FACULTY OF
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CONSERVATION OF WILD POLLINATORS IN AGRICULTURAL LANDSCAPES: THE VALUE OF CSA FARMS FOR POLLINATING INSECTS

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Preface

Ever since I was young, I have been very interested in and passionate about nature. Agriculture and nature are often placed diametrically opposite, but through my studies Agricultural Sciences, an interest was sparked to find out how both can be integrated and contribute in the search for a sustainable future. Therefore, I would first of all like to thank Prof. dr. ir. Kris Verheyen and Dr. ir. Maxime Eeraerts for making this topic available. Thank you, Maxime, for introducing me to the world of insects and sharing your valuable knowledge about it, for teaching me the tricks of fieldwork, for guiding me through the sometimes rather difficult and complicated statistical analysis, for making me think critical about our findings and to always help me if certain things did not go smoothly or unexpected problems arose. Thank you, Kris, for always being ready to answer questions and for the constructive and positive feedback.

In addition, I would like to thank many other people who are involved with the project, both directly and indirectly. First of all, a huge thank you to all the CSA-farmers and managers of the nature reserves we visited for giving us permission to carry out our fieldwork. Without you it would have been impossible to conduct this study. I would also like to express my enormous gratitude to Jens D'Haeseleer and Jef Hendrix for verifying my bee and hoverfly identifications and correcting errors. Thanks also to Augustijn De Ketelaere who identified all the wasps. Without the knowledge of the three of you, there might still be many errors in the dataset and therefore threaten the reliability of the results. Next, I would also like to thank my fellow student Jasper Olivier for joining me on two sampling days and, given our largely overlapping research topic, for the many consultations and answers to my questions.

Last but not least, my family and friends also deserve a big thank you. Thanks to my parents, I was able to start the studies that interested me and their unconditional support, despite all the stress and difficult periods that sometimes accompanied it, brought me to where I am today. It was also nice to see that my interest also fascinated them, which made me even more motivated to complete this research successfully. And also to the rest of my family and friends: thank you, for always being there for me, for providing the necessary relaxation, for believing in me and for wanting to stop at every flower being visited by a bee. Thanks to all of you.

<div align="right">Jutta Crois, June 2024</div>

Abstract (EN)

The past decades have been characterized by biodiversity and insect diversity loss. The conversion of valuable habitats to areas intended for intensive food production makes agriculture one of the main causes of these losses. Recently, more attention has been paid to agricultural diversification practices (e.g. intercropping, agroforestry, variety mixtures) to prevent the loss of (pollinating) insects. Since community supported agriculture (CSA) represents a small-scale form of agriculture, typified by extensive crop diversification, this thesis investigates the value of these farms in providing floral resources for wild pollinators.

In late summer 2023, pollinating insects were caught at sixteen different locations in Flanders, both on a CSA farm and in semi-natural grasslands (SNG). Indeed, SNG are considered the most valuable habitats in terms of floral supply for pollinators in late summer. This study now shows that vegetation cover and species richness are similar for both habitats and that flower abundance is even higher for the CSA habitat. Pollinator abundance and species richness are also comparable. However, vegetation and pollinator community composition differ between the two habitats, making them complementary. Hence, CSA can be considered a valuable habitat for pollinators. Furthermore, flower abundance was found to significantly positively affect the abundance of all pollinators and hoverflies. In contrast, the proportion of agriculture in the surrounding area had a significant negative effect on the hoverfly abundance. Flower abundance and/or richness and the percentage agriculture in the surrounding area had no significant effect on the abundance and/or richness of other pollinators.

Samenvatting (NL)

De voorbije decennia worden gekenmerkt door een verlies aan biodiversiteit en insectendiversiteit. De omschakeling van waardevolle habitats naar arealen voor intensieve voedselproductie maakt landbouw tot één van de hoofdoorzaken van deze verliezen. Recent gaat echter steeds meer aandacht uit naar landbouwdiversificatie (bv. *intercropping, agroforestry*, *variety mixtures*) om de teloorgang van (bestuivende) insecten tegen te gaan. Aangezien *community supported agriculture* (CSA) een kleinschalige vorm van landbouw vertegenwoordigt, die getypeerd wordt door een uitgebreide gewasdiversificatie, wordt in deze thesis onderzocht wat de waarde van dit type landbouw is in het bieden van *floral resources* voor wilde bestuivers.

In de nazomer van 2023 werden op zestien verschillende locaties in Vlaanderen bestuivende insecten (bijen, zweefvliegen, vlinders, wespen) gevangen, zowel op CSA-boerderijen als in semi-natuurlijk graslanden (SNG). SNG worden namelijk als meest waardevolle habitats gezien met betrekking tot de bloemvoorziening voor bestuivers in de nazomer. Uit dit onderzoek blijkt nu dat de vegetatiebedekking en -soortenrijkdom vergelijkbaar zijn voor beide habitats en dat de bloemabundantie zelfs hoger is in CSA's. Ook de aantallen en soortenrijkdom van bestuivers zijn vergelijkbaar. De samenstelling van de vegetatie- en bestuiversgemeenschap verschillen echter tussen beide habitats, wat hen complementair maakt. CSA-boerderijen kunnen dus als waardevolle habitat voor bestuivers beschouwd worden. Verder blijkt dat bloemabundantie een significant positief effect heeft op de abundantie van alle bestuivers en zweefvliegen. Het areaal landbouw in de omgeving had een significant negatief effect op de zweefvliegabundantie. Bloemabundantie en/of -rijkdom en het landbouwareaal in de omgeving hadden geen significant effect op de abundantie/ rijkdom van andere bestuivers.

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1. Introduction

The past decades have been characterized by a loss of biodiversity and insect diversity. Several drivers and their interactions are at the root of this, with climate change, pollution, biological factors and habitat change posing a major threat on insect populations, including pollinator populations. With regard to the driver habitat change, agriculture is often given as the main cause. In addition to the frequent use of pesticides and the destructive soil management practices, among other things, it is mainly the transition to large-scale monocultures and the associated loss of non-productive landscape elements such as hedgerows as well as diversity on the field itself that leads to homogenization of the landscape. This loss of landscape heterogeneity compromises pollinator populations, which is quite paradoxical given the importance of pollination for a large proportion of crops cultivated worldwide to meet the ever-increasing demand for food. Therefore, attention should go to on- and off-farm management practices in order to conserve or restore biodiversity, for example by decreasing field sizes or increasing the amount of semi-natural habitats. More so, these strategies improve the availability and accessibility of floral resource.

A continuous supply of floral resources is crucial for pollinating insects. Still, there is often a spatial and/or temporal mismatch between the supply of and demand for these floral resources. Complementary habitats, however, meeting the needs of pollinators throughout their active period, have the potential to bridge this gap. Especially in late summer, floral resources for pollinating insects are scarce and often only available in (semi-)natural grasslands. Although intensive agriculture is often seen as a main contributor to pollinator declines, agricultural diversification is a promising strategy in this light. But evidence regarding the benefits for pollinating insects of this type of farming is generally lacking. Therefore, a comprehensive study is conducted on the role CSA farms can play in providing floral resources during late summer.

CSA was used as a broad, umbrella term for a variety of small-scaled, diversified farming principles with crop diversification being the most important strategy. In practice, a far-reaching form of intercropping is applied on these farms and crops are regularly alternated with cover crops or green manures in an appropriate rotation. Moreover, trees and/or shrubs are often integrated. Most of these farms are also organic, but in general the amount of pesticides applied is low to zero. These farms thus provide the perfect environment to investigate the effect of crop diversification on pollinators and therefore hopefully provide answers to subsequent questions:

1. What floral resources do different habitat types (CSA farms – semi-natural grasslands) provide for pollinating insects in late summer?
2. To what extent do different habitat types support communities of wild pollinating insects?
3. What is the influence of the floral resources and the surrounding landscape on pollinators?

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2. Literature study

A. Biodiversity and insect decline: a brief summary

In 1964, the International Union for Conservation of Nature (IUCN) established the Red List of Threatened Species. Nowadays, this list encompasses more than 157,100 animal, plant and fungi species and provides information on the global extinction risk status of each of them (IUCN, 2023). More than 44,000 species on the IUCN Red List are threatened with extinction, meaning that biodiversity is declining (IUCN, 2023). That nature is declining, is also confirmed by a report from the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) which states that approximately one million animal and plant species are threatened with extinction United Nations, 2019). Despite the fact that results for insects are quite uncertain, an estimation of about 10% of the insect species being threatened is put forward in this report.

Many studies have tried to estimate and quantify biodiversity loss. For instance, Sánchez-Bayo & Wyckhuys (2019) assume that, based on several published scientific reports, the decline in insect species amounts to 41%, twice as high as the decline of vertebrate species.[1] More so, Thomas et al. (2004) conclude that, if extinction rates of invertebrates are similar with those of vertebrates and plants, the biological world potentially heads towards its sixth major extinction event. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands were investigated by Biesmeijer et al. (2006). They found that, even though it is uncertain whether the decline in plants causes a reduction in the associated pollinators or vice versa, or if both plant and pollinator declines are the result of some other factors, these linked elements in biological communities go probably down together as they face the same pressures (Biesmeijer et al., 2006).

One of the reasons why insects in particular are at greater risk of extinction or why they require different conservation measures than other taxa, is that, in most cases, they probably exhibit more habitat-specific features or have different spatial patterns of habitat specificities (Dunn, 2005). Hence, Dunn (2005) claims that it is beyond doubt that the biodiversity crisis is an insect biodiversity crisis.

In general, multiple factors lie at the root of insect decline and often these stressors simultaneously pose a challenge to insects. Still, there is no clear evidence which of the stressors or combinations of different factors are most harmful (Wagner et al., 2021). In what follows, a brief enumeration of causes of loss and threats to insect diversity decline is given, preceded by some findings from recent years.

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[1] One has to take care with interpreting these results, as Mupepele et al. (2019) argue that this paper contains methodological shortcomings and does not fully represent current knowledge about this topic: their literature search was way too limited by taking into account only certain specific terms, their approach was biased and the conclusions they draw regarding the trends and drivers of decline were unsubstantiated.

While freshwater insects show an annual increase of about 1.08%, equivalent to +11.33% per decade, the estimated decline of terrestrial insects is 0.92% per year, which equals -8.81% per decade (van Klink et al., 2020). For arthropod biomass, species numbers and abundances in grasslands, declines of 67%, 34% and 78% have been found, while declines of 41% for biomass and 36% for species numbers (there was no significant on the abundance) were reported in forests (Seibold et al., 2019). These results confirm the outcomes of a previous 27-year German study which revealed a decrease in average biomass of flying insects of 76%, reaching even 82% in midsummer (Hallmann et al., 2017).

When considering pollinators in particular, similar results are observed. For example, van Strien et al. (2019) investigated over a century of data regarding butterflies in the Netherlands and found an overall contraction of butterfly species of more than 80%. Another long-term study, carried out between 1980 and 2013 in Great Britain, revealed that a third of wild bee and pollinator species in Great Britain has decreased (Powney et al., 2019). Remarkable, however, is that the average occupancy of solitary bees decreased by 32%, while the occupancy for key pollinators visiting economically important European crops increased on average by 12% in the same period, with even an increase of 38% for eusocial bee species (Powney et al., 2019). This may be the result of the implementation of agri-environmental schemes. Indeed, the findings of Carvell et al. (2017) on the positive effects of habitat quality on the family lineage survival of bumblebees substantiate the concept of habitat restoration by means of agri-environmental schemes. However, with regard to bumblebees, the results are not always unambiguous either: historical changes in bumblebee communities showed that some species were suspected of population decline, while other communities remained stable or even tended to increase in their distribution (Cameron et al., 2011; Rollin et al., 2020).

Yet, the number of studies demonstrating increasing trends is low and these studies must be considered carefully (Wagner et al., 2021). Indeed, there is growing evidence for an overall insect decline and it appears that it is the confluence of different factors and their interactions that underlie the decrease in pollinators (Vanbergen et al., 2013). These factors are in what follows referred to as 'drivers of insect decline' and four of them are considered major causes: habitat loss, climate change, pollution and biological aspects.

II. Drivers of insect decline

Habitat change

Species extinction rates are estimated to reach the order of a thousand species per million species per decade, which mainly results from habitat destruction (Pimm & Raven, 2000). Agriculture too is considered the leading cause of biodiversity loss, amongst others due to the conversion of natural ecosystems in farmland and the implementation of more intensive management practices (Dudley & Alexander, 2017). Consequently, also pollinator populations are affected. Indeed, since the 1850s, extinction patterns of bees and flower-visiting wasps in Britain can be described by intervals

of relative stability (few species losses) alternated with phases of acceleration in decrease (more species losses) and some of these periods of greater losses seem to correspond to large-scale changes in agricultural policy and practice (Ollerton et al., 2014), such as the post-war agricultural development. As many countries strived for self-sufficiency and higher living standards after World War II, the area of arable land expanded, and farms increased in size and became more specialized (Robinson & Sutherland, 2002). Along with these changes, some other crucial developments took place: the application of modern pesticides, a growing use of inorganic fertilizers, the removal of hedgerows, a reduction in crop rotation, a more continuous cereal cultivation and, most importantly, a decrease in landscape diversity (Robinson & Sutherland, 2002).

Along the same lines, the Belgian Mansholt Plan has been suggested to have caused the strong decline in ground nesting bees after 1970, because agricultural measures such as high levels of input utilisation, ploughing practices and the lower share of perennials, reduced the opportunities for these bees to nest (Rollin et al., 2020). Another important historical event is the Green Revolution, which resulted, among others, in the frequent application of synthetic fertilisers and pesticides, the cultivation of rather genetically uniform monocultures and the removal of natural landscape elements like hedgerows and trees (Sánchez-Bayo & Wyckhuys, 2019). This last-mentioned effect has important implications, since these natural landscape elements are important nesting sites for many different bee species that occupy diverse locations (Goulson et al., 2015).

As they could not distinguish between habitat loss and habitat fragmentation, Winfree et al. (2009) concluded that both had a significant negative effect, in particular in systems with very little natural habitat. The pressure exerted on insects by habitat fragmentation has also been put forward by Vanbergen et al. (2013) and it appears that certain groups are more affected by it than others. For instance, almost 75% of the butterfly species investigated in a British study showed a decline in distribution area with species exhibiting low mobility experiencing more pressure than more mobile species (Warren et al., 2001). Migratory species have also been shown to experience less declines than less mobile species in case of an increased proportion of agricultural land (Seibold et al., 2019). Yet some species proliferate in fragments. Indeed, despite a change in species composition, these fragments can be characterized by greater densities and similar diversities of native bees compared to undisrupted habitats (Cane, 2001).

Nevertheless, specialized species with more narrow habitat and/or dietary requirements or species with a slower development or lower mobility, are more likely to experience declines than generalist, fast developing and more mobile species (Biesmeijer et al., 2006). Some solitary bee species, for instance, exhibit a relatively short flight season, meaning that the appropriate floral resources should be provided throughout their active life cycle (Goulson et al., 2015). As habitat change strongly influences the landscape structure and thereby the availability of resources, these examples confirm that this factor can undoubtedly be seen as a main driver of insect decline.

Pollution

Sources of pollution are multiple, ranging from fertilisers and pesticides applied on agricultural land to industrial chemicals like heavy metals, and sewage and landfill leachates originating from urbanised areas (Sánchez-Bayo & Wyckhuys, 2019). The impact of pesticides as well as the impact

of fertilisers are discussed below, since these two sources of pollution are relevant in the context of this thesis.

The total weight of pesticides used in Great Britain between 1990 and 2015 decreased by 48%, but areas treated in 2015 were sprayed almost twice as frequently as those treated in 1990 (Goulson et al., 2018). Apparently, the reduction in pesticide weight and use was offset by the use of insecticides with a much higher toxicity such as pyrethroids and neonicotinoids (Goulson et al., 2018). These neonicotinoid pesticides are mostly used in agriculture as seed coatings, but also as foliar sprays, in-furrow treatments and granules, and in non-agricultural regions (i.e. urban and forest areas) (Hladik et al., 2018). Since these systemic insecticides do not discriminate, not only target, but also non-target species like pollinators can be affected when they consume nectar or pollen from treated crops or when they are exposed to neonicotinoids via other exposure routes (e.g., spray drift, gutation fluid). Although most research has been on the effects on honeybees (*Apis mellifera*, hereafter "honeybees"), wild pollinators too can suffer from the detrimental effects of clothianidin, imidacloprid, thiamethoxam and other neonicotinoids, due to a similar diet (Hladik et al., 2018).

However, the detrimental effects of pesticides are not restricted to insecticides: there is increasing evidence that exposure to fungicides may also harm both managed honeybees and wild bees. Bumblebees colonies, for instance, produce fewer worker bees and smaller mother queens, and show a reduction in total bee biomass after exposure to chlorothalonil (Bernauer et al., 2015). In addition, exposure to only the scent of the commercial fungicide Manzate has been shown to modify the behaviour of bumblebees, notably by increasing their navigation time (Sprayberry et al., 2013). Yet, this kind of behavioural changes does not seem to be the result of fungicides alone. Indeed, changes in foraging behaviour of honeybees also resulted from exposure to non-lethal glyphosate concentrations (Balbuena et al., 2015). Moreover, this widely used herbicide disturbs honeybee gut microbiota composition (with different bacterial species and strains showing different susceptibility), but a normal microbial community is essential to protect the bee against opportunistic pathogens (Motta et al., 2018). Apart from these direct toxic effects, herbicides kill weeds that are often important food resources for pollinators (Aviron et al., 2023; Goulson et al., 2015). Additionally, the ease by which these weeds will be eliminated from agricultural fields will probably increase by using herbicide resistant crops (Richards, 2001).

Besides the use of pesticides, fertilizer application is also considered to put pressure on insects (Ollerton et al., 2014), especially due to the risk of leaching into the environment (Dudley & Alexander, 2017). Eutrophication and the associated alteration in floral composition can change biodiversity considerably, in particular by decreasing pollinator richness (Carvalheiro et al., 2020). More specifically, nitrogen specialists seem to fare worse than generalist pollinators and species with a nitrophilous plant preferences could even outperform those that favour nitrophobous plants. In addition, diet sources of butterfly larvae are often more restricted to certain plant genera than those of bees, making the former ones more prone to resource declines (Carvalheiro et al., 2020).

Biological aspects

For many years, honeybees have been and still are transported around the world, which has facilitated honeybee parasites and pathogens to be spread (Goulson et al., 2015). The micro-

sporidian *Nosema ceranea*, for example, can spillover from honeybees to bumblebees, where it appears to be at least equally or even more infective than in honeybees, and its presence in wild populations of bumblebees has already been demonstrated (Graystock et al., 2013). Honeybees have also been found to be a plausible source or reservoir of emerging infectious diseases (EIDs), which implies that the presence of honeybees could result in declines of wild pollinators because of spillover of these EIDs (Fürst et al., 2014). Besides honeybees, bumblebee colonies too have been domesticated and traded around the world. However, it is hardly impossible to rear pathogen-free colonies, since they are fed on honeybee-collected pollen that is often contaminated. Hence, bumblebee trade promotes the expansion of pathogens which has disastrous effects on wild populations, e.g. the local extinction of *B. dahlbomii* in South America (Goulson et al., 2015).

Another concern is that flowers are supposed to be involved in the dispersal of a variety of pollinator parasites. Host pollinators like the ubiquitous honeybees or bumblebees can contaminate flowers that are visited by non-host pollinators (Graystock et al., 2015). Hence, both shared (floral) resources and robbing food stores increase the likelihood of intertaxonomical transmission or vectoring of parasites (Evison et al., 2012). Besides their potential risk on the spread of parasites, common resources are also considered as some form of competition. Indeed, the worker size of four bumblebee species turned out to be smaller in the presence of honeybees (Goulson & Sparrow, 2009). One possible explanation is that the reduced resource level forces smaller bumblebees to leave the nest in search of pollen and nectar, but the assumption that reduced food availability in larval stages leads to smaller adults, is more likely (Goulson & Sparrow, 2009).

For the sake of completeness, two other biological factors have to be mentioned i.e. genetics and invasive species. Declining populations are demonstrated to exhibit reduced gene diversity (Cameron et al., 2011) and both alien plant and animal species may disturb native species (Sánchez-Bayo & Wyckhuys, 2019).

Climate change

Climate change is likely to affect the distribution of insects, since global patterns of abiotic factors (temperature, precipitation, relative humidity, winds and solar radiation) define the physiological limits to insect habitats (Stange & Ayres, 2010). Indeed, common bumblebee species, for instance, increasingly inhabit northern sites, for which climate change is given as potential explanation (Casey et al., 2015). In addition, it may influence insect populations in terms of alterations in floral resources (e.g. geographical mismatch between plant and pollinator) (Goulson et al., 2015).

Climate change, however, also implies the occurrence of more extreme weather events, affecting pollinator populations both directly and indirectly. Exposure to extreme temperatures can alter wild bee development and emergence, but if this emergence occurs when floral resources are not yet available, the fitness of these bees is largely affected (Walters et al., 2022). In addition, these extreme weather events can modify the quality and quantity of floral resources, which may in turn lead to less flower visits and a reduced pollination success (Walters et al., 2022). However, not only extreme heat, but also floods can have detrimental effects on local bee communities, for example on those species with underground nesting behaviour (Goulson et al., 2015).

The impact of climate change on insects stays, however, quite uncertain. Moreover, Warren et al. (2001) found that positive effects of climate change are offset by the negative impact of habitat loss, especially for sedentary and specialist species, since they cannot settle in too isolated habitat fragments. On the other hand, climate change is believed to exacerbate the abovementioned drivers of insect decline (Goulson et al., 2015). This indicates that it is important not to consider the four drivers described above as isolated factors, but to see them in a bigger picture interacting with each other.

Combined effects

In the real world, the abovementioned drivers work in combination (Figure 1) (González-Varo et al., 2013). Sometimes the combined effect of two or more drivers can be synergistic, which means that the different drivers can act simultaneously, with their total effect exceeding the sum of the individual effects (Brook et al., 2008).
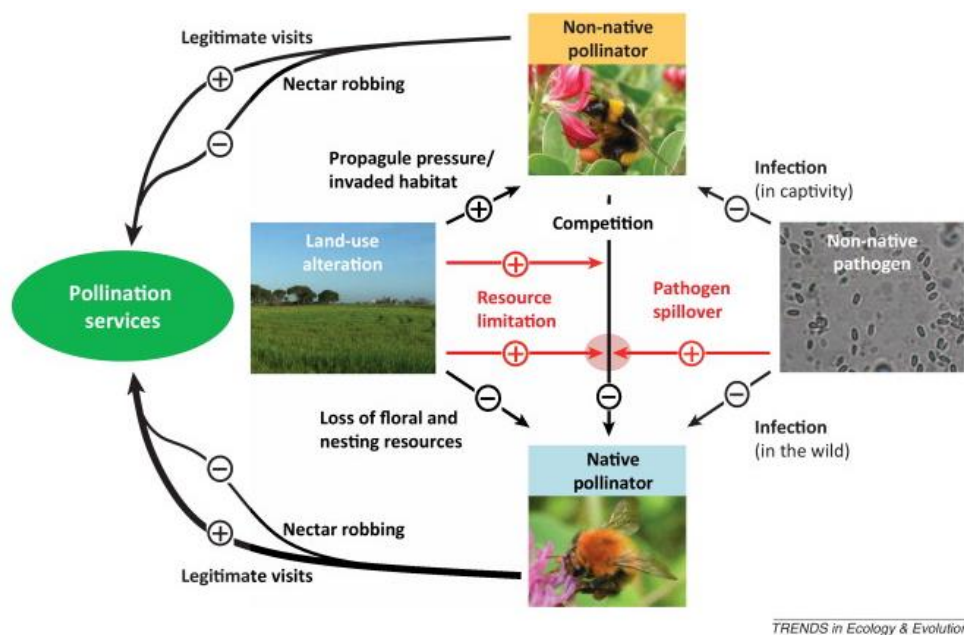
Figure 1: Schematic representation of possible combined effects between landscape alteration, invasion by a non-native pollinator and pathogen spread impacting native pollinators and their pollination services. Black arrows represent direct effects, red arrows represent (indirect) interactive effects. The positive sign denotes an increase, the negative sign denotes a decrease. From González-Varo et al. (2013)

There exists, for example, a link between pathogen prevalence and exposure to pesticides. While honeybees are known to be affected by the parasite *N. ceranea*, bumblebee colonies are exposed to a similar pathogenic microsporidian, i.e. *N. bombi*, which is associated with declining populations of *Bombus* species (Cameron et al., 2011). It has been shown that fungicides like chlorothalonil strongly predict the prevalence of *N. bombi* (McArt et al., 2017). Neonicotinoids are another type of pesticide associated with the prevalence of pathogens. These insecticides negatively affect the bees' immune response and both clothianidin and imidacloprid significantly enhanced replication of the deformed wing virus (Di Prisco et al., 2013).

Although different studies make contradictory claims about insect declines and which driver is the most important one, it is clear that, because of the wide range of ecosystem services insects provide, these reductions could lead to both ecological and economic impacts (Wagner et al., 2021). This highlights the functional significance of pollinators.

B. Functional significance of pollinating insects

For many years there was no clear consensus on how many flowering plant species are pollinated by animals until Klein et al. (2007) published their results: almost 70% of the crops worldwide benefit from animal pollination. In terms of production, however, only 35% of the global food production comes from these crops, while 60% comes from crops that do not rely on animal pollination, such as wind-pollinated cereals (Klein et al., 2007). Ollerton et al. (2011) reported their results on the importance of pollinators for plants in general (not only crops) and found even higher numbers: 78% of the temperate-zone and 94% of the tropical plants species depend on animal pollination. Considering the latitudinal diversity trend, they conclude that globally a proportion of 87.5% of all flowering plant species (i.e. 308,006 out of 352,000 species) are pollinated by animals (Ollerton et al., 2011). The vast majority of these pollinators are bees (both social and solitary), wasps, flies, beetles, butterflies and moths (Reilly et al., 2024; Vanbergen et al., 2013).

The honeybees is by far the best-known pollinator. Many farmers largely depend on managed colonies to provide pollination services to their crops and, as natural habitats are increasingly being compromised due to ongoing agricultural practices, they will become even more reliant on them (Kremen et al., 2002). Indeed, since no clear evidence was found for an overall decline of fruit and seed set with increasing distance to natural habitats, pollination services of honeybees may ensure pollination in agricultural areas, despite steep decay rates of native pollinator visitations (Ricketts et al., 2008). However, although managed honeybees are often used by farmers to pollinate their crops (Eeraerts et al., 2023; Steffan-Dewenter et al., 2001), they add to pollination services of wild insects rather than replacing them (Garibaldi et al., 2013). One must therefore be careful not to consider only honey bees as important for pollination services.

Wild insects are important too at providing pollination services, even when honeybees are abundant (Garibaldi et al., 2011; Reilly et al., 2024). Wild bees are known to make up a large part of the approximately 22,000 bee species worldwide (Goulson et al., 2015) and the global economic value of pollination as an ecosystem service delivered by these wild bees has been shown to be comparable with the pollination delivered by honeybees (Kleijn et al., 2015). More so, from a study of Garibaldi et al. (2013) it appears that visits by wild pollinators significantly increase fruit set in all of the 41 investigated crop systems, also when honeybee visits were frequent, whereas honeybee visitations increased fruit set in only 14% of the systems. Additionally, the quality of pollination, for which cross-pollination can be given as example, is better in case of wild insects compared to honeybees (Garibaldi et al., 2013).

Moreover, interactions between different species have been demonstrated to modify the behaviour and resulting pollination contribution of dominant pollinators. Indeed, the presence of non-*Apis* bees lowered the honeybee visitation rate, but increased their pollination effectiveness (Brittain et al., 2013). Non-honeybee flower visitors, for instance, improved honeybee movements among sunflower heads (Carvalheiro et al., 2011) and higher bumblebee richness and abundance

increased the visitation rate and probability of row changes of honeybees in sweet cherry orchards (Eeraerts, Smagghe, et al., 2020). Moreover, pollination requirements of a wider variety of crops is reached with higher species diversity (Kremen et al., 2002). Pollination efficiency is thus improved by a diverse pollinator community of functionally distinct species, since they complement each other both spatially and temporally due to a different behaviour (Fontaine et al., 2006; Hoehn et al., 2008).

Yet, not only ecosystem services in the form of crop pollination may be considered important in terms of biodiversity conservation. Indeed, 2% of bee species provides 80% of the crop pollination and those species are predominantly regionally common species (Kleijn et al., 2015). Therefore, conservation strategies solely based on crop pollination services would, to a certain extent, neglect those species that do not contribute to crop pollination or that are more threatened in the intensified agricultural landscape than those dominant species (Kleijn et al., 2015). Hence, it is important to find ways to support populations of different wild pollinator species. A major influencing factor here is the impact of surrounding landscape on these populations.

C. Importance of landscape and local factors for pollinator conservation

As already mentioned, insects are at risk and agriculture is believed to play a pivotal role in this. On a small scale, spatial and temporal floral resource availability is modified by agricultural intensification, the use of pesticides exposes wild pollinators to changing foraging conditions or increased risk of dying and certain management practices destroy nesting sites. On a larger scale, more land is converted to agricultural land, the environment grows into a more uniform landscape and highly valuable (semi-)natural habitats are lost and fragmented (Kremen et al., 2007).

However, not only in terms of agriculture, but also more generally, pollinators respond differently to these landscape effects. While the relative attractiveness of a plant to pollinators can, to a certain extent, determine their abundance at local scale, the structure of the pollinating community is determined by both the nesting sites and floral resources at a larger spatial scale (Steffan-Dewenter et al., 2001). Indeed, mobile organisms delivering certain ecosystem services (e.g. pollination) operate on a local scale, but in order to meet their needs and to support their populations, they often depend on a larger, landscape-level supply of these resources (Kremen et al., 2007).

Furthermore, it appears that habitat structure at the landscape level influences social bees more than solitary species (Kennedy et al., 2013). For example, it has been shown that the landscape structure influences honeybee abundance only at large scales (Steffan-Dewenter et al., 2002). This is probably due to the larger foraging distance of social bees compared to solitary bees (Greenleaf et al., 2007; Kendall et al., 2022; Kennedy et al., 2013). Moreover, research revealed that solitary wild bees exposed to less appropriate habitats and more isolated patches had larger mean body sizes (Steffan-Dewenter et al., 2002). Indeed, body size appears to best predict solitary bees' foraging range and because of the larger foraging distance of larger individuals, bee communities that are situated in disturbed habitats are characterized by large solitary bee species (Gathmann & Tscharntke, 2002).

Yet, not only the scale, but also the landscape complexity affects pollinator populations. Although in most cases mainly its negative aspects are highlighted, the future role of agricultural landscapes is of great importance in terms of conservation (Tscharntke et al., 2005). Indeed, crop heterogeneity

could improve the multitrophic biodiversity in agricultural landscapes and the amount of semi-natural habitat cover in the landscape could further improve this effect (Sirami et al., 2019). More biodiversity is harboured in complex landscapes and functional groups that are favourable in terms of agriculture, such as pollinators, are affected in a positive way by this complexity (Estrada-Carmona et al., 2022). Two dimensions are attributed to this concept of landscape complexity, i.e. landscape composition (Figure 2, x-axis) and landscape configuration (Figure 2, y-axis). One refers to composition, amongst other things, as the amount of a certain habitat, while configuration is used to explain effects of grain size, shape complexity and connectivity (Haan et al., 2020). In other words, an increasing number and/or evenness of habitat types is said to increase the compositional heterogeneity of a landscape, while more complex spatial patterns result in a higher configurational heterogeneity (Fahrig et al., 2011).
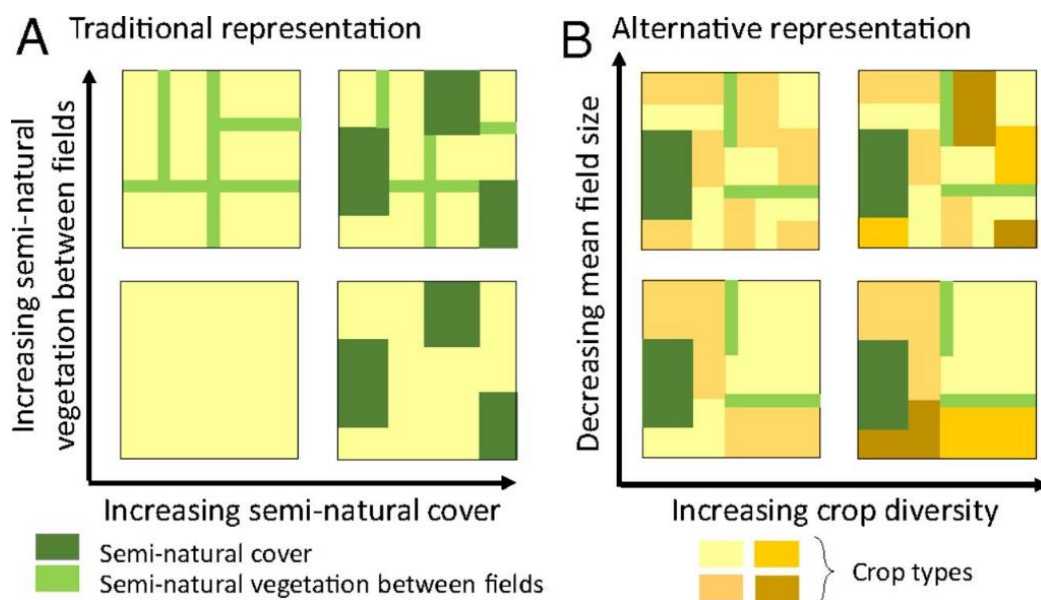
Figure 2: Two different representations of agricultural landscape heterogeneity, focusing on semi-natural (A: traditional representation) or crop heterogeneity (B: alternative representation). Each large square represents a landscape. From Sirami et al. (2019)

I.   The effect of landscape complexity

Landscape composition

The amount of (semi-)natural habitat is one way to express landscape composition and much research has been done on its effects on pollination and crop productivity. A study in the Canadian prairie temperate grassland region, for example, has shown that expanding non-crop land cover will probably not compromise crop yield and can even have a positive effect on the yield if it occurs within the field boundaries, i.e. less than 800 m from field centres (Galpern et al., 2020). Also yield stability and resistance benefit from the amount (composition) and proximity (configuration, see further) of semi-natural habitat, which most probably has to do with the influence these habitats have on pollinators (Redhead et al., 2020).

Indeed, the number of flower-visiting bee species and their abundance has been shown to increase with an increasing proportion of semi-natural habitat in the landscape (Steffan-Dewenter et al., 2001; Tscharntke et al., 2005). Adding 10% of high-quality habitats to the landscape results in a 37% increase of abundance and species richness of wild bees (Kennedy et al., 2013). However, not only wild bees, but also non-bee pollinator like flies, hoverflies, butterflies, beetles and bugs are positively affected by the proportion and/or dispersion of herbaceous semi-natural habitats (Lajos et al., 2021). More generally, Garibaldi et al. (2021) stated that at least 20% of the working landscape area should be native habitat, since this could contribute to agricultural productivity, among others by improving pollination. Empirical evidence is provided by Eeraerts (2023), who discovered that an amount of 15% semi-natural habitat serves as a threshold around cherry orchards at a 250 m scale. Below this threshold, the amount of semi-natural habitat should be increased in order to enhance crop pollination. Beyond this value, pollinator visitation does not increase (Eeraerts, 2023).

In contrast to the abovementioned results, semi-natural habitats did not show any advantageous effect on bumblebee densities, while mass-flowering crops at landscape scale, especially oilseed rape, did (Westphal et al., 2003). Rather than providing continuous and diverse resources that are typical for semi-natural habitats, these mass-flowering crops exhibit periods of high floral resource availability followed by periods of low availability and are therefore characterized by seasonal resource pulses of floral abundance (Riggi et al., 2024). The positive effects these crops can have on pollinators, however, is mainly during their flowering period. After this period, pollinating insects may be adversely affected by mass-flowering crops. For example, during mass-flowering of apple, pear and sweet cherry, the number of brood cells of *Osmia cornuta* and *O. bicornis* were not affected, since these two mason bee species could continuously collect pollen. After mass-flowering of these fruit crops, however, the number of brood cells decreased if there was a higher proportion of mass-flowering fruit crops in the surrounding landscape (200 m) (Eeraerts, Piot, et al., 2021). Moreover, species richness and abundance of flower-visiting wild pollinators in sweet cherry orchards and fruit set decreased in these landscapes with a high proportion of intensive fruit production, suggesting that these agricultural practices can weaken pollination services delivered by wild pollinators (Eeraerts et al., 2017).

Agricultural intensification, expressed at both farm and landscape level, favours yields of crops that are (almost) completely independent from pollinators much more than yields of heavily pollinator-dependent crops, and increasing dependence on pollinators has been shown to increase yield variability (Deguines et al., 2014). This implies that there is probably an important trade-off between crop pollination services on the one hand and agricultural intensification on the other (Deguines et al., 2014). In this respect, the presence of floral resources different than those provided by crops can also be beneficial. Establishing wildflower plantings adjacent to crop fields, for instance, does not only increase wild bee and hoverfly abundances, but also improves pollination services, leading to higher yields a couple of years after seeding (Blaauw & Isaacs, 2014). Likewise, ruderal plants within fields of pollinator-dependent crops can enhance diversity of flower visitors, which has been demonstrated to positively affect sunflower production in areas that are isolated from natural habitats (Carvalheiro et al., 2011). These measures, however, are rather management parameters that exert an influence at field rather than landscape level.

Yet it is important to recognise that the effect of flower strips and similar on-farm measures depends on the landscape context i.e. cleared, simple or complex landscapes. Indeed, this context influences the effectiveness of agri-environmental schemes (i.e. measures introduced in response to the increasing concern about farmland biodiversity loss) in boosting pollinator species richness and abundance (Figure 3, Scheper et al. (2013)). Effects of these agri-environmental measures are non-significant in cleared landscapes (<1% semi-natural habitat), largest in simple landscapes (1 – 20% semi-natural habitat) and smaller in complex landscapes (>20% semi-natural habitat) (Batáry et al., 2011; Scheper et al., 2013; Tscharntke et al., 2005). Moreover, a distinction exists between croplands and grasslands: agri-environmental management improved species richness only in simple, but not in complex croplands, whereas in grasslands, both species richness and abundance were positively affected regardless of the landscape complexity (Batáry et al., 2011).
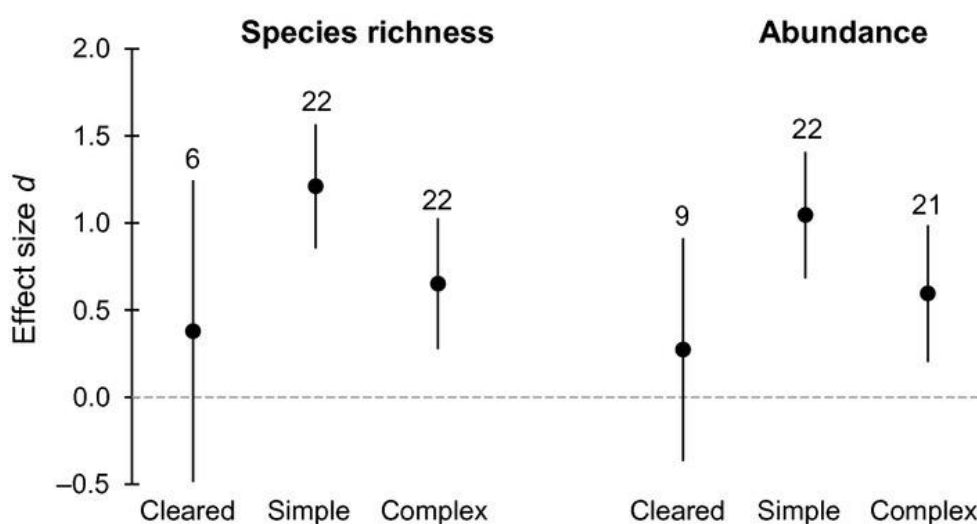
Figure 3: The effects of agri-environmental measures on species richness and abundance of pollinators for different landscape contexts (cleared, simple and complex), expressed as mean effect size. From Scheper et al. (2013)

On the contrary, Fahrig et al. (2015) found that higher compositional heterogeneity, expressed as higher crop diversity, did not result in more diversity. In addition, bee abundance was either not affected by (Pisman et al., 2022) or declined with (Hass et al., 2018) a higher degree of crop diversity. One possible explanation is that, in these studies, higher crop compositional heterogeneity was correlated with increased cultivation of intensively managed crops, such as pear (Pisman et al., 2022) or maize (Hass et al., 2018). Other research, however, revealed that decreasing crop richness negatively affected biodiversity (Sirami et al., 2019) and crop yields (Magrach et al., 2023). Effects of crop compositional heterogeneity are thus quite ambiguous.

Landscape configuration

As mentioned before, landscape configuration mainly refers to the effects of grain size, shape complexity and connectivity (Haan et al., 2020). Mean field size is one way to assess these effects and research showed that a decrease in this parameter enhances biodiversity within farmland (Fahrig et al., 2015). Indeed, lowering the mean field size from 5 to 2.75 ha resulted in a similar effect on multitrophic diversity as an expansion of semi-natural cover from 0.5 to 11% of the

landscape (Sirami et al., 2019). Moreover, the positive effects of reduced field sizes even seemed to apply if no semi-natural vegetation is present between fields (Sirami et al., 2019). However, not only biodiversity, but also crop production benefits from smaller field sizes (Magrach et al., 2023).

Field border density, related to field size, is another way to express landscape configuration. Higher densities of field borders at landscape level have been shown to increase wild bee abundance, which consequently resulted in improved seed set of plants (radish) growing in these field borders, possibly through improved connectivity (Hass et al., 2018). Indeed, pollination in fine-grained landscapes that are characterized by a high edge density is 1.7 times higher than in coarse-grained landscapes with only a low edge density (Martin et al., 2019). Besides, a pollen transfer experiment revealed that transmission rates along crop-crop borders were higher compared to continuous crop fields, making these borders potentially important for the dispersal of pollinators (Hass et al., 2018).

When it comes to configuration, also the distances to natural habitats are considered. For example, an increasing distance to natural habitats has been shown to lower mango production and to reduce the abundance and richness of flying flower-visiting species (Carvalheiro et al., 2010). The same conclusion can be drawn from the synthesis of 23 studies by Ricketts et al. (2008): both pollinator richness and visitation rate significantly declined in an exponential way as a function of isolation. At a distance of about 1.5 km from a natural habitat, species richness is reduced to about half of the richness of fields adjacent to these areas and 50% of the maximum value of visitation rates of native pollinators was found at an even smaller distance (670 m) (Ricketts et al., 2008). Contrarily, a shallower overall decline in fruit and seed set was found with increasing distance from natural habitats (Ricketts et al., 2008). A comparable study revealed that the stability and mean levels of flower visitor richness, visitation rate and this time also fruit set in agricultural areas significantly decrease as isolation from (semi-)natural areas increases (Garibaldi et al., 2011).

In general, variables that improve landscape composition and configuration, such as higher crop diversity, the presence of semi-natural habitat in the surrounding landscape and smaller field sizes can support pollinator populations and their services, because they improve the availability and accessibility of floral resource (Hemberger & Gratton, 2023). Intensively managed agricultural landscapes, however, are often characterized by a spatial mismatch between floral resource supply to pollinators and pollination demand in pollinator-dependent crops, because of a high resource discontinuity in those landscapes (Hemberger & Gratton, 2023). Hence, it is crucial to understand the importance of floral resources provided by agricultural and natural areas to pollinating insects.

II.   *The importance of floral resources*

Nowadays, pollinating insects are increasingly exposed to mass-flowering crops (e.g. oilseed rape) and fewer wildflowers are found in intensively farmed landscapes, resulting in a more monotonous diet (Goulson et al., 2015). Despite the positive influence that mass-flowering crops can have on pollinator densities (see Landscape composition), the phenology of floral resource supply should not be overlooked (Timberlake et al., 2019). Indeed, the availability of floral resources changes throughout the season within a certain year and over several years (Bishop et al., 2024), but it is crucial for pollinators to have a continuous presence of phenologically differently flowering plants during their active period, as explained below.

Importance of seasonal continuity in floral resources

During the flight season of pollinators, periods in which the nectar supply of flowering plants exceeds the energy demand of the individuals, i.e. nectar surplus, alternate with periods in which plants cannot provide enough nectar to meet the needs of the insects, i.e. nectar deficit (Timberlake et al., 2019). These nectar deficits, the so called 'hunger gaps', are twofold for bumblebees. The first gap spans the period from the beginning of the flight season until late March, a period at which the nectar production at farmlands is limited while emerging bumblebee queens have a high sugar demand. The second gap occurs in late summer, since the high nectar demand from bumblebee colonies cannot be satisfied with the amount produced between August and October (Figure 4) (Timberlake et al., 2019).
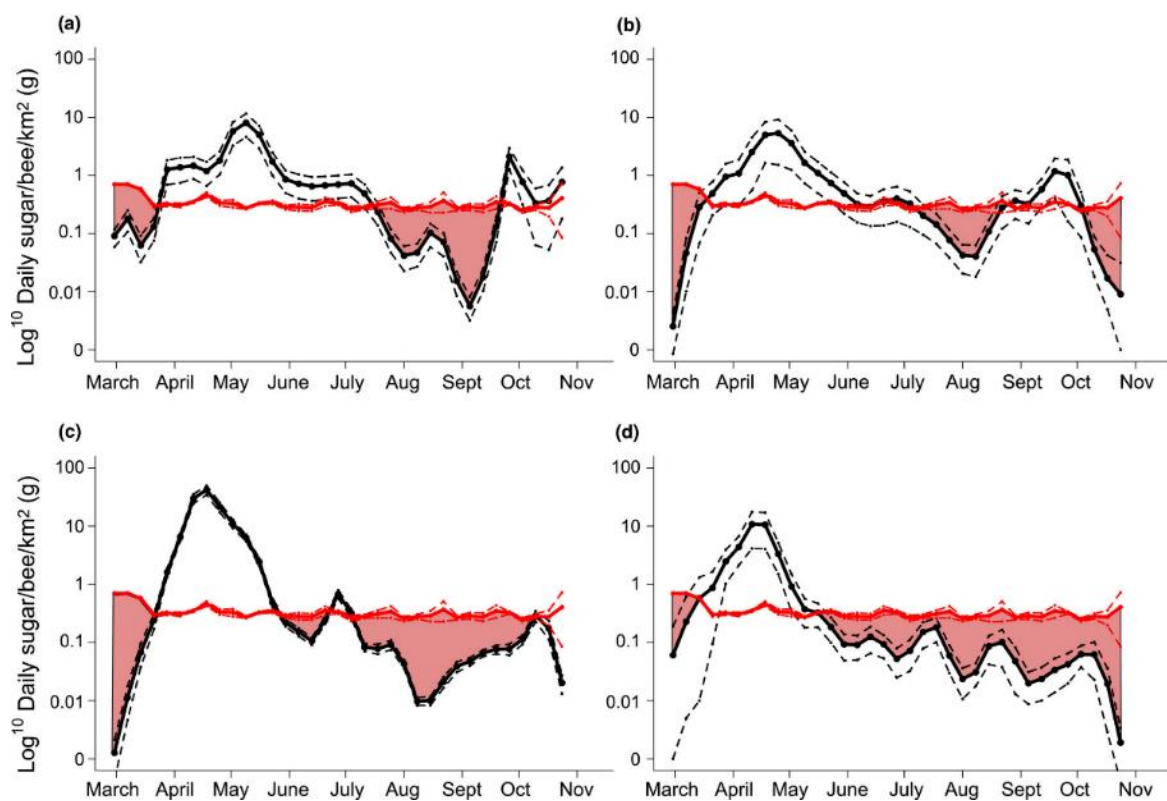
Figure 4: Comparison between the daily nectar supply and daily demand of three common bumblebee species on different farms in the UK. Black lines indicate the sugar available per individual bee. Red lines indicate the estimated mean daily sugar requirement of B. terrestris. From Timberlake et al. (2019)

As the season progresses, bumblebee and solitary bee abundances, both positively predicted by degree days, increase (Bishop et al., 2024). Indeed, 62% of the pollinator species have their population peak in July and August, making mid- and late summer resources essential for their survival (Balfour et al., 2018). The problem, however, is that landscape floral resources peak in late spring (May) and do not or only to a limited extent recover in summer, leading to a mismatch in supply and demand (Bishop et al., 2024). This coincides with the corresponding, previously mentioned hunger gap. Conservation management thus should pay attention to provide the appropriate floral resources at times when nectar and/or pollen demand is high.

Research showed, for example, that the performance of bumblebees (*B. impatiens*), expressed as colony growth and gynes production, appears to be best when resources are continuously provided (Hemberger et al., 2022). One possibility to achieve this, is by sowing fields of red clover. These late season flowers provide resources at a time when other resources are generally scare, thereby positively affecting the reproduction of bumblebees (Rundlöf et al., 2014). Complementary habitats that provide complementary floral resources in space and time therefore offer an opportunity to bridge the gap between floral resource supply and demand.

Bridging the gap with complementary habitats

Different habitats are said to complement each other over time if resources within one habitat are provided earlier or later in the year than those in another habitat due to variability in phenology (Mandelik et al., 2012). In order to sustain pollinator populations, these different habitats should complement each other in terms of floral resources, which should be provided during the entire activity period of pollinators (Figure 5, Ammann et al. (2024)). Mallinger et al. (2016), for instance, demonstrated that wild bee abundance and species richness within blooming apple orchards increase with an increasing diversity of the surrounding landscape. Floral communities in the different habitat types that made up this diverse landscape, i.e. orchards, annual croplands, grasslands and woodlands, differed in their diversity and phenology and could therefore continuously supply wild bees with floral resources during their foraging period (Mallinger et al., 2016). In addition, the floral richness in extensively managed meadows is continuously high, which coincides with a high wild bee abundance and richness, especially for rare and specialist species (Maurer et al., 2022).

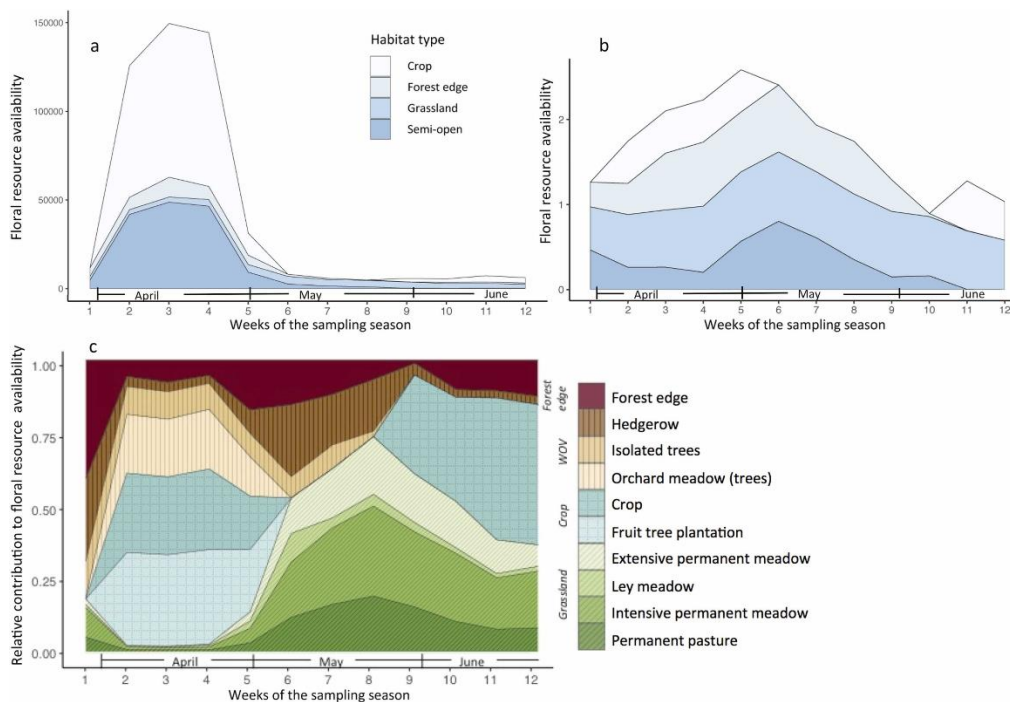*Figure 5: Temporal shift in the contribution of different habitat types (represented by different colours) over the season in terms of floral resource abundance (a), flower diversity (b, Simpson diversity) and the relative contribution to floral resources availability over time (c). From Ammann et al. (2024).*

A similar result was found by Martins et al. (2018) who showed that apple orchards and small fruit fields exhibit higher bee diversity when hedgerows, meadows and suburban areas characterize the surrounding landscape. Their study also pointed to the role agriculture can play in continuously providing floral resources. Apple orchards and small fruit fields (blueberry, raspberry) complement each other in flowering phenology, thereby supporting different wild bee genera like *Bombus* and *Andrena*. Moreover, these crops are attractive to specialist bee species and could therefore also sustain a diverse bee community at regional level (Martins et al., 2018). But not only the presence of different crops can be beneficial. The extended flowering periods of different cultivars of a certain pollinator dependent crop like sweet cherry also provide pollinators with floral resources and the different, sequentially flowering period of these sweet cherry cultivars result in an increase of pollinator richness and abundance (Eeraerts, 2022).

For agriculture in general, bee abundance and richness have been found to increase from spring, peak in mid-summer and decline through late summer and fall (Harrison et al., 2018). Field-level management, however, can add complementary floral resources. Just like orchards, hedges with trees and shrubs like willow (*Salix* sp.) or blackthorn (*Prunus spinosa*) serve as important floral resources in March and April, but are scarce in flower production later on in the season (Eeraerts, Van Den Berge, et al., 2021; von Königslöw et al., 2022). Establishing a hedge herb layer could extend this period to July or August. Flower strips too prove very useful to complement the floral supply of orchards and hedges thanks to their floral peak production in summer, i.e. from June to mid-August (von Königslöw et al., 2022). In fact, flower strips offer floral resources from April onwards, with their importance increasing during the season until July, and primarily sustain dominant crop pollinators (Maurer et al., 2022). Hence, despite the historical and current contribution of agriculture to insect decline, diversifying agriculture may offer opportunities to support populations of wild pollinators.

D. Potential of diversifying agriculture for pollinator conservation

I. *Uptake of habitat creation measures is low*

Agri-environmental schemes have been created to financially support and stimulate farmers to enhance biodiversity in their land management. One example is sowing wildflower seed mixes to provide habitats and nectar and/or pollen for pollinating insects (Wood et al. 2015; Nichols et al. 2019; Balfour & Ratnieks, 2022). Yet, there are some limitations to this measure. Firstly, sown flowers are strongly visited by bumblebees and honeybees, but the majority of (non-corbiculate) bee species forage on wild plants other than those included in flower-rich schemes, such as *Heracleum sphondylium, Hypochaeris radicata* and *Tripleurospermum inodorum* (Woods et al., 2017). These attractive wildflower species, however, are often considered as weeds in agronomic terms, making their presence or use in agriculture less preferable (Nichols et al., 2019; Baflour and Ratnieks, 2022). Moreover, different plant species contribute at different rates to the total nectar supply at farmlands: only three plant species account for 50% of the total sugar supply and only eight species contribute to 80% of the total sugar supply (i.e. *Allium ursinum, Cirsium arvense, Trifolium repens, Trifolium pratense, Heracleum sphondylium, Ranunculus acris, Rubus fruticosus* agg., *Taraxacum* agg.) (Timberlake et al., 2019). Nevertheless, the presence of other, less

productive plant species is also important, as they ensure a phenological continuous nectar supply (Timberlake et al., 2019).

However, there are also other ways to conserve biodiversity and promote ecosystem services, for example through the small-scale creation or restoration of habitats such as hedgerows (Aviron et al., 2023; Ponisio et al., 2016). Within intensive agricultural landscapes, hedgerows support the occurrences of native bees and hoverflies, but also enhance the occurrence of species that are more specialized in floral and nesting resources and of less mobile species, two types of species that are more vulnerable to habitat degradation (Kremen & M'Gonigle, 2015). Small-scale changes within the agricultural system can thus boost pollinator populations, and agri-environmental policies should therefore aim at ending and reversing the current trend of increasing field sizes (Hass et al., 2018).

According to growers, both hedgerows and flower strips are beneficial for bees and other insects, but the logistics (e.g. space, time, money) required to establish and maintain them are probably one of the largest barriers to their adoption, just like the amount of administration involved in applying for subsidies. Besides, the available information is often regarded as insufficient (Eeraerts et al., 2020). Establishing wildflower strips, for instance, seems to be one of the least desirable practices among farmers, because only a limited number of studies indicates its agronomic or economic benefits, with only two studies demonstrating yield increases to be larger than the flower strip establishment and opportunity costs (Kleijn et al., 2019). Likewise, although the importance of heterogeneity of the crop production area has been demonstrated, this was only investigated to a small extent for pollinator communities in agricultural landscapes (Hass et al., 2018). But even if research provides evidence that certain practices favour pollinator populations, farmers remain reluctant to adopt these practices given the economic uncertainty. Managing grasslands more extensively, for example, benefits both grassland bee diversity and delivery of pollination services to sunflower fields, but this management practice does not result in overall profit for the farmers (Scheper et al., 2023). Hence, the uptake of these ecosystem service enhancing management practices is made more difficult.

In addition, uncertainty about the relevance for their specific farm and conditions, the mostly indirect rather than direct effects without clear and easily observable outcomes, the greater knowledge requirements and a general lack of practical information to help farmers in adopting those nature-based management practices are reasons of concern for implementing this type of ecological intensification measures (Eeraerts et al., 2020; Kleijn et al., 2019; Scheper et al., 2023). On top of this, the effect of certain practices depends on the surrounding landscape (Scheper et al., 2013), which implies that management at a spatial scale beyond the farm should gain more attention in order to obtain the maximum effect (Gabriel et al., 2010). As it was stated by Gabriel et al. (2010): "The challenge will be to find policy levers to encourage multiple farmers within a landscape to adopt such schemes in concert, thereby creating landscape-level benefits." One type of practices that potentially help in creating habitats for pollinators in order to maintain their populations, is agricultural diversification.

II. *Agricultural diversification to the rescue?*

Diversified farming systems can be defined as "farming practices and landscapes that intentionally include functional biodiversity at multiple spatial and/or temporal scales in order to maintain ecosystem services that provide critical inputs to agriculture, such as soil fertility, pest and disease control, water use efficiency, and pollination", which can be achieved by implementing practices that are developed via traditional and/or ecological scientific knowledge (Kremen et al., 2012). Wild plant and animal communities within agricultural landscapes create diversification at the landscape level, while polycultures, non-crop plantings, mixed cropping systems (consisting of livestock or fish with crops) and crop or livestock rotation over time diversify farming systems at field scale. Within fields, different genetic varieties of a certain crop (both annual or perennial), as well as a variety of different crops can be grown together as polycultures and compost or manure application may enhance soil biodiversity (Kremen et al., 2012).

In general, diversified farming systems exhibit characteristics such as being multifunctional, organic, sustainable and eco-agricultural, but the reverse is not always true, for example in case of large-scale monocultures in organic farming that resemble more conventional, industrialized agriculture and do not, or only to a limited extent, sustain ecosystem services (Kremen et al., 2012). Since these diversified forms of agriculture can deliver a lot of ecosystem services, including biodiversity and pollination, they are believed to produce less environmental and social harm than conventional agricultural practices do, without sacrificing much in terms of mean crop productivity (Kremen & Miles, 2012).

Organic agriculture is a first example of diversified farming practices that can be beneficial for pollinators. Increasing the organic area per total crop area from 5% to 20% boosted bee species richness in fallow strips adjacent to fields by 50%, bumblebee density by 150% and solitary bee density by 60% (Holzschuh et al., 2008). If those fallow strips were adjacent to organic farming fields, bee species richness raised from average 3.95 to 6.33 species (60%), bumblebee abundance from average 3.7 to 8.5 individuals per 100 m² (130%) and solitary bee abundance from average 1.1 to 2.6 individuals per 100 m² (136%) (Holzschuh et al., 2008).

Another type of diversified farming practices is crop diversification, which is defined as "a process that makes a simplified cropping systems more diverse in time and space by adding additional crops" and can come in different forms (Hufnagel et al., 2020). Different crop diversification types that can be distinguished, are crop rotations, cover crops, agroforestry, intercropping and variety mixtures (Beillouin et al., 2021).

For example, intercropping *Vicia faba* together with wheat did not differ in number of flower visits from sole crop stands of the legume, which implies that diversifying monocultures of wheat with faba beans could potentially mitigate floral resources losses (Kirsch et al., 2023). Yet, diversification strategies based on cereal-legume intercropping to enhance flower-visiting insects in crop fields are not considered to benefit these populations strongly, since legume flowers contribute only to a small extent in the provisioning of attractive floral resources (Aviron et al., 2023). Moreover, although pollinator diversity, density and community composition can be improved, these benefits must be balanced with (potential) yield penalties, which have been shown for intercropping

flowering plants in maize systems (Norris et al., 2018). Intercropping bell pepper with flowering basil, on the contrary, resulted in wider, longer and heavier fruits with higher seed production compared to single-cropping (Pereira et al., 2015).

Likewise, intercropping trees or shrubs with arable crops, known as silvoarable agroforestry, results in an increased pollinator abundance compared with arable control fields (Staton et al., 2019). This probably follows from the favourable living conditions in those mixed-structured landscapes, which are characterized by both a higher proportion of flowering and nesting potential compared to sites without agroforestry (Kay et al., 2020). Moreover, additional management practices such as enhancing local floral resources further improve pollinator habitat suitability in several of these agroecosystems, for instance in tropical coffee agroforestry systems (Centeno-Alvarado et al., 2024). Furthermore, pollination services are expected to be somewhat higher in agroforestry systems (Kay et al., 2020). Yet, it is important to notice that most information regarding the effects of agroforestry on pollinators is gained from studies performed in (sub)tropic regions, while not much research has investigated these effects in temperate regions (Staton et al., 2019).

Increasing the availability of floral resources can also be obtained by using cover crops on fallow fields or as part of a crop rotation such as low-diversity mixtures including buckwheat and phacelia, which are mixtures that are characterized by high floral density during summer and thus by high bee visitation rates (Mallinger et al., 2019). Mass-flowering crops too are valuable, since different, phenologically complementing crops (e.g. apple and blueberry (Martins et al., 2018)) or different, sequentially flowering cultivars of the same crop (e.g. cherry (Eeraerts, 2022)) can provide floral resources for pollinators, as described before. Overall, agroforestry, crop rotation and cover crops are the strategies leading to the largest biodiversity benefits, while the positive effects of intercropping and variety mixtures on biodiversity are smaller (Beillouin et al., 2021). All these findings thus suggest that crop diversity can support populations of wild pollinator communities.

3. Study objective

In their review, Rosa-Schleich et al. (2019) investigated the ecological-economic trade-offs of diversified farming systems through an assessment of different ecological (e.g. pollination, weed control, soil health, biodiversity, pest control) and economic variables (e.g. yield, pesticide input, fertilizer input, risk) at farm level. Much evidence was found for ecological benefits like biodiversity, nutrient availability and carbon sequestration and for economic benefits such as yield, yield stability and profitability. In addition, some diversified farming practices such as the use of legumes like phacelia or lupine as cover crops, the implementation of pollination-dependent crops in a crop rotation and the presence of structural elements (e.g. hedges, field margins) can be beneficial for pollinator populations, but overall, evidence is lacking (Rosa-Schleich et al., 2019). Indeed, while some evidence exists for the effects of non-crop diversification measures on pollinators and pollination, evidence is almost completely missing for crop diversification to affect pollinators and pollination (Tamburini et al., 2020).

Therefore, more research should be done on the effects of agricultural diversification practices to understand their impact on pollinators. Crop diversification is such an agricultural diversification practice and is already being implemented on certain farms, including community supported agriculture (CSA) farms. Indeed, CSA farmers largely rely on crop diversity. Research performed in the USA by Paul (2019) revealed that, on average, 38 different crops of 115 varieties are cultivated on those farms, mainly as a risk-hedging strategy. This implies that CSA is more than just a food-producing system. Community supported agriculture can be defined as "a producer-consumer local production and marketing partnership that involves a subscription-based contract for the delivery of seasonal products from the farm" which traditionally emphasised sustainable agriculture, shared production risks, consumer involvement in production activities and authenticity of local sourcing (Woods et al., 2017).

Although the social and economic aspects of this type of agricultural system cannot be ignored, the focus here lies on the "sustainable agriculture" part of CSA. In other words, this thesis investigates how CSA farming and its associated practices like crop diversification could contribute to biodiversity, in particular by supporting wild pollinators (bees, hoverflies, butterflies and wasps), and how this agricultural habitat use relates to other habitat uses. The latter can be examined by comparing these CSAs with semi-natural areas, being species-rich grasslands. At the time of doing fieldwork, i.e. late summer, these grasslands provide important floral resources for pollinators. Therefore, semi-natural grasslands (SNGs) serve as some kind of positive control or benchmark habitat with which the CSA habitat is compared. The main research questions to investigate this, are:

1. What floral resources do different habitat types (CSA – SNG) provide for pollinating insects in late summer?
2. To what extent do different habitat types support communities of wild pollinating insects?
3. What is the influence of the floral resources and the surrounding landscape on pollinator?

The composition of the vegetation on CSAs is likely to differ from that in SNGs, as the plants in the former habitat type have been carefully chosen and sown and are mainly crops intended for

consumption, while SNG are characterized by naturally occurring plant species. Yet, since CSAs can be considered an extensive diversified agriculture with a very high degree of crop diversification on a small area, these farms can provide important floral resources for pollinating insects in late summer. Indeed, different flowering crops and varieties alternate and complement each other in their flowering period, which implies that the needs of pollinators can be met throughout the year.

Here, however, the main focus is on the floral resource provisioning in late summer. Although many crops are likely to have finished flowering by that time, we hypothesize that some agricultural crops in our study farms will still be flowering during late summer. More so, thanks to the high crop diversity, there may even be several crops still in bloom which provide pollinators with floral resources. But to what extent the CSA habitat supports communities of wild pollinating insects and how this relates to SNG is a more difficult question. Because SNG are among the most important habitats for pollinators in late summer (Ammann et al., 2024; Timberlake et al., 2019), they can serve as a positive control or benchmark to understand the value of CSA farms. Given the complementarity of floral resources in CSAs, these farms are likely to support communities of wild pollinators to a large extent, but we suspect this is mainly the case for common species and less for specialists, considering the type of floral resources these two habitats provide (i.e. cultivated crops vs. naturally occurring plants).

We also assume that the surrounding area, both at the local and landscape level, can have an impact on the abundance and species richness of the pollinators. At the former level, we suggest that a greater quantity and diversity of floral resources within each habitat type translates into higher numbers of pollinators comprising more different species. At the latter level, a higher amount of (semi-)natural habitat may support pollinator populations, both in terms of abundance and species richness, while other types of land use such as intensive agriculture or urban areas could lead to a lower number and richness of pollinators.

4. Material and methods

A. Study design and site selection

The study was conducted in Flanders, Belgium. Here, intensive agriculture is widespread and forms an important economic activity (Eeraerts et al., 2017; Jacquemin et al., 2017). A total of sixteen landscapes were selected, in which a CSA farm and SNG were chosen as habitat types that we set out to compare in this study. The distance between the different landscapes ranged from 1.48 km to 109.16 km (Figure 6).

CSA farms in this study represent highly diverse, mixed food systems. All farms produce many vegetables and fruits, and some also have livestock and grains. Most of the CSAs were certified organic farms, but in general, usage of chemical pesticides and fertilisers is low or negligible on these farms. Their vegetables are marketed through home sales, vegetable packets or the share-and-pick principle, with a combination of these strategies often applied.

A SNG was searched in the close vicinity of each CSA farms to have a paired setup, i.e. one CSA farm and one SNG in each landscape. The SNGs were selected according to the Biological Valuation Map of Flanders, which classifies the vegetation type of each plot in the region (De Saeger et al., 2023). In addition, the Biological Valuation Map of Flanders also evaluates the biological value of each plot as not valuable, biologically valuable and biologically very valuable. Hence, in a buffer zone with a radius of 1000 m around each CSA farm, we selected all biologically valuable and biologically very valuable species-rich grasslands, mesophilic hay meadows and roughened grasslands. Often, parcels had a combination of several of these vegetation types, with others such as willow thicket, shrub vegetation, sedge meadow, wet meadow grassland, embankment, marsh grassland and other grasslands of diffuse biological value alongside them. Consequently, we visited each landscape to both visit the CSA and inspect the different grasslands. Based on vegetation conditions combined with accessibility (i.e. knowledge of the owner and having granted access), we then selected one SNG per landscape. Within each landscape, the distance between the CSA and the SNG ranged from 51 m to 1,304 m.

In each habitat element, the CSA farm and the SNG, we marked two fixed transects of 25 m for data collection. These transects were positioned in the habitat elements such that they covered the representative vegetation of the whole parcel. Data were collected between the 25th of July and the 5th of September to cover the floral resources and the pollinator communities in mid- to late summer.
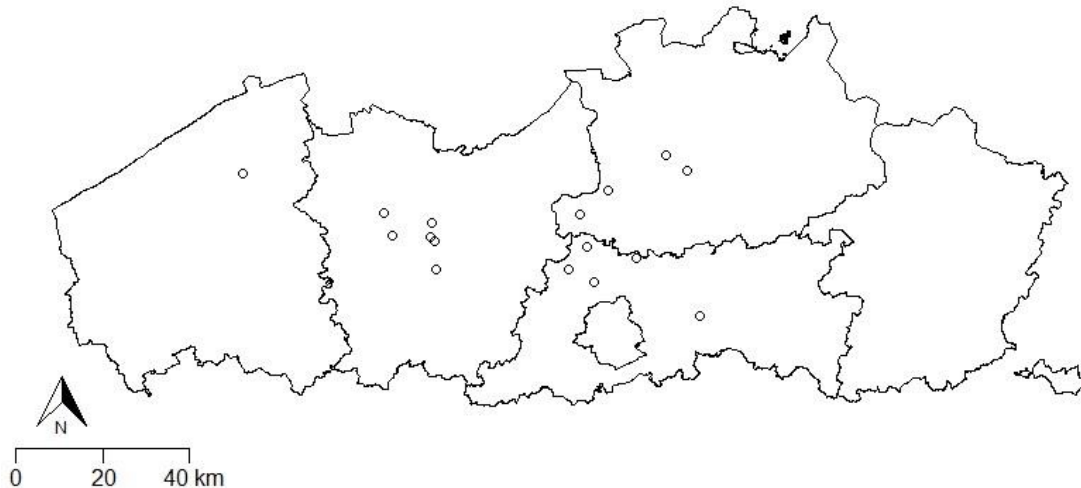
Figure 6: Overview of the different sampling landscapes in Flanders, Belgium. Within each landscape one CSA farm and one SNG site were selected for data collection.

Land cover data within the agricultural landscape-matrix was extracted from the most recent publicly available databases (Departement Landbouw en Visserij, 2023). We identified agricultural land covers surrounding the selected study sites, both CSA and SNH sites, in a circular area with 250 m, 500 m and 1000 m radius, measured from the central point between both transects of each sites. Agricultural land covers that were considered are: potato, grains and beans, vegetable fields, maize, pollinator dependent fruit crops (e.g., apple, pear, berries), sugar beets and feed crops. Maps were verified using aerial photographs. We calculated total agricultural land cover percentages within each landscape radius. The percentage of agriculture cover within 250 m, 500 m and 1000 m ranged between 0% and 84.27% (mean ± standard error: 45.67% ± 4.24%), 6.35% and 84.32% (43.82% ± 3.60%), and 6.54% and 67.13% (39.32% ± 2.91%), respectively.

B. Data collection

I. Vegetation survey

For both the CSA and SNG site, two representative transects were chosen in such a way that they mapped each habitat as closely as possible. These transects were 25 metres long and one metre wide along both sides. When the vegetation was only valuable along one side, it was chosen to delineate 1.5 m or even 2 m along that side and consequently include the other side little or not at all in the survey. This way, two transects of 50 m² were laid out each time, both on the CSA farm and in the SNG. Along these transects, the vegetation was recorded. First, by using six cover classes (Table 1), the percentage cover for the different vegetation layers was estimated. These vegetation layers were: shrub and tree layer, herb layer, moss layer, litter layer and fallow land (Table 12, Supplementary Information).

Cover Class	Percentage cover (%)
A	< 1
B	1 – 5
C	6 – 25
D	26 – 50
E	51 – 75
F	76 – 100

After the vegetation cover estimation, all plants along the transects were identified to species level. If knowledge of the plant species was lacking, the identification app *Obsidentify* was used, but only if the certainty of the observations was high enough (reliability > 90%). If species level was unknown, the plant genus was noted and/or the plant was taken to the lab for further determination. Five plant species remained undetermined and were named "Plant X" (with X = 1, 2, 3, 4 or 5) in the dataset. Only one of them was visited by pollinators. Grasses were noted as 'grass' without any further determination. Like the vegetation layers, plant species were divided into six different cover classes (cfr. Table 1). Furthermore, plants were classified according to their phenology, i.e. vegetative, flowering and bloomed.

The final step of the vegetation survey involved counting the number of flowerheads of flowering plants. For many plant species such as *Ranunculus acris*, *Trifolium repens* and *Convolvulus arvensis,* floral units comprised a single flower, while we counted the capitula for i.a. *Cirsium vulgare*, *Taraxacum officinale* and *Senecio vulgaris*, the umbels for i.a. *Achillea millefolium, Foeniculum vulgare, Daucus carota* and *Heracleum sphondylium* and the racemes for *Medicago sativa* (cfr. Plantlife's Every Flower Counts survey method (Hemmings et al., 2022)). This number then serves as a representation of the flower abundance.

II. Pollinator survey

At the beginning of each pollinator survey, four parameters were recorded, i.e. temperature, cloud cover, wind speed and the starting time of each measurement. Values for temperature and wind speed were taken from the KMI (Koninklijk Meteorologisch Instituut) app. To determine the cloud cover, we visually estimated the percentage cover of clouds relative to blue sky. Since there were no large fluctuations between temperature, cloud cover and wind speed on a certain sampling date, this data was averaged per location (Table 13, Supplementary Information). Sampling conditions on different dates, however, were different due to due to varying weather conditions in the summer of 2023. Minimum and maximum mean values are 18°C and 27.5°C, 0% and 90% and 6.3 km.h^{-1} and 28.3 km.h^{-1}.

Along each transect, all flower-visiting insects were caught with an insect net for 40 minutes in total. Sampling was always carried out in pairs by both Maxime Eeraerts and Jutta Crois (except for two locations, i.e. Londerzeel (ME), Zedelgem (JC)): after sampling 20 minutes on one transect, we switched and caught for 20 minutes on the other transect. This was mainly done to compensate for potential individual differences in sampling efforts. Hence, each habitat type was sampled for 80

minutes (two transects). If we were distracted while sampling (e.g. specimen processing, passers-by asking questions), we stopped the timer so that the 20 minutes sampling time would represent only active netting.

During sampling, the insects were kept in tubes and collected according to the plant species they were caught on. After each sampling round, we noted which and how many insects were caught on that particular plant species. Only bees, hoverflies, butterflies and wasps were collected. Specimens that could be identified to species were released after the survey, while pollinators that could not be identified in the field were taken to the laboratory and kept in the freezer for later identification. We used *Bijen – Veldgids voor Nederland en Vlaanderen* (Falk & Lewington, 2017) for the identification of bees, *Veldgids Zweefvliegen* (Bot & Van de Meutter, 2019) for hoverflies and *Veldgids Dagvlinders* (Wynhoff et al., 1999) for butterflies. The identification of bee species was checked and adjusted, if necessary, by Jens D'Haeseleer, while Jef Hendrix did the same for hoverflies. Wasps, we did not identify ourselves. Identification of these insects was performed by Augustijn De Ketelaere. If a sample was found to be none of the four pollinator types mentioned above, this sample was excluded from further analysis.

C. Data analysis

I. *What floral resources do different habitat types provide for pollinating insects in late summer?*

To answer the first research question, we used the vegetation dataset. As mentioned before, we worked with different classes, representing different coverage percentages, to estimate the cover of the vegetation. These classes, however, are qualitative, which makes it hard to perform a quantitative data analysis. Therefore, we decided to work with mean value of each cover class:

$$mean\ cover\ (\%) = \frac{lower\ limit\ (\%) + upper\ limit\ (\%)}{2}$$

Although we recognise that this method, given the wide range of coverage percentage within one class, results in a strong simplification, the use of a mean percentage instead of a letter to indicate the vegetation cover, allows us to analyse the data quantitatively.

To determine the effects of the two different habitat types on the cover, species richness and flower abundance of the vegetation, three different datasets were constructed: the complete vegetation dataset containing all plants recorded, the vegetation dataset containing the flowering plants and the vegetation dataset containing the flowering and pollinator-visited plants. We then examined whether these different datasets are correlated by using the Spearman's rank correlation coefficient method (Table 2). The interpretation of the correlation coefficients is based on Schober & Schwarte (2018).

Variable 1	Variable 2	ρ	p	Correlation
Cover all	Cover flowering	0.53	0.0016	Moderate
Cover all	Cover visited	0.50	0.0038	Moderate
Cover flowering	Cover visited	0.87	$6.70*10^{-11}$	Strong
SR all	SR flowering	0.90	$2.47*10^{-12}$	Strong
SR all	SR visited	0.56	0.00082	Moderate
SR flowering	SR visited	0.71	$6.29*10^{-6}$	Strong
FA all	FA flowering	1	$< 2.2*10^{-16}$	Very strong
FA all	FA visited	0.99	$< 2.2*10^{-16}$	Very strong
FA flowering	FA visited	0.99	$< 2.2*10^{-16}$	Very strong

Since the correlation between the three different datasets is significant for both the cover, species richness and flower abundance, we decided to continue the analysis with the visited vegetation dataset. The results of the other datasets are provided in the supplementary information (Table 15, Table 16, Figure 17 and Figure 18)

Vegetation cover, richness and flower abundance

The cover data was pooled by taking the sum of the mean cover values over the two different transects of each sampling locations, leading to sixteen unique cover values for CSA and SNG. These values may be greater than 100%, since different vegetation types can overlap. Next, the vegetation species richness for each habitat type was calculated as the number of unique plant species recorded at each sampling site. Finally, in order to investigate the effect of habitat type on the flower abundance, the number of flowerheads was summed for each plant species at each site.

The effect of habitat type on vegetation cover and species richness was analysed with a linear mixed-effect model (LME), using the lme() function in the nlme package in R (version 4.3.3). For flower abundance, a generalized linear mixed-effect model (GLMM) with a Poisson distribution was built, using the glmer() function in the lme4 package in R (R Core Team, 2024).

Composition of the vegetation community

To determine the vegetation community composition, the vegetation data was first used to compute the composition dissimilarity (function: vegdist(), package: vegan). For the cover and flower abundance, the Morisita-Horn index was chosen (e.g. Harrison et al. (2018); von Königslöw et al. (2022)), since this method takes the presence of rare species into account and is therefore useful when undersampling is suspected (Beck et al., 2013). For species richness, the Jaccard index is better suited since the richness data can be seen as incidence data, i.e. presence/absence. These dissimilarities were then used to perform a permutational multivariate analysis of variance using distance matrices (PERMANOVA, Anderson (2001)) by using the adonis2() function in the vegan package. In addition, with the betadisper() function (package: vegan) we determined multivariate

homogeneity of groups dispersions (R Core Team, 2024). For both calculations, the number of iterations was set at 1000.

Visualizing the community composition involved the use of nonmetric multi-dimensional scaling (NMDS) by using the metaMDS() function in the vegan package, with the number of iterations set at 1000. This way, the stress value was calculated and both a stress plot and NMDS plot were created (R Core Team, 2024). Finally, with the multipatt() function in the indicspecies package in R, we determined which plant species could serve as an indicator species for both habitat types by calculating the point-biserial correlation coefficients (r_{pb}) flower abundance (De Cáceres et al., 2010)

II.   To what extent do different habitat types support communities of wild pollinating insects?

The pollinator data is used to examine the effects of the two habitat types on the abundance and species richness of the pollinators. For these two parameters, five datasets were constructed: one for all pollinators and one for each of the four pollinator types (i.e. bees, hoverflies, butterflies and wasps). Since the focus is on wild pollinators, honeybees were excluded from the total pollinator and bee datasets.

Sampling conditions

First, we tested whether the sampling conditions had a significant effect on the pollinator dataset. By using Spearman's rank correlation coefficients, we found no significant correlation between temperature and pollinator abundance (all pollinators: $\rho = -0.22$, $p = 0.42$; bees: $\rho = 0.024$, $p = 0.93$; hoverflies: $\rho = -0.24$, $p = 0.37$; butterflies: $\rho = -0.40$, $p = 0.12$; wasps: $\rho = 0.40$, $p = 0.14$). The same holds true for the correlation between temperature and pollinator species richness (all pollinators: $\rho = 0.34$, $p = 0.19$; bees: $\rho = 0.28$, $p = 0.30$; hoverflies: $\rho = 0.035$, $p = 0.90$; butterflies: $\rho = -0.32$, $p = 0.23$; wasps: $\rho = 0.51$, $p = 0.051$).

We then checked whether the different sampling condition parameters (i.e. temperature, cloud cover, wind speed) are interrelated by using Spearman's rank correlation and found a significant correlation in all three cases (temperature ~ cloud cover: $\rho = -0.46$, $p = 4.15*10^{-49}$; temperature ~ wind speed: $\rho = 0.40$, $p = 1.84*10^{-36}$; cloud cover ~ wind speed: $\rho = 0.31$, $p = 9.42*10^{-22}$). We thus conclude that both temperature, cloud cover and wind speed are not correlated with pollinator abundance and species richness for all pollinating insects and across the four different pollinator types. Hence, these variables are not considered in the models that were built to answer the second research question.

Pollinator abundance and species richness

The pollinator abundance datasets was built by taking the sum of all insects caught at a certain sampling site, while species richness of the pollinators is calculated as the unique number of pollinator species visiting flowers at a certain site. Just like we did for the vegetation data, models were built to investigate the effects of habitat type on both parameters. Although some datasets had a normal distribution (abundance of all pollinators and bees, species richness of all pollinators

and hoverflies), we decided to work with GLMMs with a Poisson distribution, since both abundance and species richness can be considered as counts.

Composition of the pollinator community

The composition of the pollinator community was determined in a similar way as for the vegetation data, i.e. by computing dissimilarities that can be used to perform a PERMANOVA and to calculate the multivariate homogeneity of groups dispersions, and by using NMDS to visualize community data. For the abundance data, we chose for the Morisita-Horn index, while the Jaccard index was used for species richness data, for the same reason as explained before. Furthermore, an indicator analysis was performed. Again, the pollinator species that could serve as indicator species for CSA and SNG were determined by calculating the point-biserial correlation coefficients (r_{pb}). Both the PERMANOVA and indicator analysis are only performed for all pollinators, bees and hoverflies.

III.   What is the influence of the floral resources and the surrounding landscape on pollinator?

Since many studies pointed to the effect of landscape complexity on pollinator populations (Fahrig et al., 2011; Hass et al., 2018; Kennedy et al., 2013; Sirami et al., 2019), we investigated whether the area surrounding the different study sites has an influence on the pollinator abundance and species richness. To do this, we restricted ourselves to the abundance and species richness of all pollinators, bees and hoverflies as response variables and examined the effects of the fixed variables flower abundance (for pollinator abundance) or vegetation richness (for pollinator species richness) and percentage agriculture for three different radii, i.e. 250 m, 500 m and 1000 m, by building GLMMs with a Poisson distribution. All fixed variables were scaled.

For the nine pollinator abundance and the nine pollinator species richness models, we tested the full model for the three different landscape scales and selected that scale for which the model was the most informative, i.e. the model with the lowest AIC-value. If it appeared that more models were equally informative (ΔAIC $\leq$ 2), we looked at the marginal R^2 (method 'delta' (Gold et al., 2020)), i.e. the variance explained by the fixed factors of the model (Nakagawa & Schielzeth, 2013) and chose that model with the lowest AIC and highest marginal R^2. Hence, from the original nine models, we selected three models, one for each pollinator type. This was done for both the abundance and species richness datasets.

IV.   Data assumptions and model validation

Before each of the abovementioned models were constructed, the mean and standard error were calculated for each dataset. Then, we identified any outlier by making a boxplot, and checked whether the response variable (i.e. cover, plant species richness, flower abundance, pollinator abundance and pollinator species richness) was normally distributed by making a histogram, dot chart and Q-Q plot and by performing a Shapiro-Wilk test. The choice for LME or GLMM was based on the outcomes of these tests: LME was used for normally distributed data, while GLMM was used for data with a Poisson distribution (LME: vegetation cover and species richness, GLMM: flower abundance, pollinator abundance and pollinator richness).

To validate the model, the residuals were checked for outliers and normality in the same way as was done for the response variables. However, for the residuals of GLMMs, decisions were mainly based on the outcomes of the following functions of the DHARMa packages: simulateResiduals(), testUniformity(), testOutliers(), testDispersion() (R Core Team, 2024). If excluding outliers did not result in other effects than those from the models with outliers, we decided to leave the outliers in the dataset. Using GLMMs is considered sufficiently good so that no other models (e.g. negative binomial, glmmTMB) had to be constructed. However, if removing outliers did change the outcome, we looked at it case by case and explain the used method in the following section.

5. Results

A. General results

Of the 790 vegetation observations during our fieldwork in late summer, 767 belonged to the herb layer and 23 to the shrub and tree layer. In particular, 710 of these observed plant species, belonging to 187 unique species, are referred to as herb, of which 495 were in bloom and 277 were visited by one or more pollinators. Only two of the eight shrubs, of which we recorded four unique species, were in bloom, with only one being visited by pollinators (i.e. *Rubus idaeus*). None of the fifteen trees, belonging to ten unique species, were flowering at the time of sampling and consequently were not visited by pollinators either. The mean cover for these different layers ranges from 0.5% to 15% (mean ± standard error: 2.43% ± 1.02%) for trees, from 0.5% to 37.5% (5.75 % ± 4.55%) for shrubs and from 0.5% to 62.5% (6.71% ± 0.39) for herbs (grasses excluded). The remaining 57 plant species are grasses and thus wind-pollinated, so we did not investigate them further.

Regarding the habitats, 410 of the vegetation observations including 134 plant species were recorded at the CSA habitat, while the other 380 observations including 113 plant species were recorded at the SNG habitat. Pollinators visited 67 of these different plant species in the CSA habitat, while 49 different plant species were visited in SNG.

Altogether, we collected 2138 individuals belonging to 135 different species. Of all these pollinating insects, 245 were honeybees, 1038 were wild bees belonging to 40 species, 658 were hoverflies belonging to 44 species, 80 were butterflies belonging to eleven species and 117 were wasps belonging 39 species. We recorded 1112 and 1026 individuals belonging to 86 and 99 species on CSA farms and in SNGs, respectively. Looking specifically at wild pollinating insects, i.e. excluding honeybees from the datasets, this amounts to 945 individuals in CSAs and 948 in SNGs. Of these species, 49 were found in both habitat types (honeybees not included), making 36 species unique to the CSA habitat type and 49 to SNGs. Interestingly, species occurring in both habitats tended to occur in higher numbers than species caught only in the CSA or SNG habitat (Figure 7). These results were obtained after removing some outliers (Table 3).
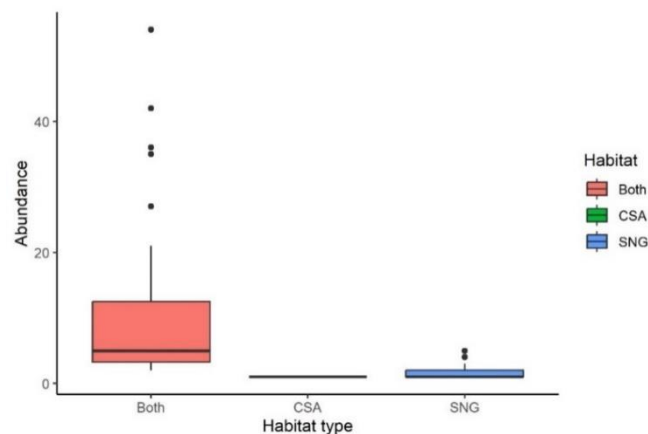
Figure 7: Distribution of abundance of the unique species for both habitats and of the species unique for the CSA and SNG habitat.

Table 3: Outliers for the abundance of the different pollinator species unique for both habitat types or for the CSA and SNG habitat.

Both		CSA		SNG	
Pollinator	**Abundance**	**Pollinator**	**Abundance**	**Pollinator**	**Abundance**
B. lapidarius	108	*Chelonus sp.*	4	*H. truncorum*	7
B. pascuorum	612	*C. panzeri*	2	*M. nigricans*	55
B. terrestris	67	*E. rufipes*	3		
E. arbustorum	81	*E. sepulcharis*	2		
E. nemorum	73	*M. ligniseca*	2		
E. tenax	188	*M. mellinum*	5		
S. scripta	99	*N. podagrica*	5		
		P. albimanus	2		

Just as shown above for the unique species for each habitat type, we detected outliers for the response variable in some cases. To find out whether these outliers considerably affected the results, we also built models where these datapoints were excluded from the dataset. In none of these cases, removing outliers changed the final outcome of a model (Table 14, Supplementary Information). Therefore, we worked with the complete datasets, including the outliers, to investigate the effects of habitat type on the vegetation and pollinators. The only exception is the butterfly abundance dataset. Yet, we decided to retain the outliers and work with the complete dataset. The reason for this is given further.

B. What floral resources do different habitat types provide for pollinating insects in late summer?

The distribution of the cover, species richness and flower abundance of the visited plant species for the two different habitats is visualized in Figure 8. Habitat type has no significant effect on the cover and species richness of visited plant species, while the flower abundance is significantly higher in the CSA habitat compared to SNG (Table 4).

Table 4: Summary of the results of the linear mixed-effect models (LME) and generalized linear mixed-effect models (GLMM) of habitat type on the vegetation cover, species richness and flower abundance for the visited vegetation dataset. The following model statistics are given: F-value for LME or z-value for GLMM (Stat), p-values (p), mean value (Mean) and standard error (SE) per variable for each habitat type.

Response variable	Fixed Variable	Model	Stat	p	Habitat type	Mean	SE
Cover	Habitat type	LME	4.38	0.054	CSA	107.97	7.57
					Nature	80.63	10.84
Species richness	Habitat type	LME	0.0066	0.94	CSA	7.56	0.62
					Nature	7.63	0.60
Flower abundance	Habitat type	GLMM	-111.00	$< 2.2*10^{-16}$	CSA	2505.19	448.39
					Nature	820.56	121.05
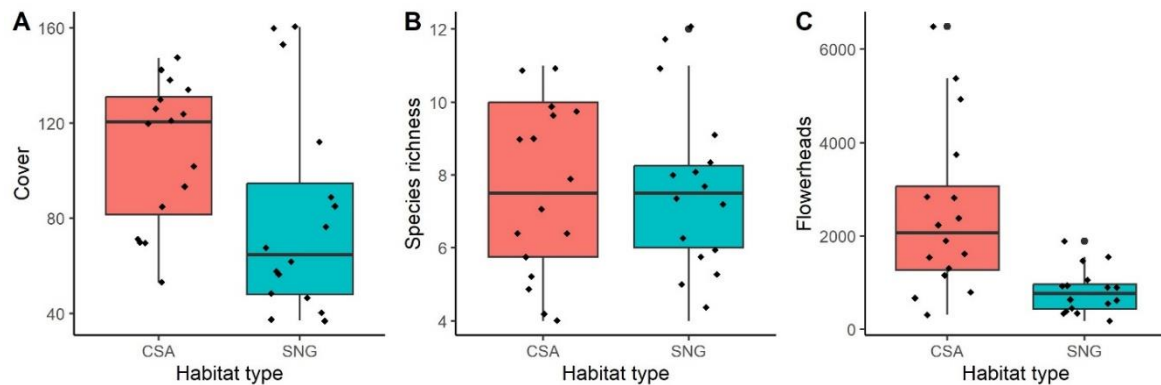
Figure 8: Distribution of the cover (A), species richness (B) and flower abundance (C) of the visited plants for the CSA (pink) and SNG (blue) habitat type.

Between different habitats, the composition of the visited vegetation communities are significantly different both in terms of cover, species richness and flower abundance. Dispersion, however, is only significantly affect by habitat type for the species richness (Figure 9, Table 5).

Table 5: Statistical results of the PERMANOVA-analysis and the corresponding distance measure used for the cover, species richness and flower abundance for the visited vegetation dataset. Centroids refers to the statistical results (F-value, p-value) of the adonis2-function. Dispersion refers to the statistical results (F-value, p-value) of the betadisper-function.

		Centroids		Dispersion		
Data	**Distance measure**	**F**	**p**	**F**	**p**	**Stress**
Cover	Morisita-Horn	3.37	0.0010	0.48	0.50	0.16
Species richness	Jaccard	3.61	0.0010	6.69	0.015	0.15
Flower abundance	Morisita-Horn	3.39	0.0010	0.39	0.54	0.15
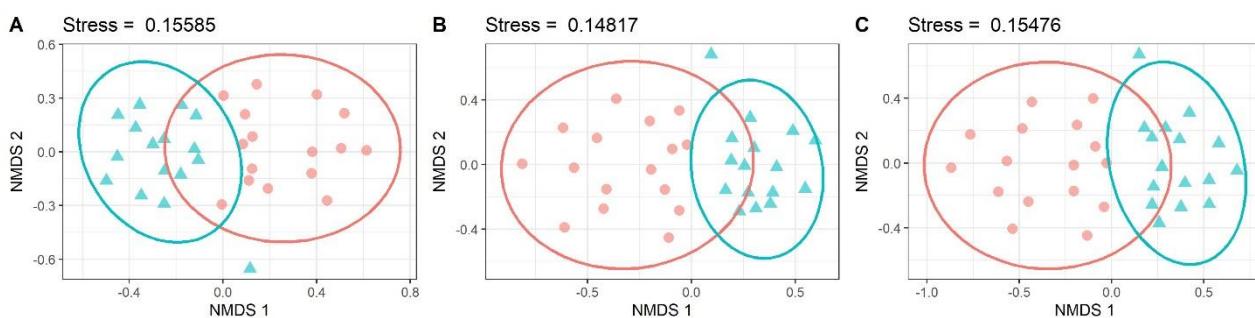
Figure 9: NMDS-plots for the cover (A), species richness (B) and flower abundance (C) of the visited vegetation dataset with the corresponding stress values. Pink circles and corresponding points refer to the CSA habitat. Blue circles and corresponding triangles refer to the SNG habitat.

The indicator analysis revealed that *Galinsoga quadriradiata* (r_{pb} = 0.329, p = 0.00599) and *Phacelia tanacetifolia* (r_{pb} = 0.267, p = 0.04096) can serve as indicator species for the visited vegetation in the CSA habitat. For SNG, these species are *Lotus corniculatus* (r_{pb} = 0.446, p = 0.016), *Heracleum sphondylium* (r_{pb} = 0.381, p = 0.018), *Lythrum salicaria* (r_{pb} = 0.35, p = 0.003), *Cirsium arvense* (r_{pb} = 0.35, p = 0.029) and *Jacobaea vulgaris* (r_{pb} = 0.313, p = 0.042). These species are a subset of the indicator species for the overall flower abundance (Table 17, Supplementary Information)

C. To what extent do different habitat types support communities of wild pollinating insects?

The distribution of the abundance and species richness of the five pollinator datasets for the two different habitats is visualized in Figure 10. Habitat type has only a significant effect on the abundance of butterflies and wasps. Other abundances and species richness for all pollinator types are not significantly different for CSA or SNG (Table 6).

Table 6: Summary of the results of the generalized linear mixed-effect models of habitat type on the pollinator abundance (AB) and species richness (SR). The following model statistics are given: z-value, p-value, mean and standard error per variable for each habitat type.

Response variable	Fixed Variable	z	p	Habitat type	Mean	SE
AB all	Habitat type	0.069	0.95	CSA	59.06	5.22
				Nature	59.25	4.58
AB bee	Habitat type	1.18	0.24	CSA	31.25	3.10
				Nature	33.63	4.61
AB hoverfly	Habitat type	0.24	0.81	CSA	20.38	4.73
				Nature	20.75	3.31
AB butterfly	Habitat type	-2.32	0.020	CSA	3.85	1.67
				Nature	2.14	0.44
AB wasp	Habitat type	-2.12	0.034	CSA	5.31	1.59
				Nature	4.36	0.75
SR all	Habitat type	0.60	0.55	CSA	14.44	1.04
				Nature	15.25	1.42
SR bee	Habitat type	0.97	0.33	CSA	5.25	0.64
				Nature	6.06	0.65
SR hoverfly	Habitat type	0.074	0.94	CSA	5.75	0.78
				Nature	5.81	0.70
SR butterfly	Habitat type	0.57	0.57	CSA	1.31	0.13
				Nature	1.57	0.25
SR wasp	Habitat type	-0.11	0.91	CSA	2.92	0.61
				Nature	2.91	0.56
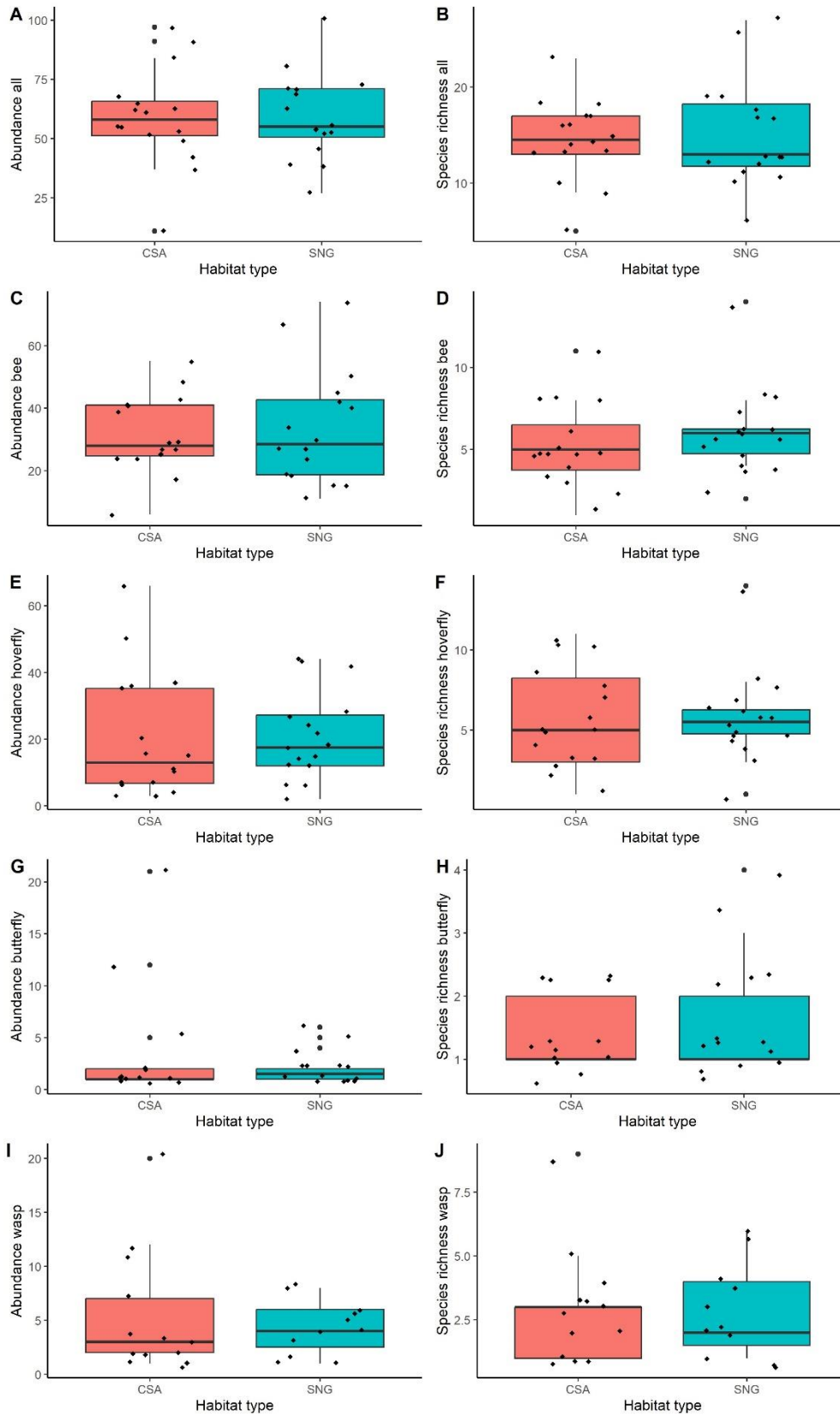
Figure 10: Distribution of the abundance (left) and species richness (right) of all pollinators (A, B), bees (C, D), hoverflies (E, F), butterflies (G, H) and wasps (I, J) for the CSA (pink) and SNG (blue) habitat type.

The composition of the pollinator community, both in terms of abundance and species richness, is significantly different within different habitats, with the abundance of all pollinators being the exception. For the dispersion, habitat type only affects hoverfly abundance and total pollinator species richness significantly (Figure 11, Table 7).
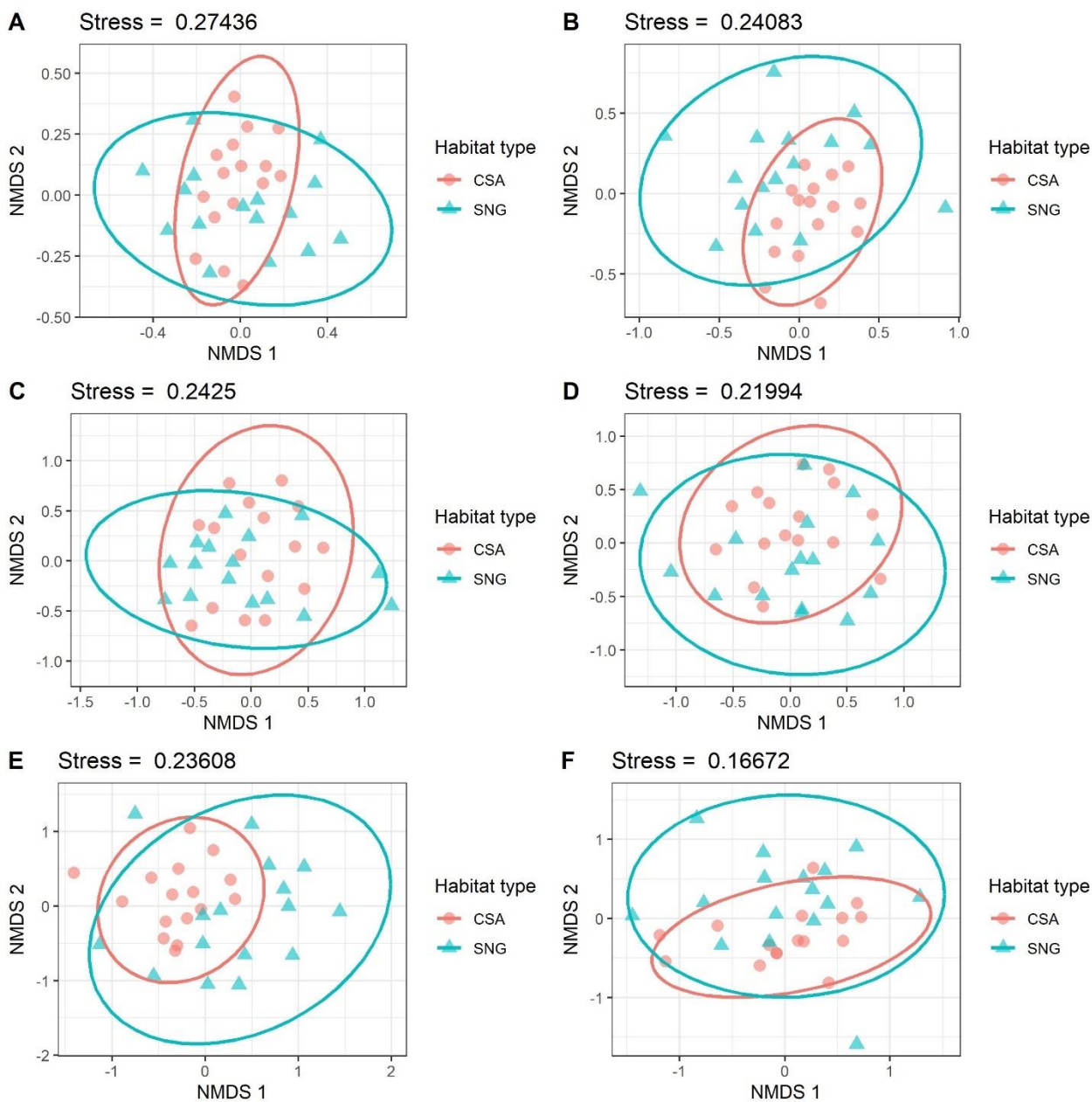
Figure 11: NMDS plots for the abundance (left) and species richness (right) for all pollinators (A, B), bees (C, D) and hoverflies (E, F) with the corresponding stress values. Pink circles and corresponding points refer to the CSA habitat. Blue circles and corresponding triangles refer to the SNG habitat.

Data	Distance measure	Centroids		Dispersion		
		F	p	F	p	Stress
AB all	Morisita-Horn	1.98	0.068	2.98	0.094	0.27
AB bee	Morisita-Horn	2.30	0.018	2.19	0.15	0.24
AB hoverfly	Morisita-Horn	2.91	0.031	5.22	0.030	0.24
SR all	Jaccard	1.82	0.0020	4.58	0.041	0.24
SR bee	Jaccard	2.03	0.0090	0.69	0.41	0.22
SR hoverfly	Jaccard	1.87	0.021	1.97	0.17	0.17

Results of the indicator analysis show that the indicator species for CSA habitats are *Hylaeus communis* (r_{pb} = 0.379, p = 0.05), *Syritta pipiens* (r_{pb} = 0.376, p = 0.026) and *Pieris rapae* (r_{pb} = 0.341, p = 0.027). For SNGs, these species are *Melitta nigricans* (r_{pb} = 0.411, p = 0.002), *Helophilus pendulus* (r_{pb} = 0.389, p = 0.027) and *Eristalis nemorum* (r_{pb} = 0.356, p = 0.036). Regarding bee and hoverfly abundances, the same species serve as indicator species.

Although honeybees were excluded from the datasets relating to the abundance (and species richness) of all pollinators and bees, we include the results regarding honeybee abundance here for completeness. First, we should mention that the abundance of honeybees is not correlated with the abundance of all pollinators (Spearman rank correlation, ρ = -0.0041, p = 0.98) and bees (ρ = 0.022, p = 0.91). Next, based on the data visualization, we already assume that honeybee abundance is higher for the CSA habitat compared to the SNG habitat (Figure 12). Indeed, the minimum and maximum honeybee abundance in the CSA habitat ranges from 1 to 35 (11.13 ± 2.30), while it only ranges between 1 and 23 (6.00 ± 1.77) in the SNG habitat. These assumptions were confirmed by building a GLMM: habitat type has a significant effect on honeybee abundance (z = -4.72, p = 2.34*10^{-6}), with the CSA habitat supporting higher abundances compared to the SNG habitat.

Figure 12: Distribution of the honeybee abundance for the CSA (pink) and SNG (blue) habitat type.

D. What is the influence of the floral resources and the surrounding landscape on pollinator?

The best models for pollinator abundance are those at the 1000 m scale for all pollinators and bees, and at the 250 m scale for hoverflies, since these models have the lowest AIC-value. Both for all pollinators and hoverflies, we found other models that were equally informative: the abundance of all pollinators at 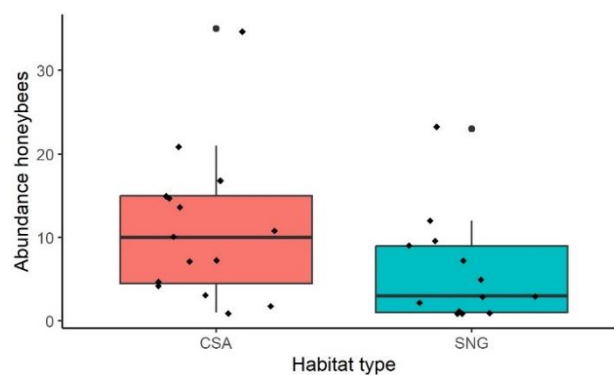the 250 m scale and the abundance of hoverflies at the 500 m scale. However, these models had a lower marginal R² (Table 18, Supplementary Information). Therefore, we only focused on the first three mentioned best models and checked if removing outliers had a significant effect on the outcome. And indeed, removing outliers from the models regarding the abundance of all pollinators and bees changed the effect of percentage agriculture from being significant to non-significant (Table 19, Supplementary Information).

Although model validation of the models with outliers showed no problems, there were quantile deviations detected for the residuals of the model for all pollinators at the 1000 m scale. None of the other tests suggested any other problems. Excluding outliers from the dataset solved the problem of quantile deviations, but testing for uniformity now resulted in a significant deviation. However, the residuals of the DHARMa package are considered to have a uniform distribution (Hartig, 2022), but visualisation and normality testing revealed that the residuals here are normally distributed. Hence, we decide to continue working with the dataset without outliers. Quantile deviations were also detected for the residuals of the bee abundance model at the 1000 m scale, albeit to a lesser extent than for the abundance model of all pollinators. Removing the outliers in the dataset, resolved all problems with the residuals. Besides, given the fact that there were no residual outliers detected, we decided to work with the dataset without outliers. Since there were no outliers present in the hoverfly abundance dataset, we had only one dataset to work with. The output of the best models for pollinator abundance we used, is given below (Table 8).

Regarding species richness, the best models with the lowest AIC are those at the 1000 m scale for all pollinators and bees and at the 500 m scale for hoverflies. For bee and hoverfly species richness, other models were also informative, i.e. the model at the 500 m scale for bee richness and the models at the 250 m and 1000 m scale for hoverflies. However, because of their lower marginal R², we decided to work with the first three mentioned best models (Table 18, Supplementary Information). For the richness of all pollinators, quantile deviations were detected, but they disappeared after removing the outliers. The residuals of the hoverfly richness model, too, showed quantile deviations, but these remained after removing outliers. Bee richness residuals had no quantile deviations. In none of the cases, however, did removing outliers have a significant effect on the outcome (Table 20, Supplementary Information). Therefore, we decided to retain the outliers. The results are given in Table 8.

Table 8: Summary of the results of the best generalized linear mixed-effect models of flower abundance or vegetation richness and percentage agriculture on the pollinator abundance (AB) and species richness (SR). For each model, the ΔAIC (difference between the AICs of the best and second best model), marginal R², model estimate, z-value and p-value are given.

Response variable	Scale	ΔAIC	R² (m)	Flower abundance/ vegetation richness			Percentage Agriculture		
				Estimate	z	p	Estimate	z	p
AB All	1000	0.9	0.17	0.053	1.97	0.049	0.062	1.46	0.14
AB Bee	1000	2.3	0.14	0.082	1.71	0.087	0.14	1.58	0.11
AB Hoverfly	250	2.0	0.18	0.20	3.48	0.00051	-0.23	-3.35	0.00080
SR All	1000	2.1	0.095	-0.053	-0.93	0.35	0.10	1.59	0.11
SR Bee	1000	1.6	0.083	-0.023	-0.25	0.81	0.15	1.49	0.14
SR Hoverfly	500	0.2	0.018	0.012	0.14	0.89	-0.062	-0.74	0.46

Neither the vegetation richness nor the percentage of agriculture significantly affect the species richness of all pollinators, bees and hoverflies. These parameters also have no significant effect on the abundance of bees. However, flower abundance significantly positively affects the abundance of all pollinators and hoverflies. The percentage of agriculture, on the contrary, has a significant negative effect on the hoverfly abundance (Figure 13). Visualisation of the non-significant relationship between flower abundance or vegetation richness and percentage agriculture on the one hand and pollinator abundance or richness on the other, is given in Figure 19 and Figure 20 (Supplementary Information).
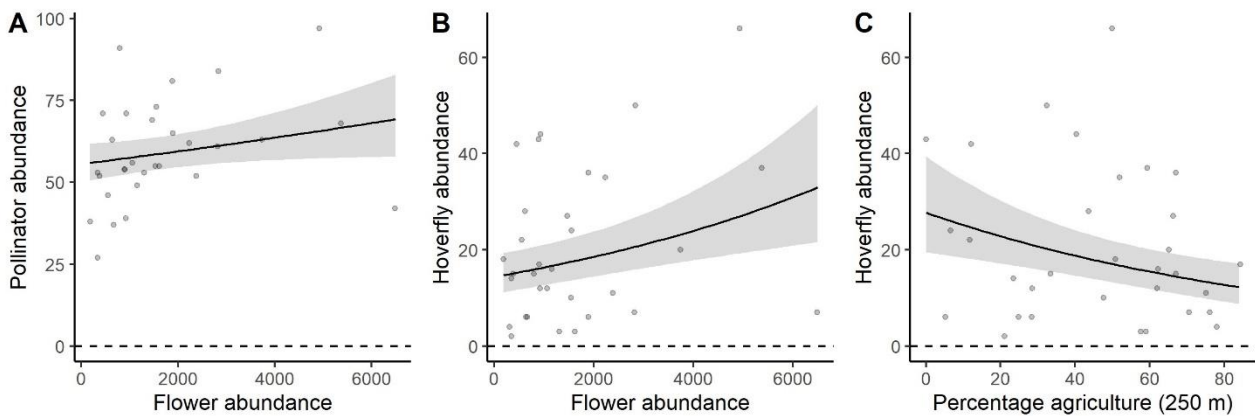
Figure 13: Relationship between the fixed variables flower abundance (A, B) and percentage agriculture (C) and the abundance of all pollinators (A) and hoverflies (B, C). The solid lines represent the significant relationship, the grey shaded area the 95 % confidence interval and the black points the raw data.

6. Discussion

A. What floral resources do different habitat types provide for pollinating insects in late summer?

In late summer, SNGs are of great importance for pollinators, since these habitat types provide pollinating insects with floral resources, which are scarce in other habitats (Ammann et al., 2024; Timberlake et al., 2019). However, at the time of doing fieldwork, many crops and other plants on the CSA farms were still in bloom, suggesting that this habitat type too can provide floral resources to meet the needs of pollinators in late summer. Indeed, vegetation cover and species richness in CSAs was similar to the cover and species richness in SNGs. More so, across the sampling landscapes, the total number of plant species visited by pollinators was even higher in CSAs (67) than in SNGs (49).

Although being characterized by a similar cover and species richness, CSAs and SNGs differ in their flower abundance. By looking at the ten most flower abundant plant species visited by insects, it is clear that the flower abundance in the CSA habitat (Table 21, Supplementary Information) exceeds the flower abundance in SNGs (Table 22, Supplementary Information). Therefore, one could argue that CSAs provide more floral resources during late summer than SNGs. However, it appears that for both habitat types the vast majority of plant species only contribute to a limited extend to the total flower abundance of that habitat type, while only a few species are characterized by an extremely high number of flowerheads (Figure 14, Figure 15).
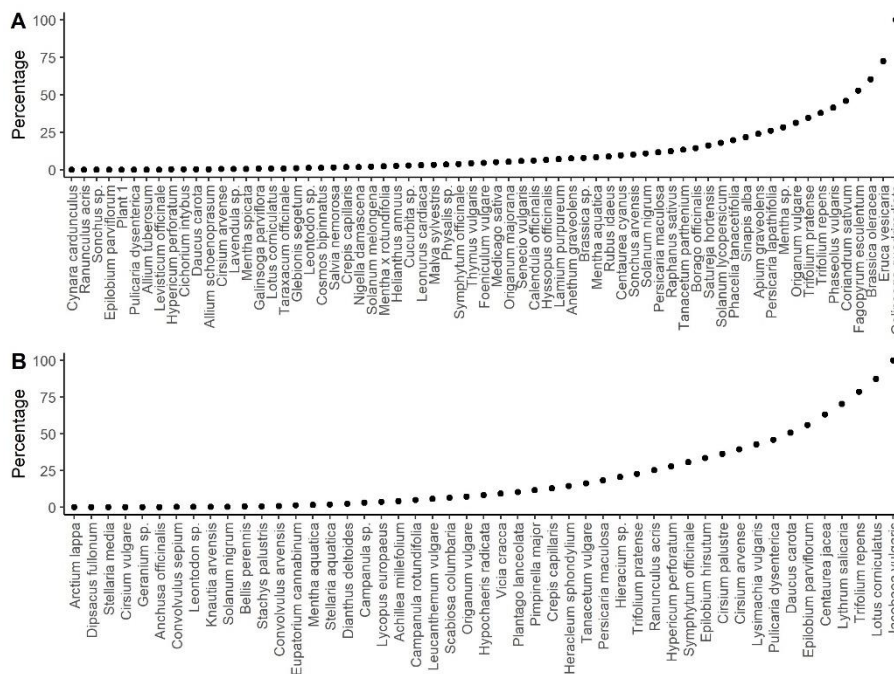
Figure 14: Contribution of all plant species to the floral resource provisioning for the CSA habitat (A) and the SNG habitat (B). Each point shows the cumulative contribution of each plant species, calculated as the mean flower abundance for that plant species by the overall mean flower abundance for that habitat type. Non-presence was taken into account by dividing the mean flower abundance of a plant species by sixteen (number of sampling sites).
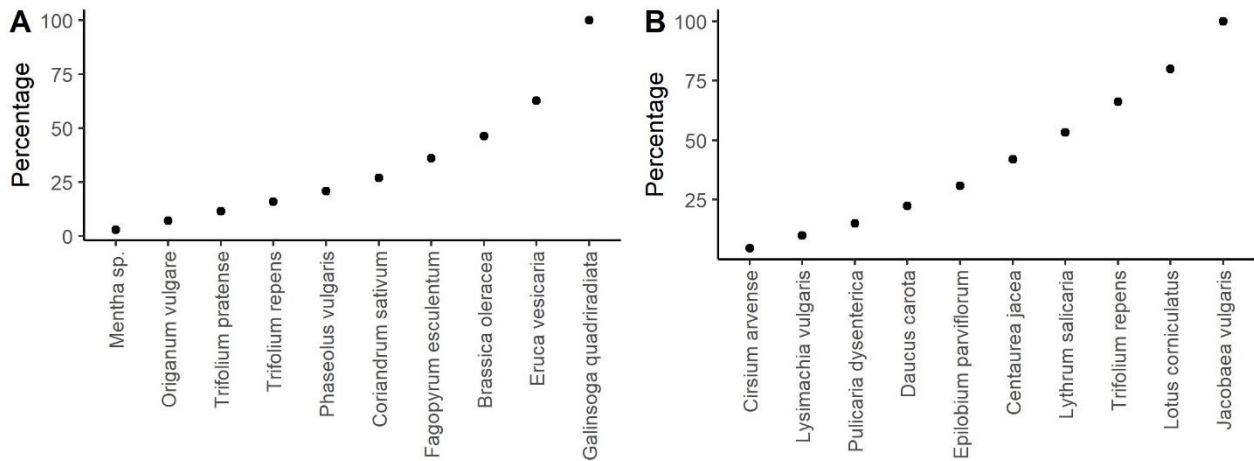
Figure 15: Contribution of the ten most flower abundant plant species to the floral resource provisioning for the CSA habitat (A) and the SNG habitat (B). Each point shows the cumulative contribution of each plant species, calculated as the mean flower abundance for that plant species by the overall mean flower abundance for that habitat type. Non-presence was taken into account by dividing the mean flower abundance of a plant species by sixteen (number of sampling sites).

But does a higher flower abundance also mean more flower visitors? The last column of Table 21 and Table 22 (Supplementary Information) already suggests that this is not the case. Indeed, pollinator abundance and species richness does not significantly differ between the two habitat types. Therefore, it is important not only to take the flower abundance of each habitat into account. The nutritional value is another important element of plants with regards to providing floral resources for pollinators, which can be derived from their nectar and pollen production. Indeed, although flower abundance exerts a strong influence on it, mainly the quality of the nectar determines flower selection by pollinators (Fowler et al., 2016). To investigate this, the FloRes database (Baden-Böhm et al., 2022) was consulted for the ten most flower abundant plant species. The volume of nectar produced per flower ranges from $4.18*10^{-5}$ ml to $5.80*10^{-3}$ ml for the CSA vegetation and from $1.53*10^{-5}$ ml to $3.24*10^{-2}$ ml for the SNG vegetation. The amount of pollen produced by plants in the CSA habitat lies between $7.03*10^{-3}$ mg and 1.15 mg, while this lies between $1.09*10^{-1}$ mg and 3.39 mg for the plants in SNGs (Table 21 and Table 22, Supplementary Information).

Based on these numbers, the nectar supply seems quite similar for both habitat types, while SNGs provide more pollen for pollinators than CSAs do. However, these values only represent the amount of nectar and pollen produced by one flower or inflorescence. Multiplying these values with the number of flowers for the different plant species, which is higher for CSAs compared to SNGs, could result in CSAs providing as much as or even more nectar and pollen compared to SNGs. Yet, this conclusion should be interpreted with caution, as only the ten most flower abundant plants were considered for each habitat, and both nectar but especially pollen data is lacking for certain species. Therefore, quantifying nectar and pollen production for the plant species recorded during fieldwork and including this information in the analysis could provide more insight into what factors drive pollinators to visit flowers.

In response to the lack of information on the quantity, quality and timing of pollen availability and the consequent lack of knowledge on how to improve food supply for pollinators, Wright et al. (2024) examined the production of plant pollen at the farm scale. They found that hedgerows provide the highest quantity of pollen per square metre unit area, followed by field margins and woodland. In contrast, pastures provided the smallest amount at this scale. This order, however, reversed when looking at the level of the whole farm (pasture > woodland > hedgerows > field margins), which can be explained by the small proportion of the land occupied by hedgerows compared to the large area occupied by pastures (Wright et al., 2024). Additionally, despite the quite effective way of flower strips and hedgerows at providing nectar and pollen, the uptake of these management practices does not always run smoothly (Eeraerts et al., 2020). Therefore, not only management practices in the form of hedgerows and field margins, but also the improvement of existing habitat such as pastures are crucial to improve the availability of resources for pollinators on farms (Wright et al., 2024).

Although SNGs and pastures are not the same, both in composition and management, it can be assumed that the findings just described also apply to SNGs. This implies that, because they are widespread in the landscape, these habitats are an important provider of floral resources, even if the amounts of nectar and pollen produced are low. And indeed, despite the generally lower levels of nectar available in late summer, SNGs are of great importance regarding nectar provisioning for pollinating insects at that time (Timberlake et al., 2019). Besides, research showed that the phenology of pollen supply is similar to that of nectar supply at a landscape level, since flower abundance in the landscape drives the availability of both resources (Wright et al., 2024). This implies that SNGs are also important pollen providers in late summer. Linking back to the findings of this thesis, this means that the high flower abundance at CSAs together with the correlation between flower abundance on the one hand and pollen and nectar production on the other, make these habitats at least as valuable as SNGs when it comes to providing floral resources. In addition, the crop diversification on these farms can be considered as another way of creating habitats for pollinators next to the implementation of hedgerows and field margins, making CSAs a possible important strategy for conservation management.

However, it is important to notice that the focus so far has been exclusively on floral resources and that the extent to which the CSA habitats can provide nesting opportunities has not been considered. It is already quite well known of SNGs that they provide important nesting sites in addition to floral resources. For instance, higher bumblebee species richness and density were found in linear habitats (i.e. "uncultivated strips of perennial grassland vegetation situated either between two cultivated fields or between a cultivated field and a road") close to grasslands compared to linear habitats at least 1 km away from this semi-natural habitat (Öckinger & Smith, 2007). According to the authors, this might be due to the presence of a higher number of suitable nesting sites in these grasslands compared to linear habitat elements or cultivated fields in the surrounding area.

Although SNG are thus of great importance, agricultural habitats can also play a role in providing nesting sites. Indeed, small-scale habitat restoration in intensive agricultural areas in the form of hedgerows, or the presence of trees and shrubs in general, promotes the occurrence of pollinator species with more specialized habitat requirements, such as cavity nesting bees (Kremen & M'Gonigle, 2015; Ponisio et al., 2016). But not only the presence of such elements as part of habitat

restoration is beneficial for pollinators. Agroforestry, one of the possible agricultural diversification practices, leads to similar results: adding single trees to an open landscape provides nesting potential for cavity nesting species (Kay et al., 2020). On-farm diversification is thus beneficial for meeting the floral resource needs of pollinators, as shown by the results of this thesis, and possibly also in terms of providing nesting opportunities.

Yet, based on the information provided in *Nederlands Soortenregister* (Naturalis, n.d.) and *Species Biodiversity Ireland* (National Biodiversity Data Centre, n.d.) and considering the species unique for the CSA habitat, SNG habitat or occurring at both habitats, the number of cavity nesting species appears to be rather low in general (Table 9). Gathering information regarding nesting habitats, however, was not the main focus of this study, so further research should investigate if there is a difference between both habitats regarding nesting behaviour.

Table 9: Nesting behaviour of the unique bee species for the CSA habitat, SNG habitat or both habitats. If species are not ground or cavity nesting, they are referred to as 'Other' with their corresponding nesting behaviour between brackets.

	Ground nesting	Cavity nesting	Other
CSA	*Andrena minutula* *Andrena nigrospina* *Lasioglossum leucopus* *Lasioglossum malacharum* *Lasioglossum zonulum*	*Megachile ligniseca*	*Bombus hypnorum (aerial nester)*
SNG	*Andrena rosae* *Dasypoda hirtipes* *Halictus rubicundus* *Lasioglossum punctatissimum* *Lasioglossum sexnotatum* *Macropis europaea* *Melitta leporine* *Melitta nigricans*	*Ceratina cyanea* *Chelostoma campanularum* *Heriades truncorum*	*Megachile willughbiella (ground & cavity)* *Sphecodes pellucidus (cleptoparasite)*
Both	*Andrena dorsata* *Andrena flavipes* *Colletes daviesanus* *Halictus tumulorum* *Lasioglossum calcaetum* *Lasioglossum fulvicorne* *Lasioglossum laticeps* *Lasioglossum leucozonium* *Lasioglossum morio* *Lasioglossum pauxillum* *Lasioglossum villosulum*	*Anthidium manicatum* *Hylaeus communis* *Megachile centuncularis*	*Bombus lapidarius (ground & underground cavity)* *Bombus pascuorum (below & above ground)* *Bombus terrestris (ground & underground cavity)* *Sphecodes monilicornis (cleptoparasite)*

Another important result is that the two habitat types differ in their vegetation composition. Indicator species for the visited vegetation in the CSA habitat are *Galinsoga quadriradiata* and *Phacelia tanacetifolia*, while *Lotus corniculatus*, *Heracleum shondylium, Lythrum salicaria*, *Cirsium arvense* and *Jacobaea vulgaris* can be considered indicator species for SNGs. Hence, because these two habitat types are characterized by different plant species, both habitat types can be considered to be complementary. Certain agricultural habitats have already been mentioned with regard to habitat complementarity, such as mass-flowering orchard crops or small fruit fields (Eeraerts, Van Den Berge, et al., 2021; Martins et al., 2018), but flower production of these types of agriculture

mainly occur in spring. Hence, the findings of this are amongst the first to illustrate that agriculture can also complement habitats in the provision of floral resources for pollinators in late summer, provided they are characterised by strong crop diversity.

Yet, in addition to crop diversity, the presence of non-crop plants also appears to be important. For example, both *Trifolium repens* and *T. pratense* belong to the ten most flower abundant plant species in the CSA habitat, with *Galinsoga quadriradiata* even being the plant species with the highest number of flowers. Some of these non-crops are intentionally sown, e.g. *Sinapis alba* and *Phacelia tanacetifolia* as green manures or *Centaurea cyanus* as part of a flower mixture for field margins. However, other species such as *Persicaria lapathifolia*, *Persicaria maculosa*, *Sonchus* sp., *Solanum nigrum, Cirsium arvense,* etc. are considered weeds. Indeed, weeds in crop fields have been proven to contribute to the abundance of many flower visitors by providing resources (Aviron et al., 2023). In addition, tolerating weeds such as *Jacobaea vulgaris* and *Cirsium arvense* may also be more beneficial for flower-visiting insects compared to sowing wildflower seed mixes. Interestingly, the cost for controlling these 'injurious weeds' is lower than the subsidies spent on planting flower species which thus have been proven to support less biodiversity (Balfour & Ratnieks, 2022). Yet their potential remains questionable because of their impact on crop yields for which they are in most cases eliminated completely. Hence, one should explore alternative weed management possibilities that support pollinator populations without comprising crop yields and income for farmers (Aviron et al., 2023; Balfour & Ratnieks, 2022).

Overall, the results confirm that CSAs can provide floral resources for pollinators in late summer. Here, CSA was used as a broad, umbrella term for a variety of (small-scaled) farming principles of which crop diversification was the most important. In practice, a far-reaching form of intercropping is applied on these farms and crops are regularly alternated with cover crops or green manures in an appropriate rotation. Moreover, trees and/or shrubs are often present on or along the field. Hence, given the wide variety of crops and non-crops together with their different flowering phenology, the CSA habitat might not only complement other habitats in late summer, also provide complementary floral resources in spring and early summer. Harrison et al. (2018) already demonstrated that bee abundance and richness are fairly evenly distributed throughout between April and September in agricultural landscapes. Yet, this will probably depend on which and how many types of crops and cultivars are grown on these farms and on their phenology. Future research should thus be carried out to confirm this hypothesis. In addition, when performing more research into this topic, it would be interesting to not only consider SNG as other habitat type, but also agricultural habitat uses such as maize fields that do not depend on insect pollination (Richards, 2001) or apple or cherry orchards which are mass-flowering crops providing floral resources at the beginning of the pollinators' active period (Eeraerts, Van Den Berge, et al., 2021).

B. To what extent do different habitat types support communities of wild pollinating insects?

Overall, almost exactly the same number of wild pollinators was caught in the CSA compared to the SNG habitat during the entire period of fieldwork, with species richness being in the same order of magnitude for both habitat types. Model building confirmed this statement by showing that, both in terms of abundance and species richness, the CSAs support pollinator communities to the same

extent as SNGs do. In other words, these types of farms, with their high levels of crop diversity, can support pollinator communities in late summer just like SNGs.

Butterfly and wasp abundance, however, were the two exceptions for which this statement does not hold (Table 14, Supplementary Information). For wasp abundance, the effect of habitat type is significant and remains significant by removing outliers. Sixty-nine individuals were caught in the CSA habitat and only 48 in the SNG habitat. Removing the datapoints from Ranst (the outlier datapoint) coincided with removing 20 datapoints, leaving only 49 datapoints left for the CSA. Still, the outcome remains the same, which is quite unexpected. Maybe this follows from the fact that after removing the outlier, the number of locations where wasps were caught is still higher for CSAs (12) compared to SNGs (11) and that the highest abundances at a certain CSA-location are 12 and 11, while this amounts only to 8 for the SNG locations.

For the butterfly abundance dataset, removing the outliers led to different results: while the effect of habitat type on butterfly abundance was significant in the dataset with outliers, this effect became non-significant by excluding these datapoints. A possible explanation can be found in the size of this dataset, which is much smaller than those of the other pollinator types. Besides, *Pieris* spp. strongly influence the outcome. Indeed, additional calculations revealed that 42 from the 80 individuals caught belong to *Pieris rapae*, six to *P. napi*, five to *P. brassicae* and eleven to *Pieris* spp., with the remaining sixteen individuals belonging to seven species. In other words, 80% of the complete dataset consists of species from the *Pieris* genus. When the outliers are removed, seventeen of the 27 individuals (63%) belong to one of the four *Pieris* species, leaving ten butterflies of five different species in the remaining dataset. Results regarding butterfly and wasp abundance should thus be interpreted with caution. Moreover, to better assess the effects of habitat type on these taxonomic groups, other protocols may be needed (e.g. Pollard Walk for butterflies).

The dominance of *Pieris* sp. is also reflected in the pollinator community composition. Despite the abundance and richness of pollinators being equal, their community composition differs between the two habitat types (cfr. Harrison et al. (2018)). This implies that the complementary resources provided by these habitats are used by different pollinator communities. Indeed, the indicator analysis reveals that *Hylaeus communis*, *Syritta pipiens* and *Pieris rapae* can serve as indicator species of CSAs, while *Melitta nigricans*, *Helophilus pendulus* and *Eristalis nemorum* fulfil this role for SNGs. These results add to the findings of Maurer et al. (2022), who discovered that different habitat types, i.e. extensive meadows, flower strips, hedgerows and intensive meadows, and forest edges harbour a relatively unique set of species. Hence, they suggest that these semi-natural habitat types, each providing complementary niches, contribute to diverse wild bee meta-communities in the agricultural landscape. Based on the results of this thesis, CSAs may be added to this list of important habitat types for pollinators. More so, just like (more continuous rather than young) flowering fields have been found to function synergistically with calcareous grasslands if provided simultaneously in the landscape (Boetzl et al., 2021), CSA farms and semi-natural grasslands too can function synergistically, hence maximizing benefits for biodiversity.

Interestingly, the SNG indicator species Melitta nigricans is known to be an oligolectic bee species. This relates to the hypothesis that, regarding their feeding habitat, the natural habitat provides more resources for specialist wild pollinators and that the CSA farms, although being characterized by a high crop diversity, harbour mostly generalist species. To answer this question, two databases

were consulted, i.e. *Nederlands Soortenregister* (Naturalis, n.d.) and *Species Biodiversity Ireland* (National Biodiversity Data Centre, n.d.), which both provide information about the feeding habitat of different pollinating insects, among others. This information regarding bee feeding habitat, is given in Table 10 and
Table 11.

Table 10: Polylectic bee species caught in the CSA, SNG or both habitats. The total number of individuals of each species caught is given between brackets.

	Polylectic
CSA	*Andrena minutula* (1)*, Andrena nigrospina* (1)*, Bombus hypnorum* (1)*, Lasioglossum leucopus* (1)*, Lasioglossum malacharum* (1)*, Lasioglossum zonulum* (1)*, Megachile ligniseca* (2)
SNG	*Andrena rosae* (1)*, Ceratina cyanea* (1)*, Halictus rubicundus* (3)*, Lasioglossum punctatissimum* (1)*, Lasioglossum sexnotatum* (3)*, Megachile willughbiella* (3)*, Sphecodes pellucidus* (1)
Both	*Andrena dorsata* (4)*, Andrena flavipes* (3)*, Anthidium manicatum* (5)*, Bombus lapidarius* (108)*, Bombus pascuorum* (612)*, Bombus terrestris* agg. (67)*, Halictus tumulorum* (2)*, Hylaeus communis* (36)*, Lasioglossum calcaetum* (5)*, Lasioglossum fulvicorne* (7)*, Lasioglossum laticeps* (4)*, Lasioglossum leucozonium* (13)*, Lasioglossum morio* (5)*, Lasioglossum pauxillum* (6)*, Lasioglossum villosulum* (2)*, Megachile centuncularis* (5)*, Sphecodes monilicornis* (5)

Table 11: Oligolectic bee species caught in the CSA, SNG and both habitats. The total number of individuals of each species caught is given between brackets.

	Oligolectic
CSA	/
SNG	*Chelostoma campanularum* (3)*, Dasypoda hirtipes* (3)*, Heriades truncorum* (7)*, Macropis europaea* (4)*, Melitta leporine* (5)*, Melitta nigricans* (55)
Both	*Colletes daviesanus* (27)

Seven bee species are unique for the CSA habitat, all being polylectic species. From the thirteen unique SNG species, seven are polylectic and the other six are oligolectic. Of all bee species that were present in both habitat types, only one is considered oligolectic while the remaining seventeen have a polylectic feeding habitat (Table 10,
Table 11). From this, it appears that specialists prefer the SNG habitat and that CSAs are mainly characterized by a generalist pollinator population, which matches previous research findings. Indeed, the majority of solitary bees species occurring in reasonable numbers on agricultural land are polylectic and exploit a wide variety of flowering plants. Moreover, the species found on the largest number of farms are those with the widest diet breadth, probably because they are able to extract pollen from a wide range of plant species (Wood et al., 2016). On the contrary, extensively managed meadows, which out of simplicity are assumed to exhibit the same properties as the SNGs under investigation here, sustain high abundance and diversity of wild bees, specialists and rare species in particular (Maurer et al., 2022).

Nevertheless, research revealed that on-farm diversification in the form of polyculture farms can serve as an important refuge for specialist bees and other pollinators that may be adversely affected by floral resource simplification due to monoculture agriculture (Guzman et al., 2019). The reason why no specialists were found in the CSAs anyway, is probably because most crops present in this habitat type are not characterised by specialist pollinators, which was the case in the study of Guzman et al. (2019), i.e. squash with specialist pollinator genera *Peponapis* and *Xenoglossa*.

Therefore, cultivating more 'specialist' crops and non-crops could positively influence specialist bee species more in the CSA habitat than in monocultures of this crop. Cultivating blueberry, for instance, could be beneficial for the bilberry mining bee *A. lapponica* (Naturalis, n.d.). Additional research should be performed to confirm or disprove this hypothesis.

C. What is the influence of the floral resources and the surrounding landscape on pollinator?

Two parameters were tested to investigate the effect of the local and landscape level resources, i.e. the flower abundance or vegetation species richness (for the pollinator abundance and richness respectively) and the effect of the percentage agriculture in the surrounding area. Butterfly and bumblebee densities have been shown to increase with increasing floral abundance (Öckinger & Smith, 2007) and also hoverfly abundance appears to be mainly determined by resource quantity factors such as the amount of floral resources (Meyer et al., 2009; Moquet et al., 2018). These findings are also reflected in the results found here, showing the significant positive effect of flower abundance on pollinator and hoverfly abundance. Most probably, this is because flower abundance largely determines pollen and nectar supply, the two essential resources for pollinating insects (Wright et al., 2024). In contrast, a significant negative effect was found for the percentage agriculture in the surrounding area on hoverfly abundance.

A higher proportion agriculture in the surrounding landscape can be related to a higher degree of landscape simplification. Indeed, here, at the most informative scale for hoverfly abundance, i.e. 250 m, the percentage of agriculture is correlated with the cover of certain arable crops (e.g. Spearman's rank correlation for potato: $\rho = 0.54$, $p = 0.032$; grains & beans: $\rho = 0.50$, $p = 0.047$; maize: $\rho = 0.60$, $p = 0.013$). This arable crop cover has been shown to negatively affect bee and hoverfly richness. In particular, increasing the arable crop cover from 30% to 80% caused a pollinator species loss of 20% (Maurer et al., 2024). However, as there are not many studies that examine the direct effect of the amount of agriculture on hoverfly populations, attention goes to research that investigates the effect of the proportion of semi-natural habitat, which is assumed to decreases with more agriculture in the area.

Both the quality and quantity of semi-natural habitat patches seem to determine the quality of the agricultural landscape for flower-visiting insects like hoverflies (Boetzl et al., 2021; Jauker et al., 2009; Kleijn & van Langevelde, 2006; Meyer et al., 2009; Moquet et al., 2018; Proesmans et al., 2019). On the one hand, hoverfly species richness was found to be positively influenced by the area of semi-natural habitat but only when flower abundance exceeded a certain minimum level, while the positive effect of flower abundance only applies in areas with a relatively high proportion semi-natural habitat (Kleijn & van Langevelde, 2006). Hoverfly density, however, appears to be not affected by the amount of semi-natural habitat (Boetzl et al., 2021). Many hoverfly species are in fact generalists and some have been shown to survive in agricultural landscapes or even play an important role in the maintenance of pollination services in these habitats which may have become unsuitable for bees (Jauker et al., 2009; Proesmans et al., 2019). This is possibly because even the presence of small grassland plots and scarce flower resources along field margins can support a variety of hoverfly species (Jauker et al., 2009).

These findings, however, do not explain the significant negative effect of agricultural percentage on abundance and the lack of significance with regard to richness of hoverflies. A possible explanation can be found in the type of semi-natural habitats. For instance, forest fragments are of great importance for hoverflies, especially for aphidophagous species and specialists. Indeed, hoverfly abundance and species richness have been shown to decrease with the distance to forests, which may be related to the role of these forests as an important larval habitat (Meyer et al., 2009; Moquet et al., 2018; Proesmans et al., 2019). If a higher proportion of agriculture results in less semi-natural habitat such as forest fragments, this can explain why the former one has a negative impact on hoverfly populations. However, different studies regarding hoverflies do not always (completely) agree with each other. Moreover, since different parameters are used in these studies (e.g. the proportion of semi-natural habitat instead of the percentage agriculture) and the effects are not always tested on the response variables investigated in this thesis (e.g. the effect flower abundance on hoverfly richness instead of hoverfly abundance), it is difficult to measure the results of this thesis against them. Therefore, the effect of floral resources and the surrounding area on hoverfly populations should be interpreted with care. Further analyses which also account for the gradient in semi-natural habitats and for the interaction between flower abundance and the proportion semi-natural habitats may provide more information.

Contrary to the expectations, however, the effect of agriculture on the abundance and species richness of all pollinators and bees is non-significant. Regarding these findings, it is important to notice that certain parameters, such as field size, were not taken into account, since the knowledge on what information is included in this parameter does not suffice to understand its possible effects. Yet, these parameters, field size in particular, can be of great importance. Sirami et al. (2019) demonstrated that lowering the mean field size from 5 to 2.75 ha resulted in a similar effect on multitrophic diversity as an expansion of semi-natural cover from 0.5 to 11% of the landscape. The maximum mean field size recorded here, was 2.30 ha and was measured within the 250 m radius. Within the 1000 m radius, the maximum mean field size only amounted to 1.34 ha, which implies that all mean field sizes are already below the size proposed by Sirami et al. (2019). Hence, the small-scale nature of the farms considered in this study, together with the relatively large proportion of edge vegetation and the high degree of crop diversity, might ensure that the abundance and species diversity of bees, and by extension all pollinators, decreases little or even not at all. This can be related to the findings of (Batáry et al., 2011), which demonstrate that agri-environmental management improves species richness only in simple, but not in complex croplands. Since the landscapes here have a rather high complexity (Figure 21, Supplementary Information), they probably already harbour relatively diverse pollinator communities.

Interestingly, the effects of the landscape complexity parameters differ for bees and hoverflies. The main reason can be found in the different breeding strategies of both pollinator types. Indeed, while hoverflies may disperse widely across the landscape because they are not restricted to single nest sites, bees collect pollen and nectar for their offspring and return to their brood cells repeatedly after foraging (Jauker et al., 2009; Kleijn & van Langevelde, 2006). Moreover, these foraging ranges are the highest for highly eusocial species (e.g. *Apis* spp.), lower for primitively eusocial (e.g. *Bombus* spp.) and solitary species. For bumblebees, these distance amounts to approximately 1000 m, while solitary bees forage no further than 300 m (Kendall et al., 2022). That the best models for bees are those at the 1000 m scale, is presumably because of the large numbers of bumblebees: 788 of the 1038 belong to one of the four *Bombus* species, i.e. *B. pascuorum* (612),

B. lapidarius (108)*, B. terrestris* agg. (67) and *B. hypnorum* (1). However, based on their wider dispersion capacity, the landscape effects might be expected to also be evaluated at the 1000 m scale for hoverflies. Yet, the best models are those at the 250 m scale for abundance and at the 500 m scale for richness, which is rather unexpected (cfr. Jauker et al. (2009)).

The effects of the two parameters thus differ for different pollinator types and go against the expectations to some extent. That the results are not always as expected, is also shown by the study of Pisman et al. (2022). They found that, in contrast to their hypothesis, orchard compositional heterogeneity in apple and sweet cherry orchards did not affect wild bumblebee and honeybee abundances, while for solitary bees, no effect was found in apple, but the effect in cherry orchards was negatively significant (Pisman et al., 2022). So in this case, but especially for this thesis, further research is recommended to explain these unexpected results.

For instance, taking into account the interaction between the percentage of agriculture and the flower abundance or vegetation richness, and not only their separate contributions, could provide more insight into the differences between the different pollinator types and the relevant scales. Including the proportion of semi-natural habitats instead of or together with the percentage agriculture, might also reveal some underlying trends which cannot be explained by the two parameters included in the models now. For example, Eeraerts et al. (2019) revealed that, independently from variations in this parameter, semi-natural habitats have a positive influence on pollinator populations regardless of intensive agriculture in the surrounding area, which highlights the regulating role of these semi-natural habitats above intensive agriculture. The region in which fieldwork was performed, however, is already rather diverse. This could explain why findings of this research and those of previous research contradict each other to some extent in terms of landscape complexity. A broader overview of the surrounding landscape is thus necessary to draw clear conclusions regarding the effect of the landscape on pollinators.

D. Some additional remarks

So far, the results showed that CSA habitats with their crop diversity as their main attribute are as valuable as SNGs in supporting pollinators in late summer. Besides, more floral resources and a lower proportion of agriculture, at least less intensive agricultural practices, are both favourable landscape parameters regarding populations of bees and hoverflies, and perhaps pollinators in general. But do these different scales also interact? In other words, do the local management practices at farm level, i.e. agricultural diversification in the form of crop diversity, reinforce the favourable effects of landscape measures such as maintaining more semi-natural habitat and vice versa?

Raderschall et al. (2021) found that, as for high proportions of semi-natural habitat, a higher degree of crop diversity increases bumblebees densities, and that this agricultural diversification strategy complements semi-natural habitat in the landscape rather than replacing it. Moreover, crop diversity enhances wild pollinator diversity, with this positive effect being higher with a higher proportion of semi-natural habitat in the surrounding landscape. Therefore, semi-natural habitats are said to complement crop diversity and strengthen its benefits for pollinators (Aguilera et al., 2020). Yet, it is important to note that the positive effects of crop diversity also depend on the type of crops

cultivated, the availability of co-flowering resources from semi-natural habitats and other crops in the landscape and the different response of different pollinators on crop diversity (Raderschall et al., 2021).

These findings also relate to the ongoing land sharing vs. land sparing debate. The reasoning behind land sharing is that the agricultural area expands, making it more wildlife-friendly but less high-yielding, and that there is less intact habitat, whereas the rationale behind land sparing is that fields with higher yields make place for wild nature elsewhere, however by being less wildlife-friendly (Green et al., 2005). Each of these approaches thus has its advantages and disadvantages and neither is perfect (Dudley & Alexander, 2017). However, promoting high-intensity agriculture with ever-increasing productivity as main purpose, does not take into account the long-term sustainability of farmland and is not necessarily translated into more nature that is spared. More attention should therefore go to multifunctional, heterogeneous and complex agricultural landscapes (land sharing) that combine both on- and off-field measures to promote biodiversity (Tscharntke et al., 2024). Hence, an agricultural landscape should look ideally like the one shown in Figure 16, for which the CSAs investigated in this study can serve as a model farm.
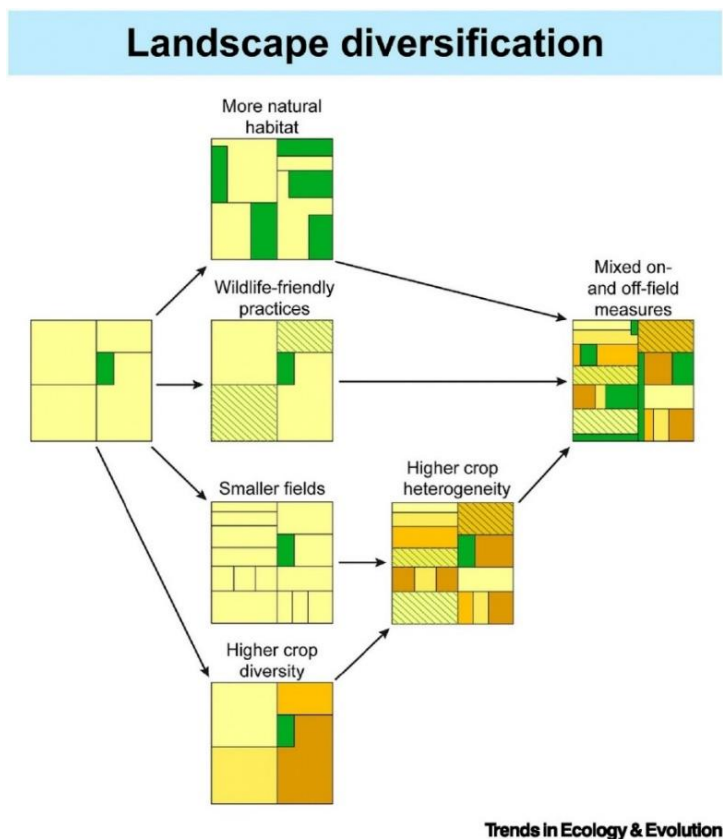

Figure 16: Potential on- and off-field measures for landscape diversification. From Tscharntke et al. (2024)

7. Conclusion

In the context of wild pollinator conservation and management, various methods of agricultural diversification are gaining attention, including community supported agriculture. The CSAs in this study represent small-scale farms characterized by a far-reaching form of crop diversification, such as intercropping, agroforestry, crop rotations, the implementation of cover crops and green manures etc. The combination of one or more of these practices appears to be a valuable method to provide floral resources for wild pollinators such as bees, hoverflies, butterflies and wasps. Indeed, the vegetation cover and species richness for both the CSAs and SNGs are comparable, with flower abundance in the former habitat even exceeding that in the latter one. The composition of the vegetation between CSAs and SNGs differs too, which implies that both habitats provide complementary floral resources for pollinating insects.

Besides providing floral resources, these habitats also support populations of wild pollinating insects at the time of doing fieldwork. Pollinator abundance and species richness did not differ between CSA farms and SNGs. However, just as for the vegetation, these two habitats differ in the composition of pollinator community they support. This reinforces the finding that CSAs and SNGs can be considered complementary habitats for pollinators during late summer, when floral resources are generally scarce. A more detailed examination of which species occurred on both habitats, however, revealed that still mainly the SNGs support specialist species. Moreover, the presence and type of nesting resources were not recorded during fieldwork, but previous research showed that mainly natural habitats that are important regarding the provision of nesting resources. Hence, given the different support both habitats provide for different pollinator populations, it is important that not one but both habitats are present.

Furthermore, considering the floral resources and proportion of agriculture in the surrounding area, some interesting results were found. Flower abundance had a significant positive effect on the abundance of all pollinators and hoverflies, which can be explained by the correlation between the amount flowers and the amount of nectar and pollen produced. On the other hand, the proportion of agriculture in the surrounding area had a significant negative effect on the hoverfly abundance, while the effect was non-significant for other pollinators. This rather unexpected finding might be explained by the small field sizes combined with the rather large amount of diversity the surrounding area.

However, the scale at which these effect were assessed, differed for the different pollinators. For all pollinators and bees, the most informative model was the one at the 1000 m scale. This was related to the high number of bumblebees recorded during fieldwork, which are characterized by a foraging distance of approximately 1 km. For hoverflies, the 250 m scale for abundance and the 500 m scale for richness were difficult to link with previous findings. Indeed, hoverflies are, due to their breeding strategy, not restricted to single nest sites and are therefore considered to disperse widely across the landscape. Hence, future research should be performed to explain these unexpected outcomes, but also to deliver additional information regarding some conclusions made in this thesis.

8. References

Aguilera, G., Roslin, T., Miller, K., Tamburini, G., Birkhofer, K., Caballero-Lopez, B., Lindström, S. A. M., Öckinger, E., Rundlöf, M., Rusch, A., Smith, H. G., & Bommarco, R. (2020). Crop diversity benefits carabid and pollinator communities in landscapes with semi-natural habitats. *Journal of Applied Ecology*, *57*(11), 2170–2179. https://doi.org/10.1111/1365-2664.13712

Ammann, L., Bosem-Baillod, A., Herzog, F., Frey, D., Entling, M. H., & Albrecht, M. (2024). Spatio-temporal complementarity of floral resources sustains wild bee pollinators in agricultural landscapes. *Agriculture, Ecosystems and Environment*, *359*. https://doi.org/10.1016/j.agee.2023.108754

Anderson, M. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*, 32–46.

Aviron, S., Berry, T., Leroy, D., Savary, G., & Alignier, A. (2023). Wild plants in hedgerows and weeds in crop fields are important floral resources for wild flower-visiting insects, independently of the presence of intercrops. *Agriculture, Ecosystems and Environment*, *348*. https://doi.org/10.1016/j.agee.2023.108410

Baden-Böhm, App, M., & Thiele, J. (2022). *The FloRes Database: A floral resources trait database for pollinator habitat-assessment generated by a multistep workflow [Dataset]*. Dryad. https://doi.org/https://doi.org/10.5061/dryad.djh9w0w29

Balbuena, M. S., Tison, L., Hahn, M. L., Greggers, U., Menzel, R., & Farina, W. M. (2015). Effects of sublethal doses of glyphosate on honeybee navigation. *Journal of Experimental Biology*, *218*(17), 2799–2805. https://doi.org/10.1242/jeb.117291

Balfour, N. J., Ollerton, J., Castellanos, M. C., & Ratnieks, F. L. W. (2018). British phenological records indicate high diversity and extinction rates among late-summer-flying pollinators. *Biological Conservation*, *222*, 278–283. https://doi.org/10.1016/j.biocon.2018.04.028

Balfour, N. J., & Ratnieks, F. L. W. (2022). The disproportionate value of 'weeds' to pollinators and biodiversity. *Journal of Applied Ecology*, *59*(5), 1209–1218. https://doi.org/10.1111/1365-2664.14132

Batáry, P., Báldi, A., Kleijn, D., & Tscharntke, T. (2011). Landscape-moderated biodiversity effects of agri-environmental management: A meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1713), 1894–1902. https://doi.org/10.1098/rspb.2010.1923

Beck, J., Holloway, J. D., & Schwanghart, W. (2013). Undersampling and the measurement of beta diversity. *Methods in Ecology and Evolution*, *4*(4), 370–382. https://doi.org/10.1111/2041-210x.12023

Beillouin, D., Ben-Ari, T., Malézieux, E., Seufert, V., & Makowski, D. (2021). Positive but variable effects of crop diversification on biodiversity and ecosystem services. *Global Change Biology*, *27*(19), 4697–4710. https://doi.org/10.1111/gcb.15747

Bernauer, O. M., Gaines-Day, H. R., & Steffan, S. A. (2015). Colonies of bumble bees (Bombus impatiens) produce fewer workers, less bee biomass, and have smaller mother queens following fungicide exposure. *Insects*, *6*(2), 478–488. https://doi.org/10.3390/insects6020478

Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J., & Kunin, W. E.

(2006). Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science*, *313*(5785), 351–354. https://doi.org/doi:10.1126/science.1127863

Bishop, G. A., Fijen, T. P. M., Raemakers, I., van Kats, R. J. M., & Kleijn, D. (2024). Bees go up, flowers go down: Increased resource limitation from late spring to summer in agricultural landscapes. *Journal of Applied Ecology*, *61*(3), 431–441. https://doi.org/10.1111/1365-2664.14576

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

Boetzl, F. A., Krauss, J., Heinze, J., Hoffmann, H., Juffa, J., König, S., Krimmer, E., Prante, M., Martin, E. A., Holzschuh, A., & Steffan-Dewenter, I. (2021). A multitaxa assessment of the effectiveness of agri-environmental schemes for biodiversity management. *Proceedings of the National Academy of Sciences*, *118*(10). https://doi.org/10.1073/pnas.2016038118/-/DCSupplemental

Bot, S., & Van de Meutter, F. (2019). *Veldgids Zweefvliegen*. KNNV Uitgeverij.

Brittain, C., Williams, N., Kremen, C., & Klein, A. M. (2013). Synergistic effects of non-Apis bees and honey bees for pollination services. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1754). https://doi.org/10.1098/rspb.2012.2767

Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. A. (2008). Synergies among extinction drivers under global change. *Trends in Ecology and Evolution*, *23*(8), 453–460. https://doi.org/10.1016/j.tree.2008.03.011

Cameron, S. A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., Solter, L. F., & Griswold, T. L. (2011). Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(2), 662–667. https://doi.org/10.1073/pnas.1014743108

Cane, J. H. (2001). Habitat Fragmentation and Native Bees: a Premature Verdict? *Ecology*, *5*(1). https://about.jstor.org/terms

Carvalheiro, L. G., Biesmeijer, J. C., Franzén, M., Aguirre-Gutiérrez, J., Garibaldi, L. A., Helm, A., Michez, D., Pöyry, J., Reemer, M., Schweiger, O., Leon van den, B., WallisDeVries, M. F., & Kunin, W. E. (2020). Soil eutrophication shaped the composition of pollinator assemblages during the past century. *Ecography*, *43*(2), 209–221. https://doi.org/10.1111/ecog.04656

Carvalheiro, L. G., Seymour, C. L., Veldtman, R., & Nicolson, S. W. (2010). Pollination services decline with distance from natural habitat even in biodiversity-rich areas. *Journal of Applied Ecology*, *47*(4), 810–820. https://doi.org/10.1111/j.1365-2664.2010.01829.x

Carvalheiro, L. G., Veldtman, R., Shenkute, A. G., Tesfay, G. B., Pirk, C. W. W., Donaldson, J. S., & Nicolson, S. W. (2011). Natural and within-farmland biodiversity enhances crop productivity. *Ecology Letters*, *14*(3), 251–259. https://doi.org/10.1111/j.1461-0248.2010.01579.x

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

Casey, L. M., Rebelo, H., Rotheray, E., & Goulson, D. (2015). Evidence for habitat and climatic specializations driving the long-term distribution trends of UK and Irish bumblebees. *Diversity and Distributions*, *21*(8), 864–875. https://doi.org/10.1111/ddi.12344

Centeno-Alvarado, D., Lopes, A. V., & Arnan, X. (2024). Shaping pollinator diversity through coffee agroforestry management: A meta-analytical approach. *Insect Conservation and Diversity*. https://doi.org/10.1111/icad.12755

De Cáceres, M., Legendre, P., & Moretti, M. (2010). Improving indicator species analysis by combining groups of sites. *Oikos*, *119*(10), 1674–1684. https://doi.org/10.1111/j.1600-0706.2010.18334.x

De Saeger, S., Dhaluin, P., Erens, R., Guelinckx, R., Hennebel, D., Jacobs, I., Kumpen, M., Van Oost, F., Spanhove, T., Leyssen, A., Oosterlynck, P., Van Dam, G., Van Hove, M., & Wils, C. (2023). *Biologische Waarderingskaart en Natura 2000 Habitatkaart, uitgave 2023*. https://doi.org/10.21436/inbor.96375305

Deguines, N., Jono, C., Baude, M., Henry, M., Julliard, R., & Fontaine, C. (2014). Large-scale trade-off between agricultural intensification and crop pollination services. *Frontiers in Ecology and the Environment*, *12*(4), 212–217. https://doi.org/10.1890/130054

Departement Landbouw en Visserij. (2023, August 23). *Landbouwgebruikspercelen LV, 2022*.

Di Prisco, G., Cavaliere, V., Annoscia, D., Varricchio, P., Caprio, E., Nazzi, F., Gargiulo, G., & Pennacchio, F. (2013). Neonicotinoid clothianidin adversely affects insect immunity and promotes replication of a viral pathogen in honey bees. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(46), 18466–18471. https://doi.org/10.1073/pnas.1314923110

Dudley, N., & Alexander, S. (2017). Agriculture and biodiversity: a review. *Biodiversity*, *18*(2–3), 45–49. https://doi.org/10.1080/14888386.2017.1351892

Dunn, R. R. (2005). Modern insect extinctions, the neglected majority. *Conservation Biology*, *19*(4), 1030–1036. https://doi.org/10.1111/j.1523-1739.2005.00078.x

Eeraerts, M. (2022). Increasing wild bee richness and abundance on sequentially flowering cultivars of a pollinator-dependent crop. *Agriculture, Ecosystems and Environment*, *325*. https://doi.org/10.1016/j.agee.2021.107745

Eeraerts, M. (2023). A minimum of 15% semi-natural habitat facilitates adequate wild pollinator visitation to a pollinator-dependent crop. *Biological Conservation*, *278*. https://doi.org/10.1016/j.biocon.2022.109887

Eeraerts, M., Borremans, L., Smagghe, G., & Meeus, I. (2020). A growers' perspective on crop pollination and measures to manage the pollination service of wild pollinators in sweet cherry cultivation. *Insects*, *11*(6), 1–8. https://doi.org/10.3390/insects11060372

Eeraerts, M., Meeus, I., Van Den Berge, S., & Smagghe, G. (2017). Landscapes with high intensive fruit cultivation reduce wild pollinator services to sweet cherry. *Agriculture, Ecosystems and Environment*, *239*, 342–348. https://doi.org/10.1016/j.agee.2017.01.031

Eeraerts, M., Piot, N., Pisman, M., Claus, G., Meeus, I., & Smagghe, G. (2021). Landscapes with high amounts of mass-flowering fruit crops reduce the reproduction of two solitary bees. *Basic and Applied Ecology*, *56*, 122–131. https://doi.org/10.1016/j.baae.2021.07.005

Eeraerts, M., Rogers, E., Gillespie, B., Best, L., Smith, O. M., & DeVetter, L. W. (2023). Landscape-level honey bee hive density, instead of field-level hive density, enhances honey bee visitation in blueberry. *Landscape Ecology*, *38*(2), 583–595. https://doi.org/10.1007/s10980-022-01562-1

Eeraerts, M., Smagghe, G., & Meeus, I. (2019). Pollinator diversity, floral resources and semi-natural habitat, instead of honey bees and intensive agriculture, enhance pollination service to sweet cherry. *Agriculture, Ecosystems and Environment*, *284*. https://doi.org/10.1016/j.agee.2019.106586

Eeraerts, M., Smagghe, G., & Meeus, I. (2020). Bumble bee abundance and richness improves honey bee pollination behaviour in sweet cherry. *Basic and Applied Ecology*, *43*, 27–33. https://doi.org/10.1016/j.baae.2019.11.004

Eeraerts, M., Van Den Berge, S., Proesmans, W., Verheyen, K., Smagghe, G., & Meeus, I. (2021). Fruit orchards and woody semi-natural habitat provide complementary resources for pollinators in agricultural landscapes. *Landscape Ecology*, *36*(5), 1377–1390. https://doi.org/10.1007/s10980-021-01220-y

Estrada-Carmona, N., Sánchez, A. C., Remans, R., & Jones, S. K. (2022). Complex agricultural landscapes host more biodiversity than simple ones: A global meta-analysis. *Proceedings of the National Academy of Sciences*, *119*(38), e2203385119. https://doi.org/doi:10.1073/pnas.2203385119

Evison, S. E. F., Roberts, K. E., Laurenson, L., Pietravalle, S., Hui, J., Biesmeijer, J. C., Smith, J. E., Budge, G., & Hughes, W. O. H. (2012). Pervasiveness of parasites in pollinators. *PLoS ONE*, *7*(1). https://doi.org/10.1371/journal.pone.0030641

Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T. O., Fuller, R. J., Sirami, C., Siriwardena, G. M., & Martin, J. L. (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, *14*(2), 101–112. https://doi.org/10.1111/j.1461-0248.2010.01559.x

Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., Javorek, S., King, D., Lindsay, K. F., Mitchell, S., & Tischendorf, L. (2015). Farmlands with smaller crop fields have higher within-field biodiversity. *Agriculture, Ecosystems and Environment*, *200*, 219–234. https://doi.org/10.1016/j.agee.2014.11.018

Falk, S., & Lewington, R. (2017). *Bijen - Veldgids voor Nederland en Vlaanderen*. Kosmos Uitgevers.

Fontaine, C., Dajoz, I., Meriguet, J., & Loreau, M. (2006). Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. *PLoS Biology*, *4*(1), 0129–0135. https://doi.org/10.1371/journal.pbio.0040001

Fowler, R. E., Rotheray, E. L., & Goulson, D. (2016). Floral abundance and resource quality influence pollinator choice. *Insect Conservation and Diversity*, *9*(6), 481–494. https://doi.org/10.1111/icad.12197

Fürst, M. A., McMahon, D. P., Osborne, J. L., Paxton, R. J., & Brown, M. J. F. (2014). Disease associations between honeybees and bumblebees as a threat to wild pollinators. *Nature*, *506*(7488), 364–366. https://doi.org/10.1038/nature12977

Gabriel, D., Sait, S. M., Hodgson, J. A., Schmutz, U., Kunin, W. E., & Benton, T. G. (2010). Scale matters: The impact of organic farming on biodiversity at different spatial scales. *Ecology Letters*, *13*(7), 858–869. https://doi.org/10.1111/j.1461-0248.2010.01481.x

Galpern, P., Vickruck, J., Devries, J. H., & Gavin, M. P. (2020). Landscape complexity is associated with crop yields across a large temperate grassland region. *Agriculture, Ecosystems and Environment*, *290*. https://doi.org/10.1016/j.agee.2019.106724

Garibaldi, L. A., Oddi, F. J., Miguez, F. E., Bartomeus, I., Orr, M. C., Jobbágy, E. G., Kremen, C., Schulte, L. A., Hughes, A. C., Bagnato, C., Abramson, G., Bridgewater, P., Carella, D. G., Díaz, S., Dicks, L. V., Ellis, E. C., Goldenberg, M., Huaylla, C. A., Kuperman, M., … Zhu, C. D. (2021). Working landscapes need at least 20% native habitat. *Conservation Letters*, *14*(2). https://doi.org/10.1111/conl.12773

Garibaldi, L. A., Steffan-Dewenter, I., Kremen, C., Morales, J. M., Bommarco, R., Cunningham, S. A., Carvalheiro, L. G., Chacoff, N. P., Dudenhöffer, J. H., Greenleaf, S. S., Holzschuh, A.,

Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M. M., Morandin, L. A., Potts, S. G., Ricketts, T. H., Szentgyörgyi, H., … Klein, A. M. (2011). Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecology Letters*, *14*(10), 1062–1072. https://doi.org/10.1111/j.1461-0248.2011.01669.x

Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A., Kremen, C., Carvalheiro, L. G., Harder, L. D., & Afik, O. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, *339*(6127), 1608–1611.

Gathmann, A., & Tscharntke, T. (2002). Foraging ranges of solitary bees. *Journal of Animal Ecology*, *71*(5), 757–764. https://doi.org/10.1046/j.1365-2656.2002.00641.x

Gold, A., Olin, N., & Wang, A. (2020, November 21). *What is the Delta Method?* https://cran.r-project.org/web/packages/modmarg/vignettes/delta-method.html

González-Varo, J. P., Biesmeijer, J. C., Bommarco, R., Potts, S. G., Schweiger, O., Smith, H. G., Steffan-Dewenter, I., Szentgyörgyi, H., Woyciechowski, M., & Vilà, M. (2013). Combined effects of global change pressures on animal-mediated pollination. In *Trends in Ecology and Evolution* (Vol. 28, Issue 9, pp. 524–530). https://doi.org/10.1016/j.tree.2013.05.008

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

Goulson, D., & Sparrow, K. R. (2009). Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. *Journal of Insect Conservation*, *13*(2), 177–181. https://doi.org/10.1007/s10841-008-9140-y

Goulson, D., Thompson, J., & Croombs, A. (2018). Rapid rise in toxic load for bees revealed by analysis of pesticide use in Great Britain. *PeerJ*, *6*. https://doi.org/10.7717/peerj.5255

Graystock, P., Goulson, D., & Hughes, W. O. H. (2015). Parasites in bloom: Flowers aid dispersal and transmission of pollinator parasites within and between bee species. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1813). https://doi.org/10.1098/rspb.2015.1371

Graystock, P., Yates, K., Darvill, B., Goulson, D., & Hughes, W. O. H. (2013). Emerging dangers: Deadly effects of an emergent parasite in a new pollinator host. *Journal of Invertebrate Pathology*, *114*(2), 114–119. https://doi.org/10.1016/j.jip.2013.06.005

Green, R. E., Cornell, S. J., Scharlemann, J. P. W., & Balmford, A. (2005). Farming and the fate of wild nature. *Science*, *307*(5709), 550–555.

Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, *153*(3), 589–596. https://doi.org/10.1007/s00442-007-0752-9

Guzman, A., Chase, M., & Kremen, C. (2019). On-Farm Diversification in an Agriculturally-Dominated Landscape Positively Influences Specialist Pollinators. *Frontiers in Sustainable Food Systems*, *3*. https://doi.org/10.3389/fsufs.2019.00087

Haan, N. L., Zhang, Y., & Landis, D. A. (2020). Predicting Landscape Configuration Effects on Agricultural Pest Suppression. *Trends in Ecology and Evolution*, *35*(2), 175–186. https://doi.org/10.1016/j.tree.2019.10.003

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

Harrison, T., Gibbs, J., & Winfree, R. (2018). Forest bees are replaced in agricultural and urban landscapes by native species with different phenologies and life-history traits. *Global Change Biology*, *24*(1), 287–296. https://doi.org/10.1111/gcb.13921

Hartig, F. (2022, September 8). *DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models*. https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html

Hass, A. L., Kormann, U. G., Tscharntke, T., Clough, Y., Baillod, A. B., Sirami, C., Fahrig, L., Martin, J. L., Baudry, J., Bertrand, C., Bosch, J., Brotons, L., Bure, F., Georges, R., Giralt, D., Marcos-García, M., Ricarte, A., Siriwardena, G., & Batáry, P. (2018). Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1872). https://doi.org/10.1098/rspb.2017.2242

Hemberger, J., & Gratton, C. (2023). Floral resource discontinuity contributes to spatial mismatch between pollinator supply and pollination demand in a pollinator-dependent agricultural landscapes. *Landscape Ecology*, *38*(12), 4439–4450. https://doi.org/10.1007/s10980-023-01707-w

Hemberger, J., Witynski, G., & Gratton, C. (2022). Floral resource continuity boosts bumble bee colony performance relative to variable floral resources. *Ecological Entomology*, *47*(4), 703–712. https://doi.org/10.1111/een.13154

Hemmings, K., Elton, R., & Grange, I. (2022). No-mow amenity grassland case study: Phenology of floral abundance and nectar resource. *Ecological Solutions and Evidence*, *3*(4). https://doi.org/10.1002/2688-8319.12179

Hladik, M. L., Main, A. R., & Goulson, D. (2018). Environmental Risks and Challenges Associated with Neonicotinoid Insecticides. *Environmental Science and Technology*, *52*(6), 3329–3335. https://doi.org/10.1021/acs.est.7b06388

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

Holzschuh, A., Steffan-Dewenter, I., & Tscharntke, T. (2008). Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos*, *117*(3), 354–361. https://doi.org/10.1111/j.2007.0030-1299.16303.x

Hufnagel, J., Reckling, M., & Ewert, F. (2020). Diverse approaches to crop diversification in agricultural research. A review. *Agronomy for Sustainable Development*, *40*(2). https://doi.org/10.1007/s13593-020-00617-4

IUCN. (2023). *The IUCN Red List of Threatened Species. Version 2023-1*. Https://Www.Iucnredlist.Org. Accessed on 6 February 2024.

Jacquemin, F., Violle, C., Rasmont, P., & Dufrêne, M. (2017). Mapping the dependency of crops on pollinators in Belgium. *One Ecosystem*, *2*. https://doi.org/10.3897/oneeco.2.e13738

Jauker, F., Diekötter, T., Schwarzbach, F., & Wolters, V. (2009). Pollinator dispersal in an agricultural matrix: Opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecology*, *24*(4), 547–555. https://doi.org/10.1007/s10980-009-9331-2

Kay, S., Kühn, E., Albrecht, M., Sutter, L., Szerencsits, E., & Herzog, F. (2020). Agroforestry can enhance foraging and nesting resources for pollinators with focus on solitary bees at the landscape scale. *Agroforestry Systems*, *94*(2), 379–387. https://doi.org/10.1007/s10457-019-00400-9

Kendall, L. K., Mola, J. M., Portman, Z. M., Cariveau, D. P., Smith, H. G., & Bartomeus, I. (2022). The potential and realized foraging movements of bees are differentially determined by body size and sociality. *Ecology*, *103*(11). https://doi.org/10.1002/ecy.3809

Kennedy, C. M., Lonsdorf, E., Neel, M. C., Williams, N. M., Ricketts, T. H., Winfree, R., Bommarco, R., Brittain, C., Burley, A. L., Cariveau, D., Carvalheiro, L. G., Chacoff, N. P., Cunningham, S. A., Danforth, B. N., Dudenhöffer, J. H., Elle, E., Gaines, H. R., Garibaldi, L. A., Gratton, C., … Kremen, C. (2013). A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*, *16*(5), 584–599. https://doi.org/10.1111/ele.12082

Kirsch, F., Hass, A. L., Link, W., & Westphal, C. (2023). Intercrops as foraging habitats for bees: Bees do not prefer sole legume crops over legume-cereal mixtures. *Agriculture, Ecosystems and Environment*, *343*. https://doi.org/10.1016/j.agee.2022.108268

Kleijn, D., Bommarco, R., Fijen, T. P. M., Garibaldi, L. A., Potts, S. G., & van der Putten, W. H. (2019). Ecological Intensification: Bridging the Gap between Science and Practice. *Trends in Ecology and Evolution*, *34*(2), 154–166. https://doi.org/10.1016/j.tree.2018.11.002

Kleijn, D., & van Langevelde, F. (2006). Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. *Basic and Applied Ecology*, *7*(3), 201–214. https://doi.org/10.1016/j.baae.2005.07.011

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

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

Kremen, C., Iles, A., & Bacon, C. (2012). Diversified farming systems: An agroecological, systems-based alternative to modern industrial agriculture. *Ecology and Society*, *17*(4). https://doi.org/10.5751/ES-05103-170444

Kremen, C., & M'Gonigle, L. K. (2015). EDITOR'S CHOICE: Small-scale restoration in intensive agricultural landscapes supports more specialized and less mobile pollinator species. *Journal of Applied Ecology*, *52*(3), 602–610. https://doi.org/10.1111/1365-2664.12418

Kremen, C., & Miles, A. (2012). Ecosystem services in biologically diversified versus conventional farming systems: Benefits, externalities, and trade-offs. *Ecology and Society*, *17*(4). https://doi.org/10.5751/ES-05035-170440

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

Kremen, C., Williams, N. M., & Thorp, R. W. (2002). Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences*, *99*(26), 16812–16816. https://doi.org/doi:10.1073/pnas.262413599

Lajos, K., Samu, F., Bihaly, Á. D., Fülöp, D., & Sárospataki, M. (2021). Landscape structure affects the sunflower visiting frequency of insect pollinators. *Scientific Reports*, *11*(1). https://doi.org/10.1038/s41598-021-87650-9

Magrach, A., Giménez-García, A., Allen-Perkins, A., Garibaldi, L. A., & Bartomeus, I. (2023). Increasing crop richness and reducing field sizes provide higher yields to pollinator-dependent crops. *Journal of Applied Ecology*, *60*(1), 77–90. https://doi.org/10.1111/1365-2664.14305

Mallinger, R. E., Franco, J. G., Prischmann-Voldseth, D. A., & Prasifka, J. R. (2019). Annual cover crops for managed and wild bees: Optimal plant mixtures depend on pollinator enhancement goals. *Agriculture, Ecosystems and Environment*, *273*, 107–116. https://doi.org/10.1016/j.agee.2018.12.006

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

Mandelik, Y., Winfree, R., Neeson, T., & Kremen, C. (2012). Complementary habitat use by wild bees in agro-natural landscapes. *Ecological Applications*, *22*(5), 1535–1546. https://doi.org/10.1890/11-1299.1

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

Martins, K. T., Albert, C. H., Lechowicz, M. J., & Gonzalez, A. (2018). Complementary crops and landscape features sustain wild bee communities. *Ecological Applications*, *28*(4), 1093–1105. https://doi.org/10.1002/eap.1713

Maurer, C., Martínez-Núñez, C., Dominik, C., Heuschele, J., Liu, Y., Neumann, P., Paxton, R. J., Pellissier, L., Proesmans, W., Schweiger, O., Szentgyörgyi, H., Vanbergen, A., & Albrecht, M. (2024). Landscape simplification leads to loss of plant–pollinator interaction diversity and flower visitation frequency despite buffering by abundant generalist pollinators. *Diversity and Distributions.* https://doi.org/10.1111/ddi.13853

Maurer, C., Sutter, L., Martínez-Núñez, C., Pellissier, L., & Albrecht, M. (2022). Different types of semi-natural habitat are required to sustain diverse wild bee communities across agricultural landscapes. *Journal of Applied Ecology*, *59*(10), 2604–2615. https://doi.org/10.1111/1365-2664.14260

McArt, S. H., Urbanowicz, C., McCoshum, S., Irwin, R. E., & Adler, L. S. (2017). Landscape predictors of pathogen prevalence and range contractions in US bumblebees. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1867). https://doi.org/10.1098/rspb.2017.2181

Meyer, B., Jauker, F., & Steffan-Dewenter, I. (2009). Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic and Applied Ecology*, *10*(2), 178–186. https://doi.org/10.1016/j.baae.2008.01.001

Moquet, L., Laurent, E., Bacchetta, R., & Jacquemart, A. L. (2018). Conservation of hoverflies (Diptera, Syrphidae) requires complementary resources at the landscape and local scales. *Insect Conservation and Diversity*, *11*(1), 72–87. https://doi.org/10.1111/icad.12245

Motta, E. V. S., Raymann, K., & Moran, N. A. (2018). Glyphosate perturbs the gut microbiota of honey bees. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(41), 10305–10310. https://doi.org/10.1073/pnas.1803880115

Mupepele, A. C., Bruelheide, H., Dauber, J., Krüß, A., Potthast, T., Wägele, W., & Klein, A. M. (2019). Insect decline and its drivers: Unsupported conclusions in a poorly performed meta-analysis on trends—A critique of Sánchez-Bayo and Wyckhuys (2019). *Basic and Applied Ecology*, *37*, 20–23. https://doi.org/10.1016/j.baae.2019.04.001

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

National Biodiversity Data Centre. (n.d.). *Species Biodiversity Ireland* . Retrieved May 18, 2024, from https://species.biodiversityireland.ie/index.php?

Naturalis. (n.d.). *Nederlands Soortenregister*.

Nichols, R. N., Goulson, D., & Holland, J. M. (2019). The best wildflowers for wild bees. *Journal of Insect Conservation*, *23*(5–6), 819–830. https://doi.org/10.1007/s10841-019-00180-8

Norris, S. L., Blackshaw, R. P., Critchley, C. N. R., Dunn, R. M., Smith, K. E., Williams, J., Randall, N. P., & Murray, P. J. (2018). Intercropping flowering plants in maize systems increases pollinator diversity. *Agricultural and Forest Entomology*, *20*(2), 246–254. https://doi.org/10.1111/afe.12251

Öckinger, E., & Smith, H. G. (2007). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, *44*(1), 50–59. https://doi.org/10.1111/j.1365-2664.2006.01250.x

Ollerton, J., Erenler, H., Edwards, M., & Crockett, R. (2014). Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science*, *346*(6215), 1360–1362. https://doi.org/10.1126/science.1257259

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

Paul, M. (2019). Community-supported agriculture in the United States: Social, ecological, and economic benefits to farming. *Journal of Agrarian Change*, *19*(1), 162–180. https://doi.org/10.1111/joac.12280

Pereira, A. L. C., Taques, T. C., Valim, J. O. S., Madureira, A. P., & Campos, W. G. (2015). The management of bee communities by intercropping with flowering basil (Ocimum basilicum) enhances pollination and yield of bell pepper (Capsicum annuum). *Journal of Insect Conservation*, *19*(3), 479–486. https://doi.org/10.1007/s10841-015-9768-3

Pimm, S. L., & Raven, P. (2000). Extinction by numbers. *Nature*, *403*(6772), 843–845. https://doi.org/10.1038/35002708

Pisman, M., Eeraerts, M., Ariza, D., Smagghe, G., & Meeus, I. (2022). Increased compositional heterogeneity of mass-flowering orchard crops does not promote wild bee abundance in orchards. *Agricultural and Forest Entomology*, *24*(1), 8–17. https://doi.org/10.1111/afe.12464

Ponisio, L. C., M'Gonigle, L. K., & Kremen, C. (2016). On-farm habitat restoration counters biotic homogenization in intensively managed agriculture. *Global Change Biology*, *22*(2), 704–715. https://doi.org/10.1111/gcb.13117

Powney, G. D., Carvell, C., Edwards, M., Morris, R. K. A., Roy, H. E., Woodcock, B. A., & Isaac, N. J. B. (2019). Widespread losses of pollinating insects in Britain. *Nature Communications*, *10*(1). https://doi.org/10.1038/s41467-019-08974-9

Proesmans, W., Bonte, D., Smagghe, G., Meeus, I., Decocq, G., Spicher, F., Kolb, A., Lemke, I., Diekmann, M., Bruun, H. H., Wulf, M., Van Den Berge, S., & Verheyen, K. (2019). Small forest patches as pollinator habitat: oases in an agricultural desert? *Landscape Ecology*, *34*(3), 487–501. https://doi.org/10.1007/s10980-019-00782-2

R Core Team. (2024). *R: A Language and Environment for Statistical Computing* (4.3.3). R Foundation for Statistical Computing, Vienna, Austria.

Raderschall, C. A., Bommarco, R., Lindström, S. A. M., & Lundin, O. (2021). Landscape crop diversity and semi-natural habitat affect crop pollinators, pollination benefit and yield. *Agriculture, Ecosystems and Environment*, *306*. https://doi.org/10.1016/j.agee.2020.107189

Redhead, J. W., Oliver, T. H., Woodcock, B. A., & Pywell, R. F. (2020). The influence of landscape composition and configuration on crop yield resilience. *Journal of Applied Ecology*, *57*(11), 2180–2190. https://doi.org/10.1111/1365-2664.13722

Reilly, J., Bartomeus, I., Simpson, D., Allen-Perkins, A., Garibaldi, L., & Winfree, R. (2024). Wild insects and honey bees are equally important to crop yields in a global analysis. *Global Ecology and Biogeography*. https://doi.org/10.1111/geb.13843

Richards, A. J. (2001). Does low biodiversity resulting from modern agricultural practice affect crop pollination and yield? *Annals of Botany*, *88*(2), 165–172. https://doi.org/10.1006/anbo.2001.1463

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

Riggi, L. G. A., Raderschall, C. A., Fijen, T. P. M., Scheper, J., Smith, H. G., Kleijn, D., Holzschuh, A., Aguilera, G., Badenhausser, I., Bänsch, S., Beyer, N., Blitzer, E. J., Bommarco, R., Danforth, B., González-Varo, J. P., Grab, H., Le Provost, G., Poveda, K., Potts, S. G., … Lundin, O. (2024). Early-season mass-flowering crop cover dilutes wild bee abundance and species richness in temperate regions: A quantitative synthesis. *Journal of Applied Ecology*, *61*(3), 452–464. https://doi.org/10.1111/1365-2664.14566

Robinson, R. A., & Sutherland, W. J. (2002). Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*, *39*(1), 157–176. https://doi.org/10.1046/j.1365-2664.2002.00695.x

Rollin, O., Vray, S., Dendoncker, N., Michez, D., Dufrêne, M., & Rasmont, P. (2020). Drastic shifts in the Belgian bumblebee community over the last century. *Biodiversity and Conservation*, *29*(8), 2553–2573.

Rosa-Schleich, J., Loos, J., Mußhoff, O., & Tscharntke, T. (2019). Ecological-economic trade-offs of Diversified Farming Systems – A review. *Ecological Economics*, *160*, 251–263. https://doi.org/10.1016/j.ecolecon.2019.03.002

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

Sánchez-Bayo, F., & Wyckhuys, K. A. G. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*, *232*, 8–27. https://doi.org/10.1016/j.biocon.2019.01.020

Scheper, J., Badenhausser, I., Kantelhardt, J., Kirchweger, S., Bartomeus, I., Bretagnolle, V., Clough, Y., Gross, N., Raemakers, I., Vilà, M., Zaragoza-Trello, C., & Kleijn, D. (2023).

Biodiversity and pollination benefits trade off against profit in an intensive farming system. *Proceedings of the National Academy of Sciences of the United States of America*, *120*(28). https://doi.org/10.1073/pnas.2212124120

Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S. G., Rundlöf, M., Smith, H. G., & Kleijn, D. (2013). Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss - a meta-analysis. *Ecology Letters*, *16*(7), 912–920. https://doi.org/10.1111/ele.12128

Schober, P., & Schwarte, L. A. (2018). Correlation coefficients: Appropriate use and interpretation. *Anesthesia and Analgesia*, *126*(5), 1763–1768. https://doi.org/10.1213/ANE.0000000000002864

Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J. C., Linsenmair, K. E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E. D., Vogt, J., Wöllauer, S., & Weisser, W. W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, *574*(7780), 671–674. https://doi.org/10.1038/s41586-019-1684-3

Sirami, C., Gross, N., Baillod, A. B., Bertrand, C., Carrié, R., Hass, A., Henckel, L., Miguet, P., Vuillot, C., Alignier, A., Girard, J., Batáry, P., Clough, Y., Violle, C., Giralt, D., Bota, G., Badenhausser, I., Lefebvre, G., Gauffre, B., … Fahrig, L. (2019). Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(33), 16442–16447. https://doi.org/10.1073/pnas.1906419116

Sprayberry, J. D. H., Ritter, K. A., & Riffell, J. A. (2013). The Effect of Olfactory Exposure to Non-Insecticidal Agrochemicals on Bumblebee Foraging Behavior. *PloS One*, *8*(10), e76273. https://doi.org/10.1371/journal.pone.0076273

Stange, E. E., & Ayres, M. P. (2010). Climate Change Impacts: Insects. In *eLS*. Wiley. https://doi.org/10.1002/9780470015902.a0022555

Staton, T., Walters, R. J., Smith, J., & Girling, R. D. (2019). Evaluating the effects of integrating trees into temperate arable systems on pest control and pollination. In *Agricultural Systems* (Vol. 176). Elsevier Ltd. https://doi.org/10.1016/j.agsy.2019.102676

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., & Tscharntke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, *83*(5), 1421–1432. https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2

Steffan-Dewenter, I., Münzenberg, U., & Tscharntke, T. (2001). Pollination, seed set and seed predation on a landscape scale. *Proceedings of the Royal Society B: Biological Sciences*, *268*(1477), 1685–1690. https://doi.org/10.1098/rspb.2001.1737

Tamburini, G., Bommarco, R., Cherico Wanger, T., Kremen, C., Van Der Heijden, M. G. A., Liebman, M., & Hallin, S. (2020). Agricultural diversification promotes multiple ecosystem services without compromising yield. *Science Advances*, *6*(45). https://www.science.org

Thomas, J. A., Telfer, M. G., Roy, D. B., Preston, C. D., Greenwood, J. J. D., Asher, J., Fox, R., Clarke, R. T., & Lawton, J. H. (2004). Comparative Losses of British Butterflies, Birds, and Plants and the Global Extinction Crisis. *Science*, *303*(5665), 1879–1881. https://doi.org/10.1126/science.1095046

Timberlake, T. P., Vaughan, I. P., & Memmott, J. (2019). Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *Journal of Applied Ecology*, *56*(7), 1585–1596. https://doi.org/10.1111/1365-2664.13403

Tscharntke, T., Batáry, P., & Grass, I. (2024). Mixing on- and off-field measures for biodiversity conservation. In *Trends in Ecology and Evolution*. Elsevier Ltd. https://doi.org/10.1016/j.tree.2024.04.003

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity - Ecosystem service management. *Ecology Letters*, *8*(8), 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

United Nations. (2019, May 6). *UN Report: Nature's Dangerous Decline 'Unprecedented'; Species Extinction Rates 'Accelerating.'* Https://Www.Un.Org/Sustainabledevelopment/Blog/2019/05/Nature-Decline-Unprecedented-Report/.

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

van Strien, A. J., van Swaay, C. A. M., van Strien-van Liempt, W. T. F. H., Poot, M. J. M., & WallisDeVries, M. F. (2019). Over a century of data reveal more than 80% decline in butterflies in the Netherlands. *Biological Conservation*, *234*, 116–122. https://doi.org/10.1016/j.biocon.2019.03.023

Vanbergen, A. J., Garratt, M. P., Vanbergen, A. J., Baude, M., Biesmeijer, J. C., Britton, N. F., Brown, M. J. F., Brown, M., Bryden, J., Budge, G. E., Bull, J. C., Carvell, C., Challinor, A. J., Connolly, C. N., Evans, D. J., Feil, E. J., Garratt, M. P., Greco, M. K., Heard, M. S., … Wright, G. A. (2013). Threats to an ecosystem service: Pressures on pollinators. *Frontiers in Ecology and the Environment*, *11*(5), 251–259. https://doi.org/10.1890/120126

von Königslöw, V., Fornoff, F., & Klein, A. M. (2022). Wild bee communities benefit from temporal complementarity of hedges and flower strips in apple orchards. *Journal of Applied Ecology*, *59*(11), 2814–2824. https://doi.org/10.1111/1365-2664.14277

Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R., & Stopak, D. (2021). Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(2). https://doi.org/10.1073/PNAS.2023989118

Walters, J., Zavalnitskaya, J., Isaacs, R., & Szendrei, Z. (2022). Heat of the moment: extreme heat poses a risk to bee–plant interactions and crop yields. *Current Opinion in Insect Science*, *52*. https://doi.org/10.1016/j.cois.2022.100927

Warren, M. S., Hill, J. K., Thomas, J. A., Asher, J., Fox, R., Huntley, B., Roy, D. B., Telfer, M. G., Jeffcoate, S., & Harding, P. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, *414*(6859), 65–69.

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

Winfree, R., Aguilar, R., Vázquez, D. P., Lebuhn, G., & Aizen, M. A. (2009). A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology*, *90*(8), 2068–2076. https://doi.org/10.1890/08-1245.1

Wood, T. J., Holland, J. M., & Goulson, D. (2016). Diet characterisation of solitary bees on farmland: dietary specialisation predicts rarity. *Biodiversity and Conservation*, *25*(13), 2655–2671. https://doi.org/10.1007/s10531-016-1191-x

Woods, T., Ernst, M., & Tropp, D. (2017). *Community Supported Agriculture: New Models for Changing Markets*. https://doi.org/10.22004/ag.econ.316239

Wright, E. K., Timberlake, T. P., Baude, M., Vaughan, I. P., & Memmott, J. (2024). Quantifying the production of plant pollen at the farm scale. *New Phytologist*. https://doi.org/10.1111/nph.19763

Wynhoff, I., van Swaay, C., & van der Made, J. (1999). *Veldgids Dagvlinders*. KNNV Uitgeverij.

9. Supplementary information

A. Data collection

Table 12: Vegetation cover, expressed as one of the six cover classes (Table 1), of the five different vegetation layers for the two transects in each habitat at the sixteen sampling location. A = < 1%, B = 1% – 5%, C = 6% – 25%, D = 26% - 50%, E = 51% - 75%, F = 76% - 100%.

Location	Type	Transect	Shrub and tree	Herb	Moss	Litter	Fallow
Gontrode	CSA	1	C	F	B	C	C
Gontrode	CSA	2	0	F	A	C	C
Gontrode	Nature	3	0	F	A	A	A
Gontrode	Nature	4	0	F	B	B	B
Afsnee	CSA	1	C	E	A	A	D
Afsnee	CSA	2	A	D	A	A	D
Afsnee	Nature	3	0	F	A	B	A
Afsnee	Nature	4	A	F	B	B	B
Zemst	CSA	1	0	F	A	A	B
Zemst	CSA	2	0	F	A	A	A
Zemst	Nature	3	A	F	B	A	A
Zemst	Nature	4	0	E	B	C	C
Destelbergen	CSA	1	D	E	A	A	C
Destelbergen	CSA	2	0	E	A	B	D
Destelbergen	Nature	3	0	F	A	A	A
Destelbergen	Nature	4	0	F	B	A	A
Londerzeel	CSA	1	0	F	0	B	C
Londerzeel	CSA	2	0	E	0	C	C
Londerzeel	Nature	3	0	F	C	C	B
Londerzeel	Nature	4	C	F	C	C	B
Schelle	CSA	1	0	F	0	0	B
Schelle	CSA	2	0	F	0	0	0
Schelle	Nature	3	0	F	0	B	0
Schelle	Nature	4	A	F	0	B	0
Ranst	CSA	1	0	E	A	A	E
Ranst	CSA	2	0	E	A	A	E
Ranst	Nature	3	0	F	A	A	A
Ranst	Nature	4	0	F	A	A	A
Heverlee	CSA	1	0	E	A	B	D
Heverlee	CSA	2	0	D	A	D	C
Heverlee	Nature	3	0	F	A	B	B
Heverlee	Nature	4	C	F	B	A	B
Merchtem	CSA	1	0	F	0	0	B

Merchtem	CSA	2	0	F	A	A	D
Merchtem	Nature	3	0	F	A	A	A
Merchtem	Nature	4	0	F	A	A	A
Oppem	CSA	1	0	F	A	A	D
Oppem	CSA	2	0	D	A	A	D
Oppem	Nature	3	0	F	A	A	A
Oppem	Nature	4	0	F	A	A	B
Vinderhoute	CSA	1	0	E	A	C	B
Vinderhoute	CSA	2	0	F	A	C	A
Vinderhoute	Nature	3	0	F	A	A	A
Vinderhoute	Nature	4	0	F	A	A	A
Zedelgem	CSA	1	0	F	0	A	C
Zedelgem	CSA	2	0	E	0	B	C
Zedelgem	Nature	3	0	E	B	B	B
Zedelgem	Nature	4	0	E	B	B	B
Puurs	CSA	1	0	F	A	A	C
Puurs	CSA	2	0	F	0	A	B
Puurs	Nature	3	0	F	B	B	B
Puurs	Nature	4	A	E	A	B	A
Emblem	CSA	1	0	F	A	B	B
Emblem	CSA	2	0	E	A	B	E
Emblem	Nature	3	0	F	A	A	A
Emblem	Nature	4	0	F	A	A	A
Heusden	CSA	1	0	E	A	C	C
Heusden	CSA	2	0	F	0	B	D
Heusden	Nature	3	0	F	A	A	A
Heusden	Nature	4	0	F	A	A	A
Gentbrugge	CSA	1	0	F	A	A	C
Gentbrugge	CSA	2	0	F	A	B	C
Gentbrugge	Nature	3	0	F	A	A	A
Gentbrugge	Nature	4	0	F	A	B	A

Table 13: Mean sampling conditions for the sixteen sampling sites. Time start and time end represent the starting time of the first sampling round and the ending time of the last sampling round at each location.

Location	Date	Time start	Time end	Temperature (°C)	Cloud cover (%)	Wind speed (km.h⁻¹)
Londerzeel	25/07/2023	14:30	17:43	19	35	15
Gontrode	26/07/2023	11:10	16:20	18.7	50	15
Afsnee	28/07/2023	15:00	17:30	21	72.5	20
Zemst	29/07/2023	14:30	18:20	22.5	55	17.5
Londerzeel	30/07/2023	13:50	*NA*	20.3	32.5	28.3
Destelbergen	1/08/2023	12:00	16:45	19	90	25
Schelle	9/08/2023	13:50	16:55	20.5	32.5	15
Ranst	10/08/2023	13:00	15:30	22.5	0	7.5
Heverlee	11/08/2023	13:00	15:25	27.5	25	13.8
Merchtem	14/08/2023	11:30	15:30	24.3	15	11.3
Oppem	15/08/2023	10:40	14:10	23.3	37.5	12.5
Vinderhoute	16/08/2023	11:10	14:20	22.3	20	11.3
Zedelgem	11/08/2023	11:00	17:00	21.3	87.5	11.3
Puurs	24/08/2023	10:30	*NA*	22.7	76.7	6.3
Emblem	29/08/2020	11:50	14:45	18	70	8.8
Heusden	4/09/2023	11:40	14:30	22	18	11.2
Gentbrugge	5/09/2023	12:10	14:50	27	0	8

B. Results

I. General results

Table 14: Information regarding the datasets with outliers. For each outlier, the value of the corresponding parameter (vegetation cover, vegetation species richness (SR), vegetation flower abundance (FA), pollinator abundance (AB) and pollinator species richness) is given between brackets. The following model statistics (Stat) are given: the z-value and p-value for the models with outliers (z_1, p_1) and for the models without outliers (z_2, p_2).

Data	Outlier	z_1	p_1	z_2	p_2
Vegetation cover flowering	Destelbergen, SNG (*290.5*)	0.96	0.34	3.46	0.084
Vegetation SR all	Schelle, CSA (*37*)	2.06	0.17	1.09	0.31
Vegetation FA all	Emblem, CSA (*6810*) Merchtem, CSA (*5664*) Oppem, CSA (*7152*) Zedelgem, CSA (*5294*)	-124.54	$< 2.2 * 10^{-16}$	-67.33	$< 2.2 * 10^{-16}$
Vegetation FA flowering	Emblem, CSA (*6810*) Merchtem, CSA (*5664*) Oppem, CSA (*7152*) Zedelgem, CSA (*5294*)	-124.54	$< 2.2 * 10^{-16}$	-67.33	$< 2.2 * 10^{-16}$
Vegetation FA visited	Merchtem, CSA (*5375*) Oppem, CSA (*6485*) Zedelgem, CSA (*4927*)	-111.00	$< 2.2 * 10^{-16}$	5125.50	$< 2.2 * 10^{-16}$
Pollinator AB all	Vinderhoute, CSA (*11*) Londerzeel, SNG (*101*)	0.069	0.95	-1.57	0.12
Pollinator AB bee	Merchtem, SNG (*74*)	1.18	0.24	-0.27	0.79
Pollinator AB butterfly	Heusden, CSA (*5*) Londerzeel, CSA (*21*) Zedelgem, CSA (*12*) Afsnee, SNG (*4*) Ranst, SNG (*6*) Schelle, SNG (*5*)	-2.32	0.020	0.33	0.74
Pollinator AB wasp	Ranst, SNG (*20*)	-2.12	0.034	-17.21	$< 2.2 * 10^{-16}$
Pollinator SR all	Heverlee, SNG (*26*) Oppem, SNG (*27*)	0.60	0.55	-0.58	0.56
Pollinator SR bee	Heverlee, CSA (*11*) Heverlee, SNG (*14*)	0.97	0.33	0.80	0.42
Pollinator SR hoverfly	Oppem, SNG (*14*)	0.074	0.94	-0.57	0.57
Pollinator SR butterfly	Afsnee, SNG (*4*)	0.57	0.57	0.17	0.87
Pollinator SR wasp	Ranst, CSA (*9*)	-0.11	0.91	0.71	0.48

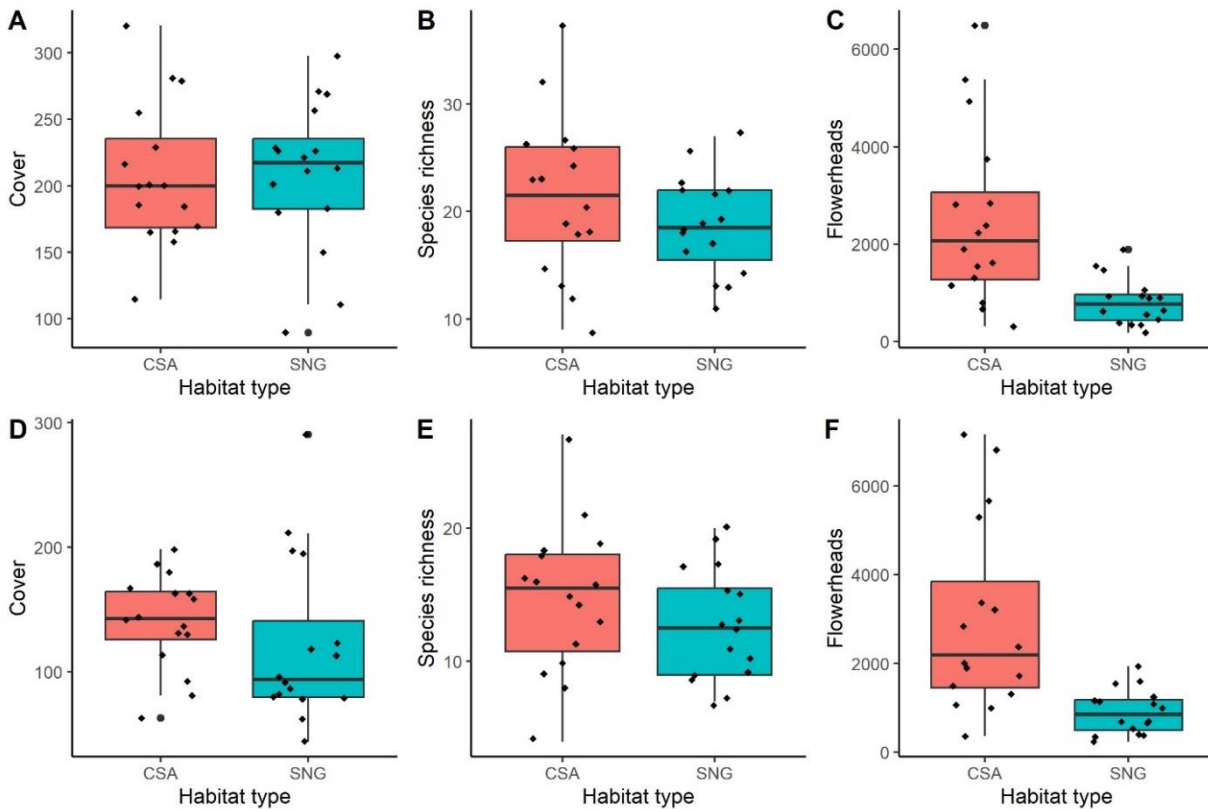## II. What floral resources do different habitat types provide for pollinating insects in late summer?

Figure 17: Distribution of the cover (A, D), species richness (B, E) and flower abundance (C, F) of the complete (first row) and flowering (second row) plants for the CSA (pink) and SNG (blue) habitat type

Table 15: Summary of the results of linear mixed-effect models (LME) and generalized linear mixed-effect models (GLMM) of habitat type on the vegetation cover, species richness (SR) and flower abundance (FA) for the complete (all) and flowering (flower) vegetation dataset. The following model statistics are given: F-value for LME or z-value for GLMM (Stat), p-values, mean and standard error (SE) per variable for each habitat type.

| Response variable	Fixed Variable	Model	Stat	p	Habitat type	Mean	SE
Cover all	Habitat type	LME	0.0012	0.97	CSA	207.69	13.44
					Nature	208.38	14.10
Cover flower	Habitat type	LME	0.96	0.34	CSA	140.63	9.56
					Nature	121.78	16.73
SR all	Habitat type	LME	2.06	0.17	CSA	21.38	1.85
					Nature	18.75	1.17
SR flower	Habitat type	LME	1.64	0.22	CSA	14.69	1.40
					Nature	12.69	1.04
FA all	Habitat type	GLMM	-124.54	$< 2.2*10^{-16}$	CSA	2972.56	533.75
					Nature	917.00	125.81
FA flower	Habitat type	GLMM	-124.54	$< 2.2*10^{-16}$	CSA	2972.56	533.75
					Nature	917.00	125.81
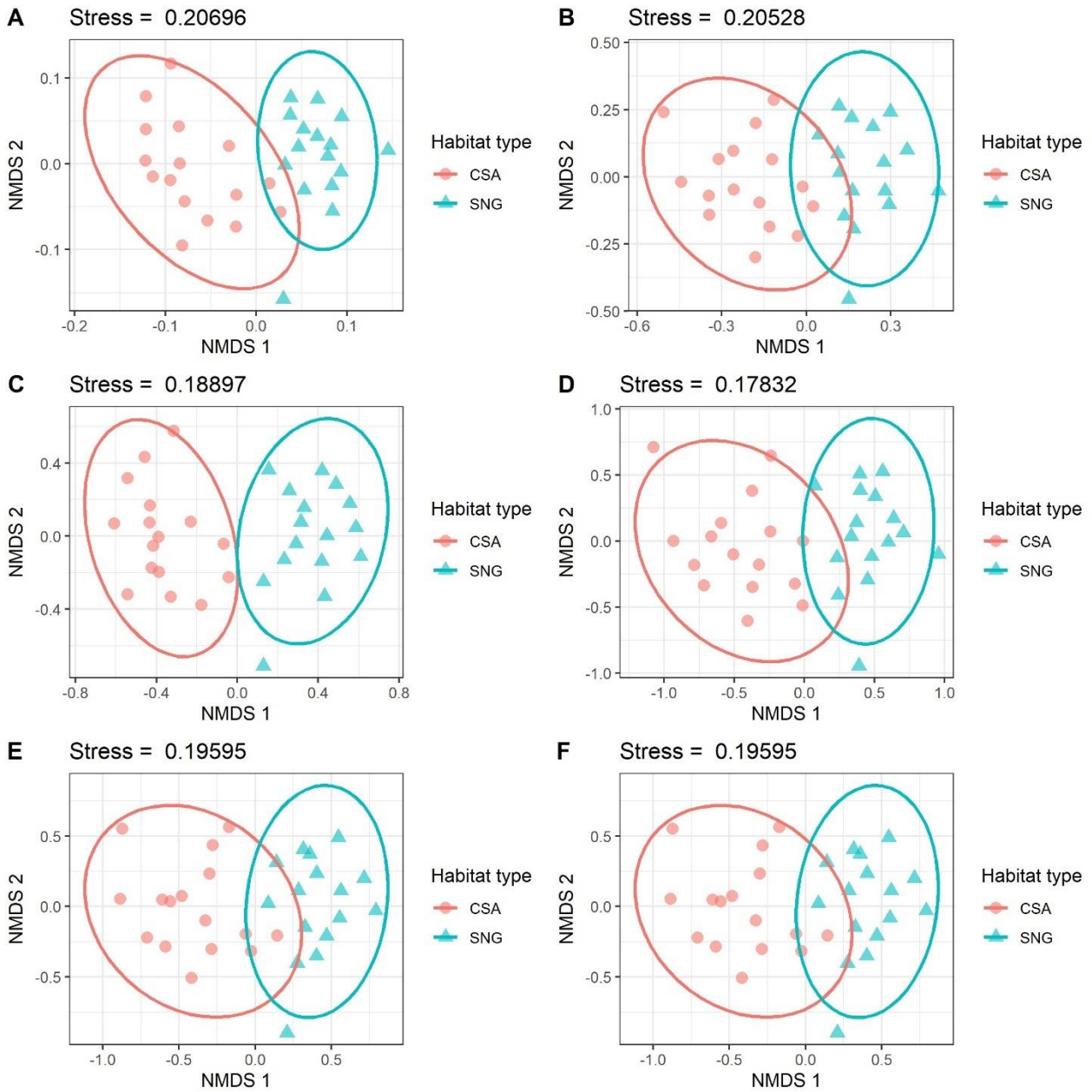
Figure 18: NMDS plots for the cover (A, B), species richness (C, D) and flower abundance (E, F) of the complete (left) and flowering (right) vegetation dataset with the corresponding stress values.

Table 16: Statistical results of the PERMANOVA-analysis and the corresponding distance measure used for the cover, species richness (SR) and flower abundance (FA) for the complete (all) and flowering (flower) vegetation datasets. Centroids refers to the statistical results (F-value, p-value) of the adonis2-function. Dispersion refers to the statistical results (F-value, p-value) of the betadisper-function.

Data	Distance measure	Centroids F	p	Dispersion F	p	Stress
Cover all	Morisita-Horn	5.18	0.0010	10.61	0.0028	0.21
Cover flowering	Morisita-Horn	3.37	0.0010	0.25	0.62	0.21
SR all	Jaccard	4.48	0.0010	0.0049	0.94	0.19
SR flowering	Jaccard	3.85	0.0010	0.84	0.37	0.18
FA all	Morisita-Horn	3.73	0.0010	0.012	0.91	0.20
FA flowering	Morisita-Horn	3.73	0.0010	0.012	0.91	0.20

Table 17: Indicator species of all plant species (left) and the flowering plant species (right) for each habitat type with their corresponding point-biserial correlation coefficients (r_{pb}) a p-value.

All plant species				**Flowering plant species**			
Habitat	Plant species	r_{pb}	p	Habitat	Plant species	r_{pb}	p
CSA	Lamium purpureum	0.43	0.0030	CSA	Lamium purpureum	0.43	0.0030
CSA	Sonchus sp.	0.43	0.020	CSA	Sonchus sp.	0.43	0.015
CSA	Foeniculum vulgare	0.36	0.040	CSA	Foeniculum vulgare	0.36	0.042
CSA	Galinsoga quadriradiata	0.35	0.0010	CSA	Galinsoga quadriradiata	0.35	0.0010
CSA	Coriandrum sativum	0.33	0.048	CSA	Solanum nigrum	0.33	0.017
CSA	Solanum nigrum	0.33	0.011	CSA	Phacelia tanacetifolia	0.27	0.038
CSA	Phacelia tanacetifolia	0.27	0.045	CSA	Senecio vulgaris	0.25	0.036
CSA	Senecio vulgaris	0.25	0.039	SNG	Lotus corniculatus	0.45	0.0090
SNG	Lotus corniculatus	0.45	0.010	SNG	Heracleum sphondylium	0.39	0.0040
SNG	Heracleum sphondylium	0.39	0.0020	SNG	Cirsium arvense	0.38	0.011
SNG	Cirsium arvense	0.38	0.010	SNG	Lythrum salicaria	0.35	0.0010
SNG	Lythrum salicaria	0.35	0.0010	SNG	Jacobaea vulgaris	0.32	0.023
SNG	Jacobaea vulgaris	0.32	0.019	SNG	Centaurea jacea	0.28	0.048
SNG	Centaurea jacea	0.28	0.034				

III. What is the influence of the floral resources and the surrounding landscape on pollinator?

Table 18: AIC, ⊿AIC and marginal R² values for the generalized linear mixed-effect models regarding the effect of flower abundance or vegetation richness and percentage agriculture on the pollinator abundance (AB) and species richness (SR).

Response variable	Scale	AIC	⊿AIC	R² (m)
AB All	250	332.6	0.5	0.17
AB All	500	336.1	4	0.089
AB All	1000	332.1	0	0.21
AB Bee	250	311.9	4.4	0.0070
AB Bee	500	312.2	4.7	0.0037
AB Bee	1000	307.5	0	0.16
AB Hoverfly	250	375	0	0.18
AB Hoverfly	500	377	2	0.18
AB Hoverfly	1000	384.4	9.4	0.067
SR All	250	200.5	2.6	0.0079
SR All	500	200	2.1	0.022
SR All	1000	197.9	0	0.095
SR Bee	250	152	2.1	0.0029
SR Bee	500	151.5	1.6	0.021
SR Bee	1000	149.9	0	0.083
SR Hoverfly	250	164.8	0.2	0.011
SR Hoverfly	500	164.6	0	0.018
SR Hoverfly	1000	165	0.4	0.0063

Table 19: Summary of the results of the best generalized linear mixed-effect models with and without (n.o.) outliers of flower abundance or vegetation richness and percentage agriculture on the pollinator abundance (AB) and species richness (SR). For each model, the ⊿AIC (difference between the AICs of the best and second best model), marginal R², model estimate, z-value and p-value are given.

| Response variable	Scale	⊿AIC	R² (m)	Flower abundance/ vegetation richenss			Percentage Agriculture		
				Estimate	z	p	Estimate	z	p
AB All	1000	0.5	0.21	0.055	2.01	0.045	0.12	2.00	0.046
AB All (n.o.)	1000	0.9	0.17	0.053	1.97	0.049	0.062	1.46	0.14
AB Bee	1000	4.4	0.16	-0.014	-0.33	0.74	0.17	2.08	0.037
AB Bee (n.o.)	1000	2.3	0.14	0.082	1.71	0.087	0.14	1.58	0.11
AB Hoverfly	250	2.0	0.18	0.20	3.48	0.00051	-0.23	-3.35	0.00080
SR All	1000	2.1	0.095	-0.053	-0.93	0.35	0.10	1.59	0.11
SR All (n.o.)	1000	0.7	0.028	-0.027	-0.49	0.63	0.049	0.87	0.39
SR Bee	1000	1.6	0.083	-0.023	-0.25	0.81	0.15	1.49	0.14
SR Bee (n.o.)	1000	0.5	0.032	0.0058	0.065	0.95	0.078	0.87	0.38
SR Hoverfly	500	0.2	0.018	0.012	0.14	0.89	-0.062	-0.74	0.46
SR Hoverfly (n.o.)	500	0.2	0.018	0.0051	0.061	0.95	-0.059	-0.71	0.48
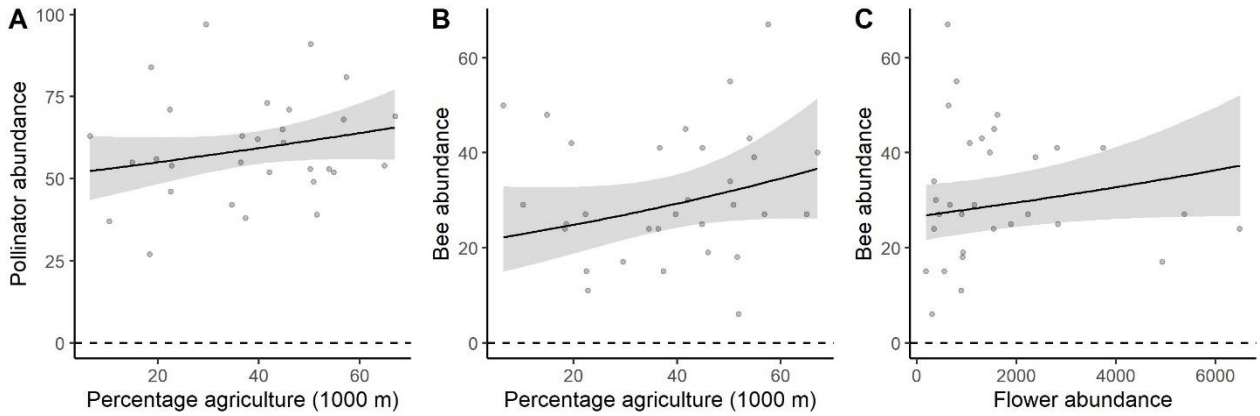
Figure 19: Relationship between the fixed variables percentage agriculture (A, B) and flower abundance (C) and the abundance of all pollinators (A) and bees (B, C). The solid lines represent the non-significant relationship, the grey shaded area the 95 % confidence interval and the black points the raw data.
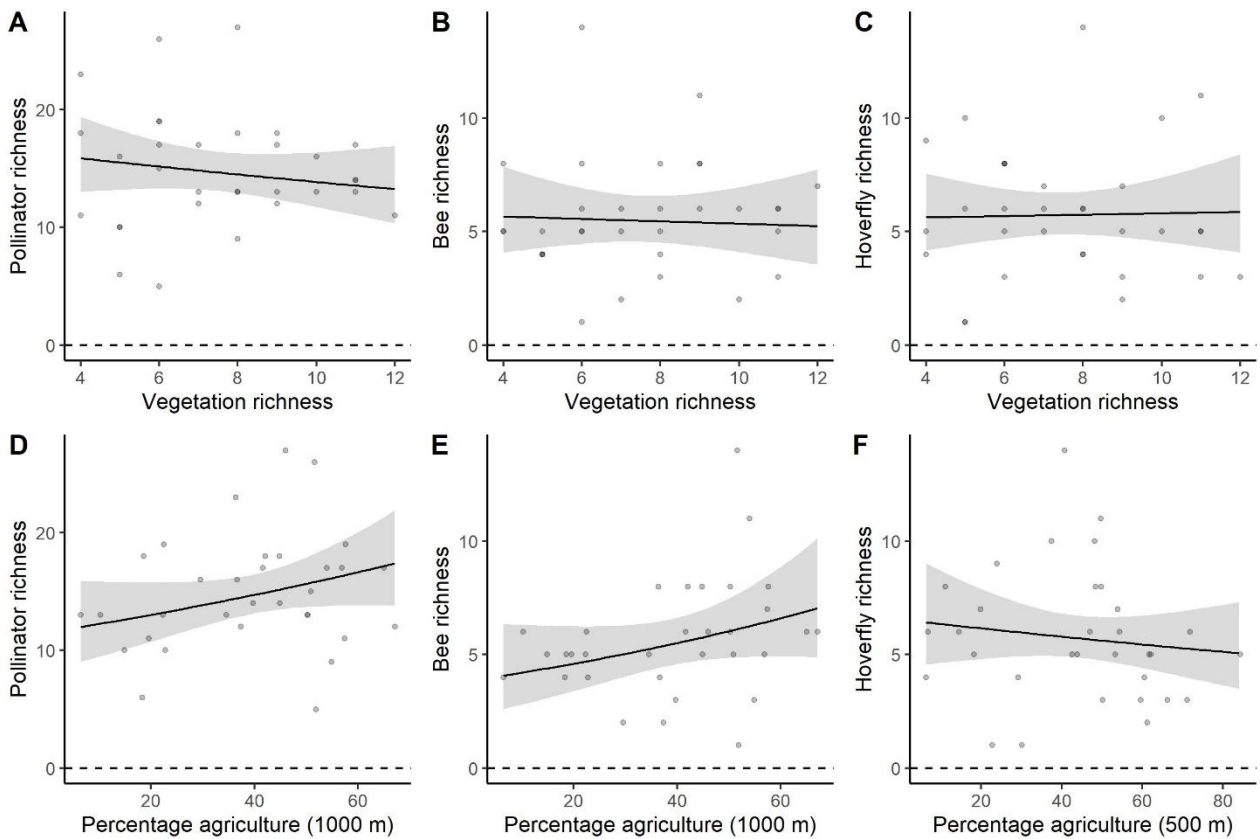

Figure 20: Relationship between the fixed variables vegetation richness (first row) and percentage agriculture (second row) and the species richness of all pollinators (A, D), bees (B, E) and hoverflies (C, F). The solid lines represent the non-significant relationship, the grey shaded area the 95 % confidence interval and the black points the raw data.

C. Discussion

Table 20: Summary of the results of generalized linear mixed-effect models of flower abundance on pollinator abundance, with the model statistics being the z-value and p-value.

Response variable	Fixed Variable	z	p
Abundance all	Flower abundance	2.19	0.028
Abundance bee	Flower abundance	-0.27	0.79
Abundance hoverfly	Flower abundance	1.55	0.12
Abundance butterfly	Flower abundance	1.78	0.075
Abundance wasp	Flower abundance	1.85	0.064

Table 21: The ten visited plant species with the highest flower abundance and their nectar volume per single flower or inflorescences (ml), pollen per single flower or inflorescences (mg) and number of caught pollinators for the CSA habitat. Flower abundance is expressed as mean flower abundance, calculated as the sum of the number of flowerheads per plant species, divided by the number of sampling locations (16).

Plant species	Flower abundance	Nectar (ml)	Pollen (mg)	Number of pollinators
Galinsoga quadriradiata	688	-	-	28
Eruca vesicaria	306	$8.31*10^{-4}$	-	89
Brassica oleracea	188	$1.31*10^{-3}$	1.15	79
Fagopyrum esculentum	172	$1.25*10^{-4}$	$9.48*10^{-2}$	43
Coriandrum sativum	113	-	-	50
Phaseolus vulgaris	88	$5.80*10^{-3}$	$8.00*10^{-1}$	33
Trifolium repens	85	$9.04*10^{-4}$	$6.40*10^{-1}$	17
Trifolium pratense	81	$5.19*10^{-3}$	$6.19*10^{-1}$	28
Origanum vulgare	76	$4.18*10^{-5}$	$7.03*10^{-3}$	43
Mentha sp.	56	-	-	16

Table 22: The ten visited plant species with the highest flower abundance and their nectar volume per single flower or inflorescences (ml), pollen per single flower or inflorescences (mg) and number of caught pollinators for the SNG habitat. Flower abundance is expressed as mean flower abundance, calculated as the sum of the number of flowerheads per plant species, divided by the number of sampling locations (16).

| Plant species	Number of flowerheads	Nectar (ml)	Pollen (mg)	Number of pollinators
Jacobaea vulgaris	103	$3.20*10^{-3}$	$2.67*10^{-1}$	63
Lotus corniculatus	70	-	-	36
Trifolium repens	66	$9.04*10^{-4}$	$6.40*10^{-1}$	30
Lythrum salicaria	58	$4.25*10^{-4}$	-	125
Centaurea jacea	57	$3.24*10^{-2}$	$1.09*10^{-1}$	117
Epilobium parviflorum	43	$6.55*10^{-4}$	3.39	9
Daucus carota	38	$1.20*10^{-3}$	$3.96*10^{-1}$	50
Pulicaria dysenterica	26	-	-	22
Lysimachia vulgaris	26	$1.53*10^{-5}$	-	8
Cirsium arvense	24	$1.23*10^{-3}$	2.73	51
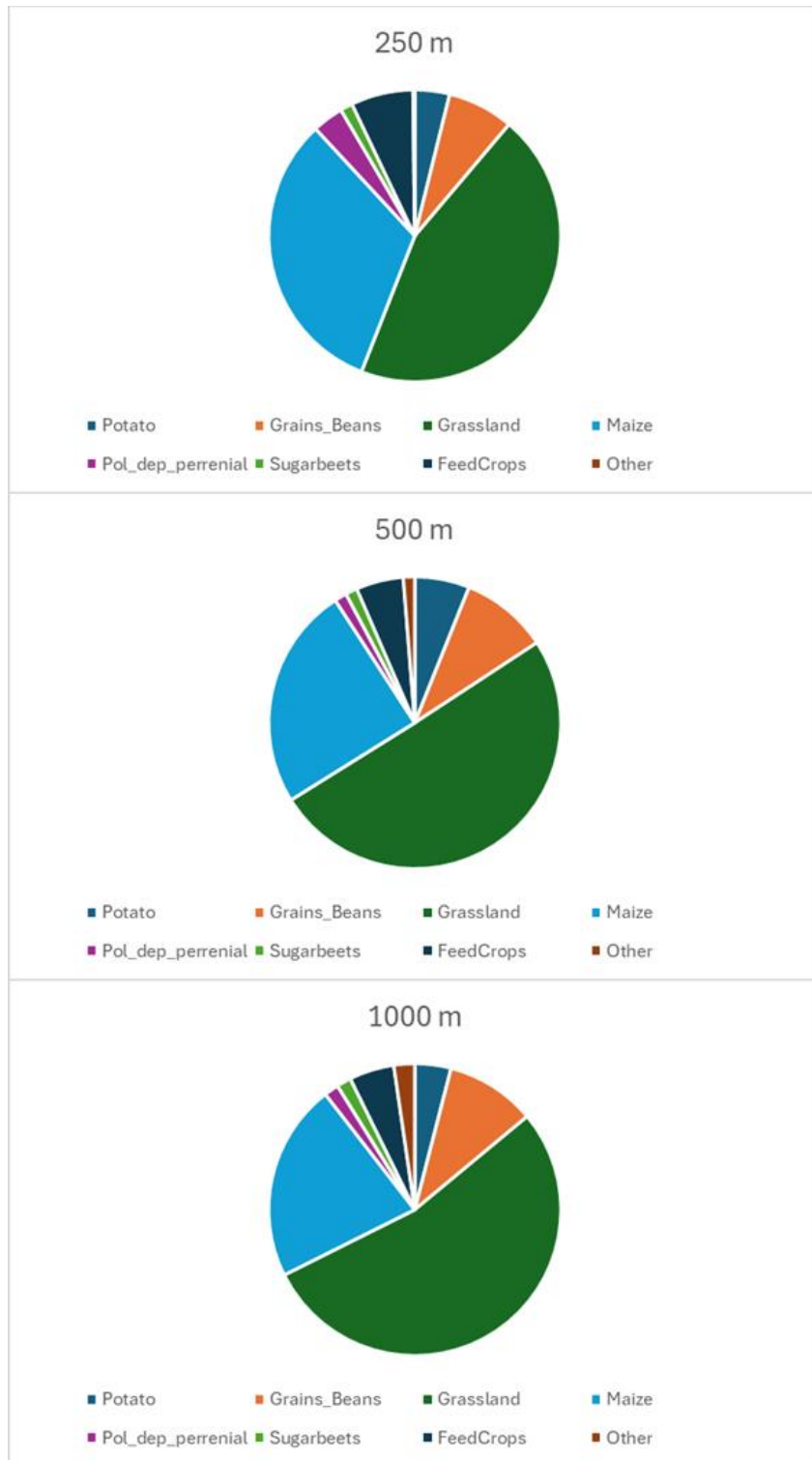
Figure 21: Pie chart with the share of each different crop type for the three different radii. The values for the cover of each crop type is calculated as the mean value over the sixteen different locations and over both habitat types.