gray et al., 2010)
	2007/08	21.6%	31.0%	
	2015/16	18.0%	NA	(Brodschneider et al., 2016)
	2016/17	20.4%	NA	(Brodschneider et al., 2018)
	2017/18	23.7%	NA	(Gray et al., 2019)
	2018/19	18.9%	NA	(Gray et al., 2020)
Serbia	2016/17	24.1%	NA	(Brodschneider et al., 2018)
	2017/18	7.4%	NA	(Gray et al., 2019)
	2018/19	25.4%	NA	(Gray et al., 2020)
Slovakia	2009/10	8.0%	NA	(van der Zee et al., 2012) cf. Chlebo and Čápek 2016; 7.1%
	2010/11	6.0%	NA	(Chlebo and Čápek, 2016)

	2011/12	9.7%	NA	(Chlebo and Čápek, 2016)
	2012/13	6.1%	NA	(Laurent et al., 2016) cf. Chlebo and Čápek 2016; 9.5%
	2013/14	2.5%	NA	(Laurent et al., 2016) cf. Chlebo and Čápek 2016; 8.8%
	2014/15	10.0%	NA	(Chlebo and Čápek, 2016)
	2015/16	8.2%	NA	(Brodschneider et al., 2016)
	2016/17	16.2%	NA	(Brodschneider et al., 2018)
	2017/18	10.0%	NA	(Gray et al., 2019)
	2018/19	15.5%	NA	(Gray et al., 2020)
Slovenia	2015/16	14.2%	NA	(Brodschneider et al., 2016)
	2016/17	19.2%	NA	(Brodschneider et al., 2018)
	2017/18	29.9%	NA	(Gray et al., 2019)
	2018/19	32.0%	NA	(Gray et al., 2020)
Spain	2009/10	18.9%	NA	(van der Zee et al., 2012)
	2012/13	10.2%	NA	(Laurent et al., 2016)
	2013/14	5.5%	NA	(Laurent et al., 2016)
	2015/16	22.1%	NA	(Brodschneider et al., 2016)
	2016/17	27.6%	NA	(Brodschneider et al., 2018)
	2017/18	26.2%	NA	(Gray et al., 2019)
	2018/19	24.5%	NA	(Gray et al., 2020)
Sweden	2008/09	14.6%	NA	(van der Zee et al., 2012)
	2009/10	28.5%	NA	
	2012/13	28.7%	NA	(Laurent et al., 2016)
	2013/14	15.4%	NA	(Laurent et al., 2016)
	2015/16	15.9%	NA	(Brodschneider et al., 2016)
	2016/17	15.2%	NA	(Brodschneider et al., 2018)
	2017/18	14.9%	NA	(Gray et al., 2019)
	2018/19	11.4%	NA	(Gray et al., 2020)
Switzerland	2007/08	17.3%	NA	(Charrière and Neumann, 2010)
	2008/09	9.1%	NA	(Charrière and Neumann, 2010; van der Zee et al., 2012)
	2015/16	9.9%	NA	(Brodschneider et al., 2016)
	2016/17	20.8%	NA	(Brodschneider et al., 2018)
	2017/18	13.8%	NA	(Gray et al., 2019)
	2018/19	13.6%	NA	(Gray et al., 2020)
Ukraine	2015/16	9.9%	NA	(Brodschneider et al., 2016)

		2016/17	17.9%	NA	(Brodschneider et al., 2018)
		2017/18	11.3%	NA	(Gray et al., 2019)
		2018/19	11.2%	NA	(Gray et al., 2020)
	UK	2008/09	16.0%	NA	(van der Zee et al., 2012)
		2009/10	36.5%	NA	
	Wales	2015/16	22.4%	NA	(Brodschneider et al., 2016)
		2016/17	19.8%	NA	(Brodschneider et al., 2018)
		2017/18	26.6%	NA	(Gray et al., 2019)
		2018/19	9.8%	NA	(Gray et al., 2020)
North America	Canada	2002/03	22%	NA	(Currie et al., 2010)
		2003/04	19%	NA	
		2004/05	15%	NA	
		2005/06	14%	NA	
		2006/07	37%	NA	
		2007/08	35%	NA	
		2008/09	34%	NA	
		2009/10	21%	NA	(CAPA, 2010)
		2010/11	29.3%	NA	(CAPA, 2011)
		2011/12	15.3%	NA	(CAPA, 2012)
		2012/13	28.6%	NA	(CAPA, 2013)
		2013/14	25%	NA	(CAPA, 2014)
		2014/15	16.4%	NA	(CAPA, 2015)
		2015/16	26.9%	NA	(CAPA, 2016)
		2016/17	25.1%	NA	(CAPA, 2017)
		2017/18	30.7%	NA	(CAPA, 2018)
		2018/19	37.7%	NA	(CAPA, 2019)
		2019/20	22.2%	NA	(CAPA, 2020)
	Mexico	2016/17	25.3%	NA	(Brodschneider et al., 2018)
		2017/18	19.6%	NA	(Gray et al., 2019)
		2018/19	16.4%	NA	(Gray et al., 2020)
	USA	2006/07	31.8%	NA	(vanEngelsdorp et al., 2007)
		2007/08	35.8%	NA	(vanEngelsdorp et al., 2008)
		2008/09	29%	NA	(vanEngelsdorp et al., 2010)
		2009/10	34.4%	NA	(vanEngelsdorp et al., 2011)
		2010/11	29.9%	NA	(vanEngelsdorp et al., 2012)
		2011/12	22.5%	NA	(Spleen et al., 2013)

		2012/13	30.6%	45.2%	(Steinhauer et al., 2014)
		2013/14	23.7%	34%	(Lee et al., 2015)
		2014/15	22.3%	40.6%	(Seitz et al., 2016)
		2015/16	26.9%	40.5%	(Kulhanek et al., 2017)
		2016/17	21.1%	33.2%	(Steinhauer et al., 2017)
		2017/18	30.7%	57.8%	(Bruckner et al., 2018)
		2018/19	37.7%	58.2%	(Bruckner et al., 2019)
		2019/20	22.2%	54.2%	(Bruckner et al., 2020)
South America	Argentina	2012	13%	NA	(Molineri et al., 2018)
		2013	13%	NA	
		2014	14%	NA	
		2015	11%	NA	
Africa	Algeria	2015/16	13.2%	NA	(Brodschneider et al., 2016)
		2016/17	10.8%	NA	(Brodschneider et al., 2018)
		2017/18	9.8%	NA	(Gray et al., 2019)
		2018/19	10.5%	NA	(Gray et al., 2020)
	South Africa	2009/10	NA	29.6%	(Pirk et al., 2014)
		2010/11	NA	46.2%	
Oceania	New Zealand	2015	10.73%	NA	(Brown et al., 2018)
		2016	9.78%	NA	
		2017	9.84%	NA	(Brown and Robertson, 2018)
		2018	10.21%	NA	(Brown and Robertson, 2019)
		2019	10.46%	NA	(Stahlmann-Brown et al., 2020)
		2020	11.30%	NA	(Stahlmann-Brown et al., 2021)
East Asia	China	2010/11	9.7%	NA	(Liu et al., 2016)
		2011/12	12.0%	NA	
		2012/13	8.5%	NA	
		2013/14	8.4%	NA	(Tang et al., 2020)
		2014/15	10.5%	NA	
		2015/16	8.8%	NA	
		2016/17	8.1%	NA	
West Asia	Iran	2018/19	22.1%	NA	(Gray et al., 2020)
	Israel	2009/10	11.2%	NA	(van der Zee et al., 2012)
		2015/16	10.5%	NA	(Brodschneider et al., 2016)
		2016/17	14.6%	NA	(Brodschneider et al., 2018)
		2017/18	8.2%	NA	(Gray et al., 2019)

	2018/19	6.6%	NA	(Gray et al., 2020)
Turkey	2009/10	25.8%	NA	(van der Zee et al., 2012)
	2015/16	7.7%	NA	(Brodschneider et al., 2016)

Table 03 | Current commercially reared bumble bee species worldwide and the location of their use. *Bombus terrestris* is divided into two subspecies.

(sub-)species reared	**Continents**	**Countries or regions**	**Company**
Bombus atratus Franklin	South America	All	Biobest Argentina
Bombus canariensis Pérez	Africa	Canary Islands	Biobest Belgium, Koppert, Agrobio
Bombus hortorum Linnaeus	Oceania	New Zealand	Trap-nested
Bombus huntii Greene	North America	Western Canada	Biobest Canada
Bombus ignitus Smith	East Asia	Japan	Biobest Belgium
Bombus impatiens Cresson	North America	All	Koppert, Biobest Canada
	Central and South America	All	Biobest Mexico, Koppert
Bombus ruderatus Fabricius	Oceania	New Zealand	Trap-nested
Bombus terrestris dalmatinus Dalla Torre *	Europe, Africa, Asia	All	Biobest Belgium, Biobest Antalya, Biobest China, STB control, Koppert, Agrobio
	South America	Chile	Biobest Belgium, Agrobio
	Oceania	New Zealand	Zonda
Bombus terrestris audax Harris	Europe	UK	Biobest Belgium, Agrobio

* Probably a hybrid population from many subspecies of *B. terrestris*

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Supplementary Material Chapter IV

On farm experience shape farmer knowledge, perceptions of pollinators and management practices

Supplementary Methodology

General survey design

Within a facilitated workshop, all authors decided on the insect pollinated crops to focus this study on. One criterion was availability, *i.e.* number of farmers in each country, and the other criteria were variation within the pollinator community of the crops and variation in their pollinator dependency, resulting into four crops: apple (*Malus domestica*), avocado (*Persea americana*), kiwifruit (*Actinidia deliciosa*) and oilseed rape (*Brassica napus* L. or OSR). The survey was then designed in English and was translated by the surveyors for each country and proofread by another independent person. Growers were contacted either personally (*e.g.* at grower workshops), via email, via standard mail or through an online platform, which was promoted in different ways. Growers received a letter of introduction in addition to the survey.

Literature review: flower visitor abundances per crop and country

To understand if farmer perceptions are linked to relative abundances of pollinators per crop and country, we performed a literature review. We included studies in which data could be grouped into the same seven functional pollinator groups as in the questionnaire (i.e. honey bees, bumble bees, other bees, flies, butterflies, beetles, other pollinators). For each country-crop combination, we aimed to identify one or more studies recording relative flower visitor abundance (see Supplementary Table 02). If several studies were found, the average relative abundance was calculated. If no suitable study from a target country was found, studies from neighbouring countries were used (see Supplementary Table 02). The only country-crop combination for which we could not identify a suitable study to match our survey data was Israel-Avocados and therefore this combination was excluded from the following analysis. To link those with farmer perceptions, we calculated the median rating of pollinators per crop and country.

Pollination biology of crops investigated

1. Apple (*Malus domestica*)

Worldwide, apple is an economically important crop. In 2019, apple was cultivated on 4.7 million ha globally with a total harvest of 87 million tonnes (FAOSTAT, 2021). Apple is highly pollinator-dependent (Free, 1993) and, for a successful fruit set, most apple varieties need a cross-compatible pollinizer cultivar (Delaplane and Mayer, 2000). As predominant pollinators for apple flowers, bees and hoverflies are mentioned (Delaplane and Mayer, 2000; Klein et al., 2007), with bees accounting for most of the pollination (Garratt et al., 2016).

2. Avocado (*Persea americana*)

The demand for avocados is growing steadily. While in 2000 2.8 million tonnes were produced worldwide, already in 2010 the number reached 3.9 million tonnes and in 2019 7.2 million tonnes (FAOSTAT, 2021). In 2019, avocado was cultivated on 0.7 million ha globally (FAOSTAT, 2021). The pollination of avocados is complex due to its dichogamous flowering behaviour. Flowers open for half a day as functional females, close after a few hours, and then reopen as male flowers (Free, 1993). While in some parts of the world avocados can self-pollinate or the pollen transfer is mediated by wind, as found in the US (Davenport, 2019), in other areas insects are required for successful pollination (Ish-Am and Lahav, 2011). This difference might be a result of different climatic regions (Davenport, 2019). In Mexico, its native range, flies were the most abundant flower visitors, followed by honey bees and wasps (Pérez-Balam et al., 2012).

3. Kiwifruit (*Actinidia deliciosa*)

In 2019, Kiwifruit was cultivated on 0.3 million ha and 4.3 million tonnes were harvested globally (FAOSTAT, 2021). Kiwifruit is a functionally dioecious vine, meaning that it has distinct male and female individuals. Therefore, sufficient pollen transfer from males to female plants is crucial for kiwifruit production (Sáez et al., 2019). In its native range, kiwifruit can be pollinated by insects and by wind (Craig et al., 1988), but the most common pollination strategy is artificial pollination since kiwifruits are not so attractive to bees due to their lack of nectar reward (Sáez et al., 2019).

4. Oilseed rape (*Brassica napus*)

Oilseed rape (OSR) was grown on 34 million ha and 70.5 million tonnes were harvested globally in 2019 (FAOSTAT, 2021). This mass-flowering crop is self-compatible, can be wind-pollinated but also benefits from pollination by insects (Stanley et al., 2013). As it produces large quantities of nectar, OSR is very attractive to insect pollinators (Williams et al., 1986). It has been shown that both bees and flies are effective pollinators of OSR (Phillips et al., 2018).

Supplementary Table 01 | Study regions and data collection. Number of questionnaires per country.

Country	**Surveyor**	**Contact information**	**Crop**	**Number of questionnaires**
Australia	Brad Howlett; Megan Gee	brad.howlett@plantandfood.co.nz	Avocado	44
Belgium	Maxime Eeraerts	maxime.eeraerts@ugent.be	Apple	21
Germany	Julia Osterman	jul.osterman@gmail.com	Apple	44
			OSR	30
Guatemala	Patricia Landaverde-González	patylandavr@gmail.com	Avocado	20
			OSR	22
Israel	Omri Avrech; Yael Mandelik	yael.mandelik@mail.huji.ac.il	Apple	31
			Avocado	32
New Zealand	Brad Howlet; Megan Gee	brad.howlett@plantandfood.co.nz	Apple	28
			Avocado	74
			Kiwifruit	31
Mexico	Flor Itzel Trujillo-Elisea	fitrujillo@ecosur.edu.mx	Avocado	31
Poland	Aleksandra Langowska, Zbigniew Koltowski;	aleksandra.langowska@up.poznan.pl	Apple	32
			OSR	35
		zbigniew.koltowski@inhort.pl		
Slovenia	Danilo Bevk	danilo.bevk@nib.si	Apple	30
Spain	Marcos Miñarro	mminarro@serida.org	Apple	30
United Kingdom (UK)	Lorna Cole; Michael P. D. Garratt; Brad Howlett	lorna.Cole@sruc.ac.uk m.p.garratt@reading.ac.uk	OSR	25

Supplementary Table 02 | Flower visitor abundances in percentage per crop and country

Survey country farmers perception	Crop (common name)	Number	Data holder	Location of study on flower visitor abundance	Source
Australia	Avocado	1	unknown	Australia	(Vithanage, 1986)
		2	brad.howlett@plantandfood.co.nz	Australia	(Evans and Goodwin, 2011)
		3	brad.howlett@plantandfood.co.nz	Australia	(Willcox et al., 2019)
Belgium	Apple	1	muriel.quinet@uclouvain.be	Belgium	(Quinet et al., 2016)
Germany	Apple	1	jul.osterman@gmail.com	Germany	unpublished
	Oilseed rape	1	jul.osterman@gmail.com	Germany	unpublished
Guatemala	Avocado	1	unknown	Mexico	(Ish-Am et al., 1999)
		2	Quezada-Euan: qeuan@uady.m	Mexico	(Perez-Balam et al., 2012)
		3	qeuan@tunku.uady.mx	Mexico	(Can-Alonzo et al., 2005)
	Oilseed rape	1	rihannon.fiction@gmail.com	Mexico	(Escobedo-Kenefic, 2020)
Israel	Apple	1	yael.mandelik@mail.huji.ac.il	Israel	unpublished
New Zealand	Apple	1	unknown	New Zealand	(Palmer-Jones and Clinch, 196
	Avocado	1	brad.howlett@plantandfood.co.nz	New Zealand	(Read et al., 2017)
		2	brad.howlett@plantandfood.co.nz	New Zealand	(Evans and Goodwin, 2011)
	Kiwifruit	1	brad.howlett@plantandfood.co.nz	New Zealand	(Howlett et al., 2017)
Mexico	Avocado	1	unknown	Mexico	(Ish-Am et al., 1999)
		2	Quezada-Euan: qeuan@uady.m	Mexico	(Perez-Balam et al., 2012)
		3	qeuan@tunku.uady.mx	Mexico	(Can-Alonzo et al., 2005)
Poland	Apple	1	unknown	Poland	(Jabłoński et al., 1981)
		2	unknown	Poland	(Wilkaniec, 1990)
	Oilseed rape	1	jul.osterman@gmail.com	Germany	unpublished
Slovenia	Apple	1	danilo.bevk@nib.si	Slovenia	(Bevk, D, Prešern, J., Pislak, M
Spain	Apple	1	mminarro@serida.org	Spain	(Miñarro and García, 2018)
		2	unknown	Spain	(Vicens and Bosch, 2000)
United Kingdom (UK)	Oilseed rape	1	m.p.garratt@reading.ac.uk	UK	(Dainese et al., 2019)

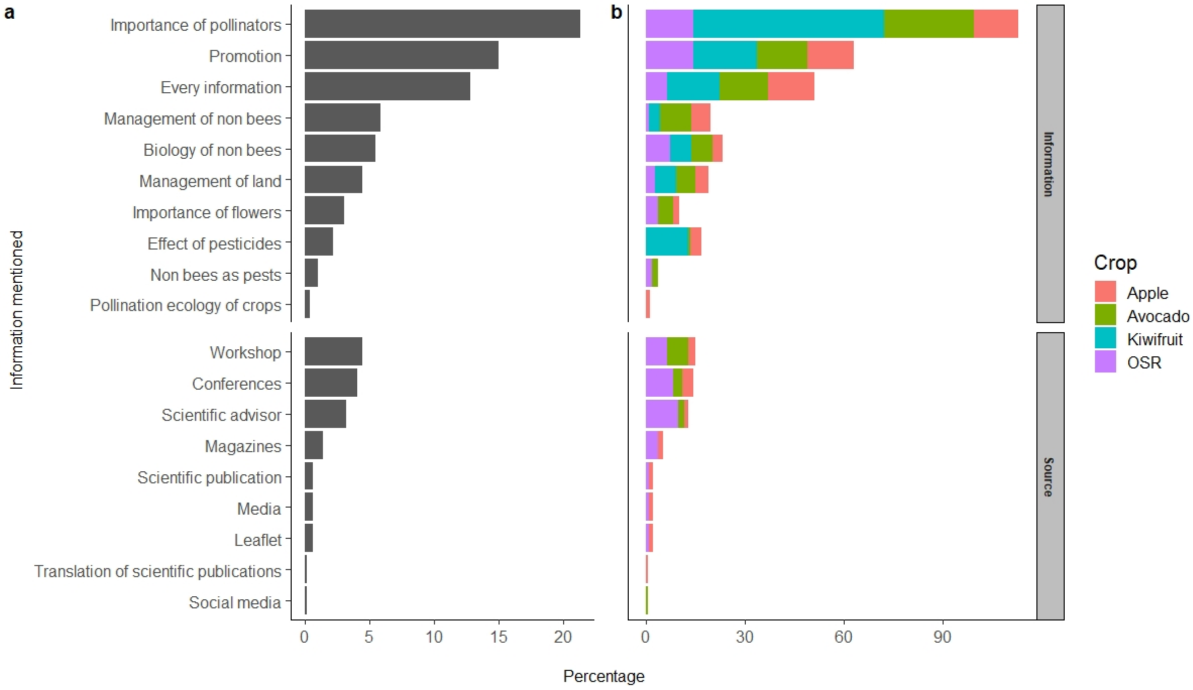
Supplementary Table 03 | Estimates and test statistics of the generalised linear models relating farmer knowledge of pollinator groups with their pollinator management practices.

Comparison	**DF**	**$\chi2$**	***P***
Providing honey bee hives			
Honey bee score	1	23.09	< **0.001**
Bumble bee score	1	1.57	0.211
Other bee score	1	0.75	0.386
Median non-bee score	1	0.04	0.834
Crop	3	4.55	0.208
Country	10	89.00	< **0.001**
Organic	1	0.05	0.819
Providing bumble bee nests			
Honey bee score	1	0.25	0.799
Bumble bee score	1	11.48	< **0.001**
Other bee score	1	3.34	0.067
Median non-bee score	1	1.78	0.183
Crop	3	16.54	< **0.001**
Country	10	38.48	< **0.001**
Organic	1	0.75	0.386
Providing other bees			
Honey bee score	1	0.01	0.924
Bumble bee score	1	0.00	0.972
Other bee score	1	4.56	**0.033**
Median non-bee score	1	0.00	0.945
Crop	3	18.95	< **0.001**
Country	10	22.71	**0.012**
Organic	1	0.00	0.963

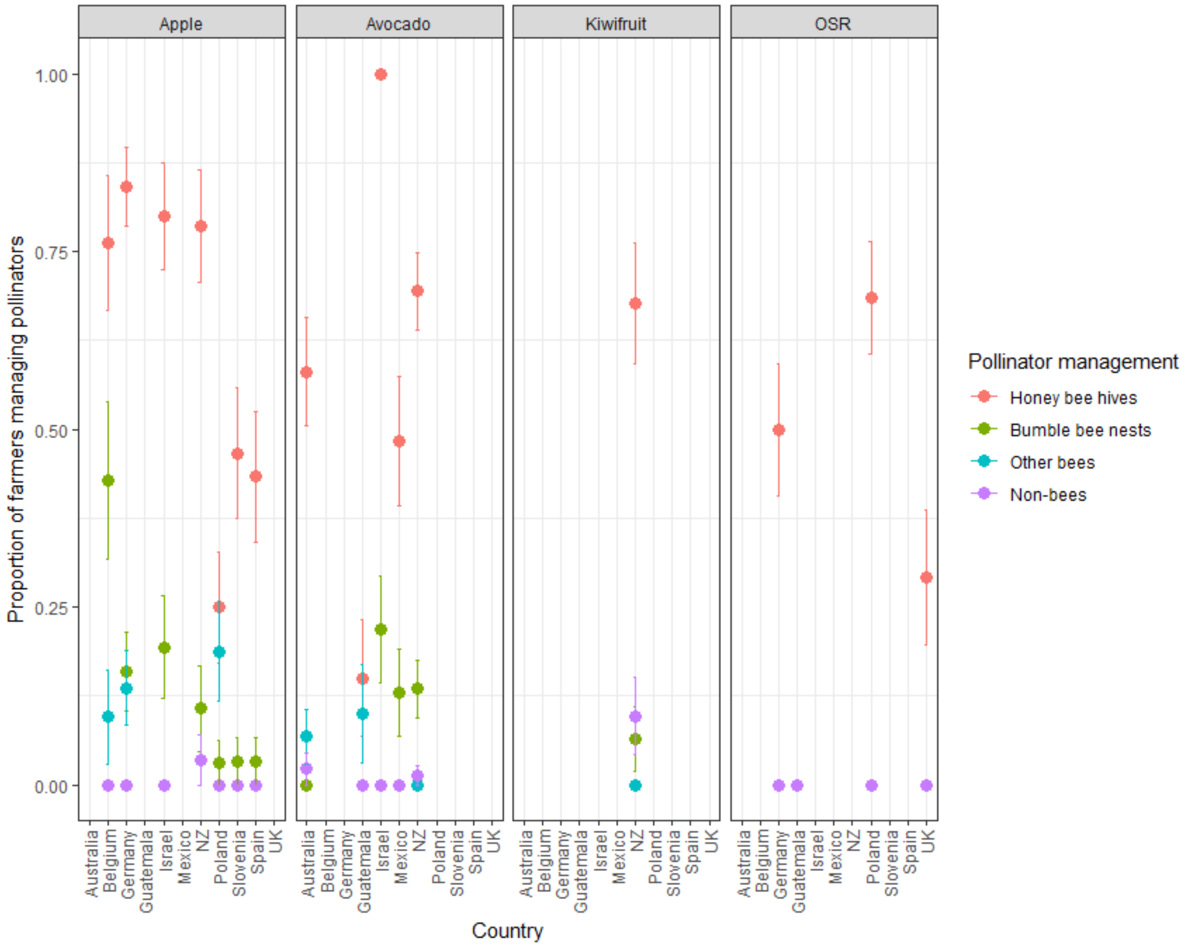
Supplementary Table 04 | Estimates and test statistics of the generalised linear models relating farmer knowledge of pollinator groups with their on-farm pollinator friendly measures.

Comparison	**DF**	**$\chi 2$**	***P***
Floral strips establishment			
Honey bee score	1	0.622	0.430
Bumble bee score	1	0.086	0.769
Other bee score	1	0.425	0.514
Median non-bee score	1	13.994	**< 0.001**
Subsidies	1	83.378	**< 0.001**
Crop	3	2.434	0.487
Organic	1	0.011	0.916
Hedgerow management			
Honey bee score	1	1.210	0.271
Bumble bee score	1	3.014	0.082
Other bee score	1	0.033	0.856
Median non-bee score	1	2.696	0.101
Subsidies	1	10.294	**0.001**
Crop	3	10.665	**0.014**
Organic	1	1.327	0.249
Other pollinator friendly management			
Honey bee score	1	0.011	0.917
Bumble bee score	1	0.094	0.367
Other bee score	1	0.814	0.367
Median non-bee score	1	1.270	0.260
Country	10	52.086	**< 0.001**
Crop	3	0.702	0.873
Organic	1	1.717	0.190

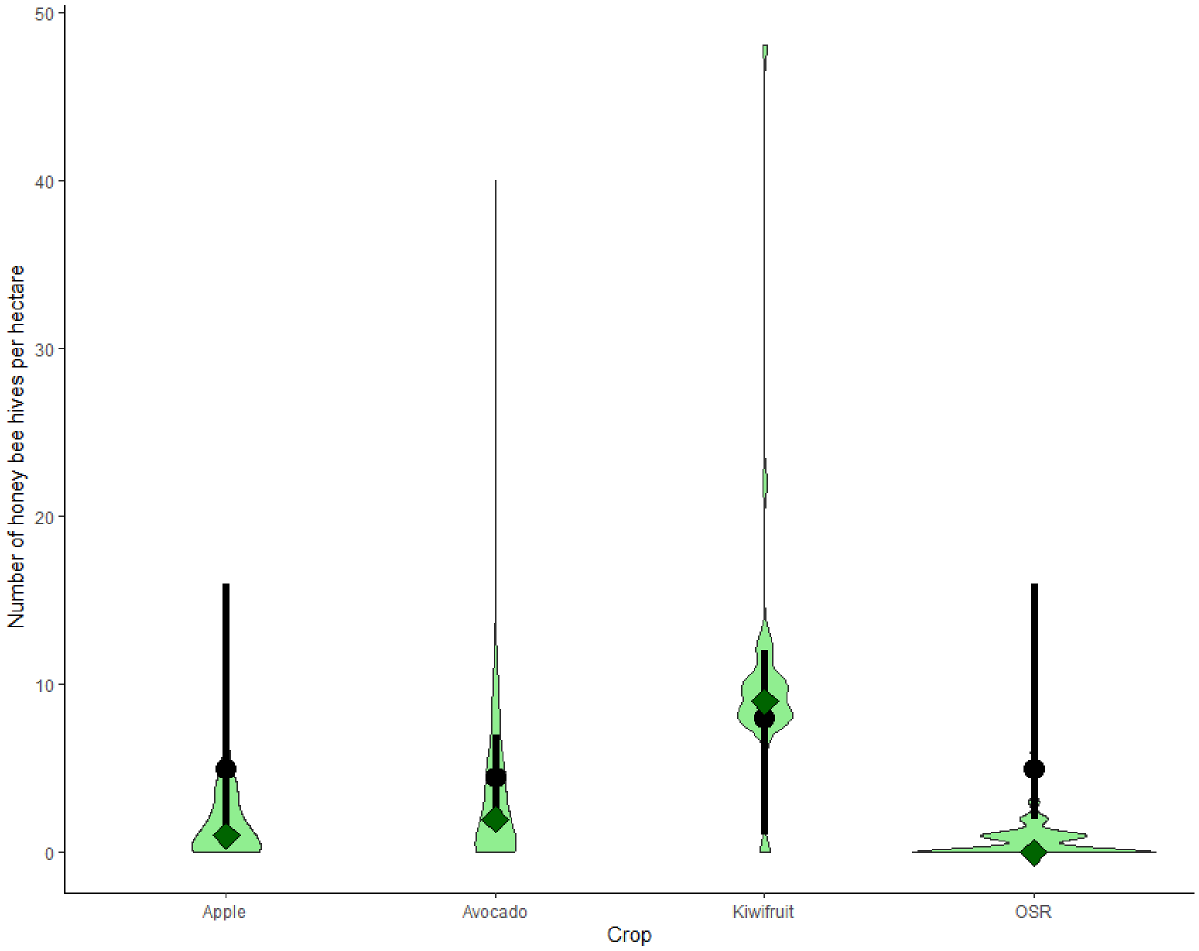
Supplementary Figures



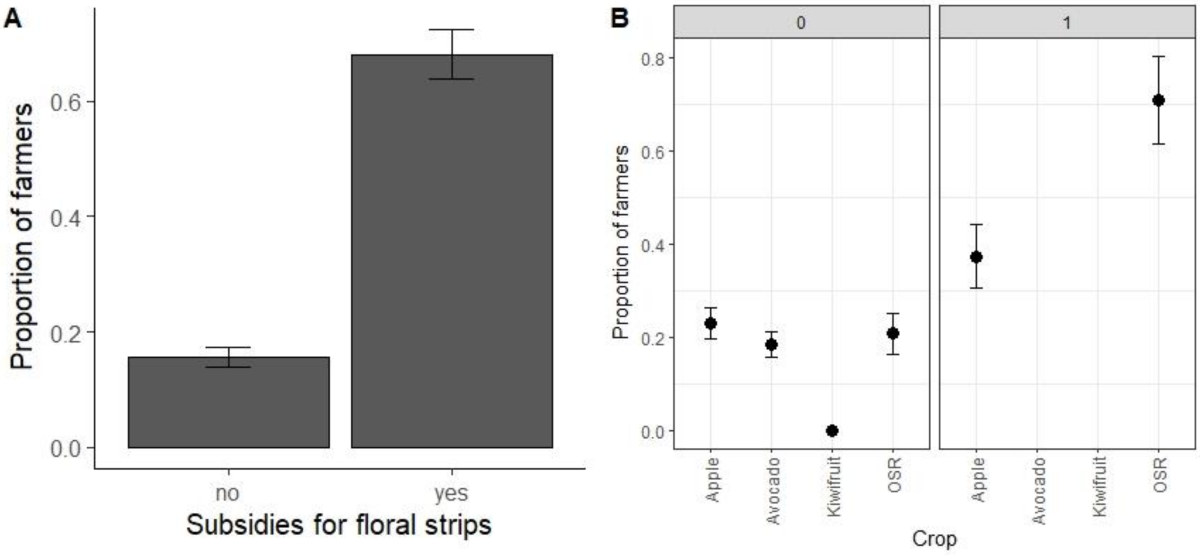
Supplementary Figure 01 | Stated information and source of information wanted by farmers in regards to non-bees in overall percentage (a) and percentage per crop (b).



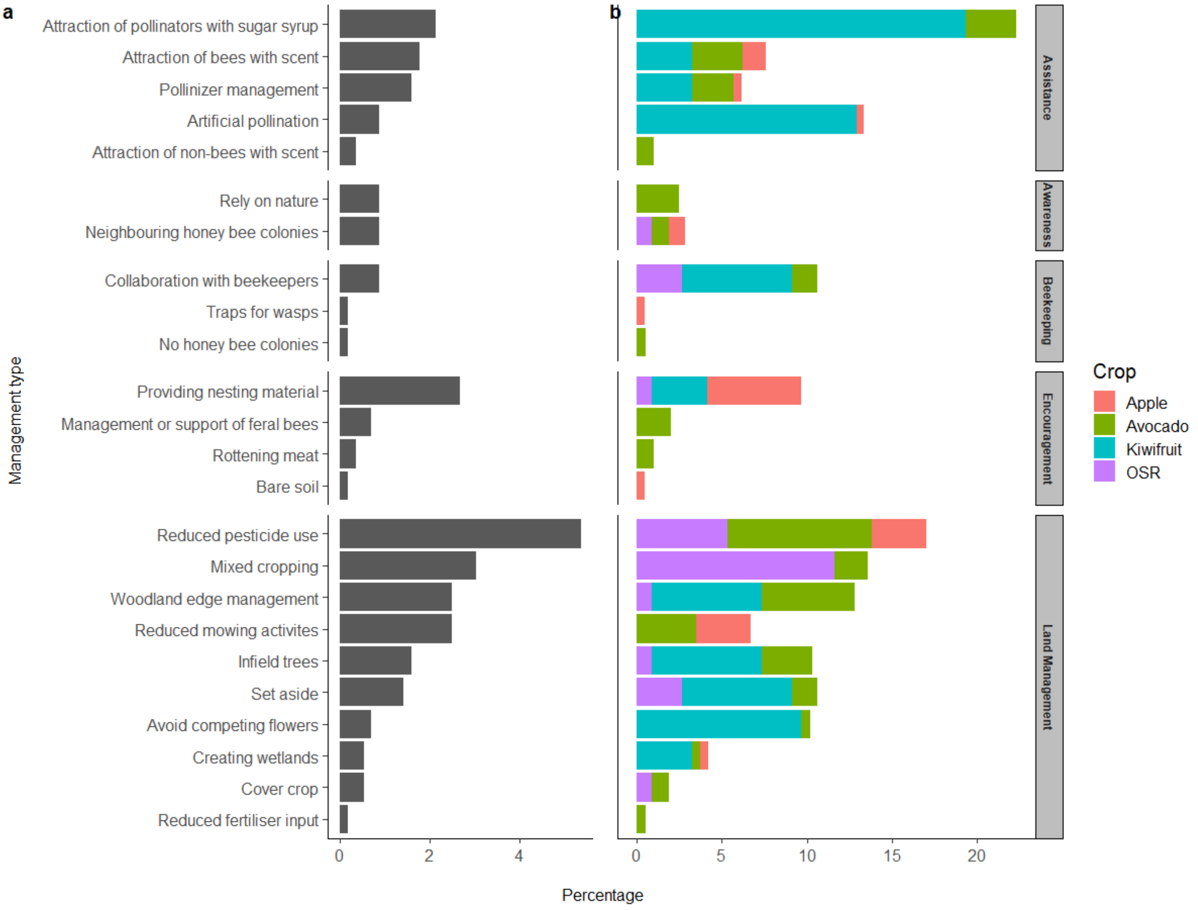
Supplementary Figure 02 | Mean proportion of farmers managing pollinators per crop, country and management type. Error bars indicate ±1 SE.



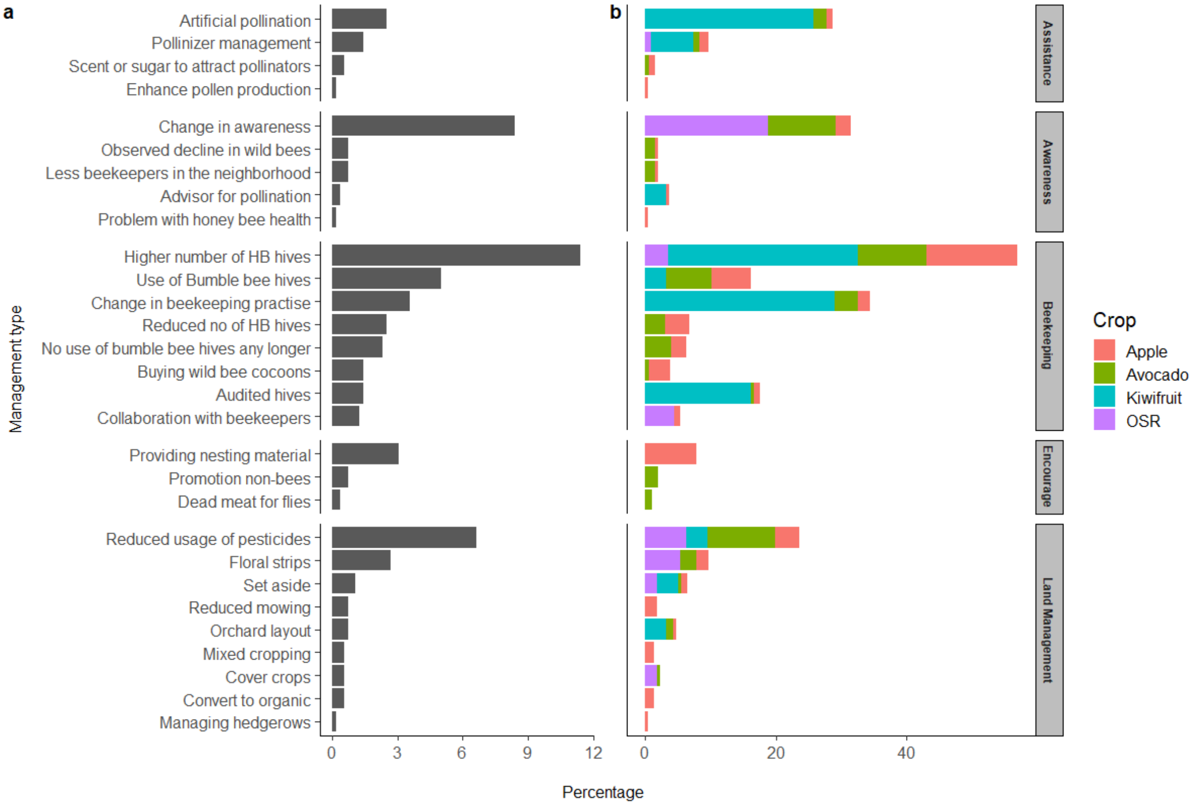
Supplementary Figure 03 | Data distribution of number of honey bee hives per hectare according to crops (in light green, violin plot). Dark green diamonds represent the median hive number per hectare per crop. Black dots represent the mean number of hives and the black line the range of hives per hectare recommended by studies (reviewed in Rollin and Garibaldi, 2019).



Supplementary Figure 04 | Mean proportion of farmers implementing (A) floral strips with and without subsidies and (B) hedgerows depending on subsidies and crop type. Error bars indicate ±1 SE.



Supplementary Figure 05 | Stated management types implemented to enhance biodiversity and pollination delivery by farmers (apart from floral strips and hedgerow management) in overall percentage (a) and percentage per crop (b).



Supplementary Figure 06 | Stated changes in pollination management in the last 10 years by farmers in overall percentage (a) and percentage per crop (b).

Supplementary Literature

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Grower Survey

Number Farm Crop Area (ha)

1) How many crops do you grow?

2) What crops do you grow that require insect pollination?

Please complete this for ________________ crop

Please specify

3) Are you certified Organic? Yes/No Please circle one

4) What is the overall area (ha) of your insect pollinated crop? ____________

5) How important are these pollinators for your crop? (score 0: if not at all, 1: if minor pollinators, 2: if somewhat important and 3: if very important)

Bees

Honeybees	0	1	2	3
Bumblebees	0	1	2	3
Other bees	0	1	2	3

Non-bees

Flies	0	1	2	3
Beetles	0	1	2	3
Moths/Butterflies	0	1	2	3
Others? Please specify	0	1	2	3

If you believe non-bees can pollinate your crop, please complete Q. 6-8 Otherwise please go to Q.9

6) Why are non-bee pollinators useful for your crop? Please tick

☐ they are more reliable pollinators than bees

☐ they visit my crop when bees aren't active

☐ they provide additional pollination above what bees can do

☐ Other (please specify) ________________________________

7) What % do you think non-bees contribute to your crop yield? __________

8) How did you become aware that non-bees can contribute pollination to your crop? Please tick

I have seen them ☐

Other growers ☐

Farm advisor or agronomist ☐

Grower workshops ☐

Through grower resources (magazine, pamphlet) ☐

Other media (e.g. radio, tv, internet) ☐

Scientists (publications, discussions) ☐

Other (please specify) ☐

9) How do you manage or try to promote pollinators in your crop? Please tick

Provide floral strips for bees ☐ non-bees ☐

Manage hedgerows for bees ☐ non-bees ☐

Supply honeybees ☐ bumblebees ☐ other bees ☐ non-bees ☐

Other practices? Please specify ____

10) How many honeybees hives do you provide per /ha? ____ bumblebees /ha? ____ others (please specify) /ha? ____

11) Has your approach to pollination management changed in the last ten years? How?
____

____

12) Do you believe non-bee pollinators can play a more important role in your crop pollination in the future? Yes/No Please circle and explain why below:

____
____

____

13) What further information would you like to help you utilise non-bees better?

____
____

About this survey

This study was initiated under the COST Super B programme, http://www.superb-project.eu/ and involves the collaboration of scientists from universities and research organisations across numerous countries including from Europe, Oceania and Africa.

The aim of this survey is to improve understanding of current crop grower knowledge regarding the diversity and value of pollinators within their crops. Growers will be surveyed across a number of countries to determine comparative knowledge and whether future strategies to improve pollination can be applied at a global scale. It will therefore provide information that can assist with future research priorities and determine whether scientific knowledge is being transferred adequately to growers.

We aim to publish the data alongside scientific knowledge and recommend strategies to improve the transfer of knowledge between growers and scientists. We will also aim to provide a summary of our findings to participating growers, should they request it (this data should be available by January 2019). Information gathered will be kept strictly confidential and any resulting publications will ensure participants can not be identified. Please contact us if you wish to withdraw your answers at any stage following survey completion. For this purpose you may wish to mark your survey with a code that you can easily refer to.

For further information about this survey and research please email either:

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Curriculum vitae

Name: Julia Osterman (formerly Goss)

Date of birth: 25.07.1988

Place of birth: Schweinfurt, Germany

Nationality: German

06/18 – 05/19	Parental leave
Since 2017:	PhD student, Martin-Luther-University Halle-Wittenberg, Institute of Biology, General Zoology, Halle (Saale), Germany Doctoral thesis: The ecology of crop pollination and its integration into farm management to ensure sustainable and stable crop yields. Supervised by: Prof. Dr. Robert J. Paxton
2016 – 2017	Internship at the Non-profit-organization “Yunkawasi”, Peru. Research focus: Andean bear population density in a region in the Andes. Training in: Camera trapping, behavioral observations of bears in the field, nature conservation.
2015 – 2016	Work for Kaminsky Naturschutzplanung GmbH
07/15 – 04/16	Parental leave
2012 –2014	**Environmental Science –Soil, Water and Biodiversity** University of Hohenheim and Swedish University of Agricultural Science (SLU), Master of Science Master Thesis: Neonicotinoids and honeybee health: The effect of the neonicotinoid clothianidin, applied as a seed dressing in *Brassica napus*, on pathogen and parasite prevalence and quantities in free-foraging adult honeybees (*Apis mellifera*). Supervised by: Dr. Joachim de Miranda, Prof. Dr. Ingemar Fries
10/09 –07/12	**Environmental Science** with minor subject **hydrology** Albert-Ludwigs-University Freiburg Bachelor of Science Bachelor thesis: Winter habitat selection of capercaillies (*Tetrao urogallus*) in the Italian Alps. Supervised by: Prof. Dr. Ilse Storch

Contributions at scientific conferences and workshops

November 2020	Scandinavian Association for Pollination Ecology (SCAPE), University of Northam, UK (online): Enhancing mason bee populations for sweet cherry pollination. Talk.
March 2020	Bienentagung, Martin-Luther University Halle-Wittenberg, Halle (Saale), Germany (canceled due to Corona): Towards integrated species and habitat management for sustainable crop pollination through an understanding of the knowledge of farmers. Poster.
October 2019	Ecosystem Service Partnership (ESP) world conference, Hannover, Germany: Managing the ecosystem service of pollination in agro-ecosystems. Talk.
September 2016	12th ALTER-Net Summer School, Peyresq, France: The influence of a mass flowering crop on the ecosystem service pollination in apple orchards: facilitation or competition? Poster.
September 2014	12th international symposium of the ICP-PR bee protection group, Ghent, Belgium: Neonicotinoids and honeybee health: Does field level clothianidin influence the prevalence and loads of honeybee (*Apis mellifera*) parasites and pathogens? Poster.
November 2013	ELLS annual conference and scientific student conference, Vienna, Austria: Biodiversity aspects of different biomass crops - is miscanthus better than rape? Poster

Publication list

6. Osterman J., Aizen M. A., Biesmeijer J. C., Bosch J., Howlett B. G., Inouye D. W., Jung Ch., Martins D. J., Medel R., Pauw A., Seymour C. L., Paxton R. J. Global trends in the number and diversity of managed pollinator species. *Agriculture, Ecosystems & Environment*, 322, 107653. (**Chapter III)**

5. Osterman W., Cornejo F., **Osterman J.** (2021). An Andean bear population hotspot in Northern Peru. *URSUS*, 32e, 1-10.

4. **Osterman J.**, Theodorou P., Radzevičiūtė R., Schnitker P., Paxton R. J. (2021). Apple pollination is ensured by wild bees when honey bees are drawn away from orchards by a mass co-flowering crop. *Agriculture, Ecosystems & Environment*, 315, 107383. (**Chapter I**)

3. Theodorou P., Herbst S., Kahnt B., Landaverde-González P., Baltz L., **Osterman J.**, Paxton R. J. (2020). How do bee and floral diversity co-vary within an urban ecosystem? The role of urban fragmentation. *Scientific Reports*, 10, 21756.

2. **Osterman J.**, Wintermantel D., Locke B., Jonsson O., Semberg E., Onorati P., Forsgren E., Rosenkranz P., Rahbek-Pederson T., Bommarco R., Smith H. G., Rundlöf M., de Miranda J. R.

(2019). Clothianidin seed-treatment has no detectable negative impact on honeybee colonies and their pathogens. *Nature Communications,* 10, 692.

1. Wintermantel D., Locke B., Andersson G. K. S., Semberg E., Forsgren E., **Osterman J.**, Rahbek-Pederson T., Bommarco R., Smith H. G., Rundlöf M., de Miranda J. R. (2018). Field-level clothianidin exposure affects bumblebees but generally not their pathogens. *Nature Communications,* 9, 5446.

Papers close to submission, submitted or under revision

Osterman J., Landaverde-González P., Garrat M. P. D., Gee M., Mandelik Y., Longowska A., Miñarro M., Cole L. J., Eeraerts M., Bevk D., Avrech O., Koltowski Z., Trujillo-Elisea F. I., Paxton R. J., Boreux V., Seymour C. L., Howlett B. G. On-farm experiences shape farmer knowledge, perceptions of pollinators and management practices (**Chapter IV**, under revision in *Global Ecology and Conservation*).

Mazi S., **Osterman J.**, Paxton R. J. Only a subset of wild bees boots the pollination of *Cajanus cajan* L. (Fabaceae), an important crop plant, in Cameroon (in preparation).

Osterman J., Benton F., Hellström S., Luderer-Pflimpfl M., Pöpel-Eisenbrandt A.-K., Stoykova B., Theodorou P., Ulbricht Ch., Paxton R. J. Managing mason bees enhance pollination services in sweet cherry orchards (**Chapter II**, in preparation).

Stoykova B., **Osterman J**., Benton F., Wild C., Heidinger I., Ulbricht C., Paxton R.J. Wild bee nesting material enhances mason bee abundance in an early-flowering crop (in preparation).

Hellström S., **Osterman J**., Osterman W., Paxton R.J. *Osmia brevicornis,* a new model organism for organisms for pesticide exposure experiments? (in preparation).

Public science articles

Osterman J. & Paxton R. J. (2021). Honigbienen fliegen auf Raps, Apfelblüten haben das Nachsehen. Obstbau, 05, pp. 277 – 279.

Baltz L. M., **Osterman J.**, Benton F., Theodorou P., Mrozek J., Paxton R. (2020). Was summt und brummt in deutschen Apfelanlagen. Obstbau, 12, pp. 694-698.

Osterman J. & Baltz L. M. (2020). Bienenschutz im Siedlungsbereich. Stadt+Grün, Oktober, pp. 49-52.

Osterman J. & Wintermantel D. (2019). Weniger Hummel-Königinnen durch Clothianidin. bienen&natur, 5, pp. 18-19.

Schönfeld P. & **Goss J**. (2014). Straßenbaumarten und ihre Ansprüche an den pH-Wert. PRO BAUM, 2, pp. 11-14.

Outreach

- Radio guest on MDR THÜRINGEN with Billy Wulff (29.08.21)
- Press release: Gefährdete Brillenbären in Peru: Forschende finden Paddington Bär (23.08.2021)
- Radio guest on MDR THÜRINGEN with Nadine Witt (14.05.2021)
- Press release: Honigbienen fliegen auf Raps, Apfelblüten haben das Nachsehen (05.05.2021)
- Co-developed an educational trail for the German garden show in Erfurt about bees ecology and conservation
- Interviewed for the newspaper MZ about pollination in sweet cherry orchards
- Press release: Feldversuch mit Neonicotinoiden: Honigbienen sind deutlich robuster als Hummeln (19.04.2019)
- Contribution to the blog "Agrardebatten" of the University of Göttingen, Germany
- Invited speaker for the annual fruit grower conference in Erfurt, Germany (17.01.2019)
- **Goss, J.**: Hummeln - unterschätze Bestäuber im Garten. MDR Garten. Broadcasted on TV (07.06.2015)

Awards and grants

2020	Granted host for the DAAD RISE program
2018	Grant for women in science (Frauenförderung) from the Martin-Luther University Halle-Wittenberg
2014	Best poster presentation at the ICPPR conference in Ghent
2014	Helmut-Aurenz-Scholarship for financing a research project in Europe
2013	Best poster presentation at the ELLS students’ conference in Vienna
2013	Germany Scholarship financed by Karl Schlecht foundation

Eidesstattliche Erklärung

Münnerstadt, den 29.09.2021

Hiermit erkläre ich an Eides statt, dass diese Arbeit, in der gegenwärtigen bzw. in einer anderen Fassung, von mir bisher weder an der Naturwissenschaftlichen Fakultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch an einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion eingereicht wurde.

Ich erkläre weiterhin, dass ich mich bisher noch nicht um den Doktorgrad beworben habe.

Ferner erkläre ich, dass ich diese Arbeit selbstständig und nur unter Zuhilfenahme der angegebenen Quellen und Hilfsmittel angefertigt habe. Die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen sind als solche kenntlich gemacht worden.

Julia Osterman

Declaration of own contribution to the original articles presented in this thesis

I. **Julia Osterman**, Panagiotis Theodorou, Rita Radzevičiūtė, Pascal Schnitker, Robert J. Paxton (2021): Apple pollination is ensured by wild bees when honey bees are drawn away from orchards by a mass co-flowering crop, oilseed rape. *Agriculture, Ecosystems & Environment* 315, 107383.

Design of the project: 70%
Collection of field data: 50%
Experimental work: 100%
Data analysis: 80%
Writing of the paper: 80%

II. **Julia Osterman**, Frances Benton, Sara Hellström, Meike Luderer-Pflimpfl, Ann-Kathrin Pöpel-Eisenbrandt, Bilyana Stoykova, Panagiotis Theodorou, Christin Ulbricht, Robert J. Paxton. Managed mason bees enhance pollination services in sweet cherry orchards (in preparation).

Design of the project: 100%
Collection of field data: 40%
Data analysis: 100%
Writing of the paper: 90%

III. **Julia Osterman**, Marcelo A. Aizen, Jacobus C. Biesmeijer, Jordi Bosch, Brad G. Howlett, David W. Inouye, Chuleui Jung, Dino J. Martins1, Rodrigo Medel, Anton Pauw, Colleen L. Seymour, Robert J. Paxton (2021). Global trends in the number and diversity of managed pollinator species. *Agriculture, Ecosystems & Environment* 322, 107653.

Literature review: 50%
Data collection for synthesis: 100%
Data analysis: 100%
Writing the paper: 50%

IV. **Julia Osterman**, Patricia Landaverde-González, Michael P. D. Garratt, Megan Gee, Yael Mandelik, Aleksandra Langowska, Marcos Miñarro, Lorna J. Cole, Maxime Eeraerts, Danilo Bevk, Omri Avrech, Zbigniew Koltowski, Flor Itzel Trujillo-Elisea, Robert J. Paxton, Virgine Boreux, Colleen L. Seymour, Brad G. Howlett. On-farm experiences shape farmer knowledge, perception of pollinators, and management practices (under revisions in *Global Ecology and Conservation*).

Design of the project: 40%
Data collection for synthesis: 90%
Data collection (survey): 10%
Data analysis: 100%
Writing of the paper: 80%