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The importance of small forest fragments for pollination services in agricultural landscapes

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Thesis submitted in fulfilment of the requirements for the degree of Doctor (PhD) in Applied Biological Sciences: Forest and Nature management

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Abstract

Agricultural landscapes in North-Western Europe have undergone drastic changes since the second half of last century. Because of agricultural intensification, and associated changes in agricultural practices, productivity has strongly increased. However, this went along with a decline in biodiversity in farmland. In these intensively managed agricultural landscapes, small fragments of semi-natural habitat can play an important role in conservation of biodiversity.

In many agro-landscapes, forests make up a big share of the total area of semi-natural habitat. These forests are, however, often very small and highly fragmented. Small forest patches and the biodiversity they harbour, deliver important ecosystem services to society. These services range from regulating services, such as nutrient cycling, hydrological regulation or biological pest control, to provisioning services, such as delivering food and wood, and cultural services, such as recreational and aesthetic services. Over the last few years, more research has been performed on the role these forest fragments play in enhancing ecosystem services in agricultural landscapes. However, the role these fragments play in providing pollination services, an important regulating ecosystem service, has barely been investigated.

Pollination of wild plants and agricultural crops is in the temperate zone largely dependent on insects and plays an important economical and ecological role. However, several taxa of pollinators show a clear decline over the last decades, thus threatening this service. Small forest fragments may play an important role in conserving insect pollinators in these agricultural landscapes. Forest patches can provide both food sources, being nectar and pollen, and reproductive habitat. In this research, we looked at the role that local and landscape characteristics play in conserving and structuring the pollinator community. Furthermore, we investigated whether this resulted in an increase in pollination services. In our research, we focused on bees and hoverflies, two of the most important and best characterized pollinators.

Based on our results, it is clear that small forest fragments containing suitable foraging and reproductive habitat harbour a rich and diverse pollinator community. Old forests with a rich herb layer can play an important role as foraging habitat and as refuges for forest-dependent hoverflies. Sun-exposed forest edges with high amounts of suitable nesting habitat for ground-nesting bees can also contribute to enhancing pollinator diversity and abundance. A diverse and abundant pollinator community will lead to a better provision of pollination services, both to agricultural crops and wild plants.

Samenvatting

Landbouwlandschappen in Noord-West Europa hebben grote wijzigingen ondergaan sinds de tweede helft van de twintigste eeuw. Door intensivering van de landbouw en de hiermee geassocieerde veranderde landbouwpraktijken, is de productiviteit sterk gestegen. Dit ging echter ten koste van de biodiversiteit in deze landschappen. In deze intensief gebruikte landbouwgebieden kunnen kleine fragmenten semi-natuurlijk habitat een belangrijke rol spelen in het behoud van biodiversiteit.

In veel landbouwlandschappen vormen bossen een belangrijk aandeel van de totale hoeveelheid semi-natuurlijk habitat. Deze bossen zijn echter vaak zeer klein en versnipperd. Kleine bosfragmenten, en de biodiversiteit die ze herbergen, leveren belangrijke ecosysteemdiensten aan de maatschappij, gaande van regulerende diensten zoals nutriëntencyclering, regelen van waterhuishouding of biologische bestrijding, tot voorzienende diensten, zoals voedsel en hout of culturele diensten, zoals recreationele en esthetische diensten. De laatste jaren is er meer onderzoek verricht naar de rol die deze kleine bosfragmenten spelen in landbouwlandschappen. De rol van deze bosfragmenten in het voorzien van bestuiving, een belangrijke regulerende ecosysteemdienst, is echter amper onderzocht.

Bestuiving van wilde planten en landbouwgewassen is in de gematigde streken grotendeels afhankelijk van insecten, en speelt een belangrijke economische en ecologische rol. Verschillende taxa van bestuivers tonen echter de laatste decennia een duidelijke achteruitgang, waardoor deze dienst in gevaar dreigt te komen. Kleine bosfragmenten kunnen in deze landschappen een belangrijke rol spelen in het behoud van de bestuiversgemeenschap. Deze bosjes kunnen zowel voedselbronnen, in de vorm van nectar en pollen, als larvaal of nesthabitat voorzien voor verschillende soorten bestuivers. In dit onderzoek keken we naar de rol die deze lokale landschaps- en boskenmerken spelen in het behouden en structureren van de bestuiversgemeenschap, en in welke mate dit resulteerde in een toename in bestuivingsdiensten. We focusten voor ons onderzoek op bijen en zweefvliegen, twee van de belangrijkste en best gekende bestuivers.

Op basis van deze resultaten blijkt dat kleine bosfragmenten, mits de aanwezigheid van geschikt foerageer- en voortplantingshabitat, een rijke bestuiversgemeenschap kunnen herbergen. Oude bossen met een rijke kruidlaag kunnen een belangrijke rol spelen als foerageerhabitat en als leefgebied voor bosbewonende zweefvliegen. Bosranden die – al dan niet door gericht beheer – rijk zijn aan nestplaatsen voor grondbewonende bijen, kunnen ook een grote bijdrage leveren in het verhogen van de diversiteit en abundantie van wilde bijen. Een diverse en abundante bestuiversgemeenschap kan op zijn beurt dan weer leiden tot een betere voorziening van bestuiving aan zowel landbouwgewassen als wilde planten.

Chapter 1: Introduction

1. Biodiversity loss

With an estimated 1.25 million currently described eukaryotic species, and estimates of about 8.75 million extant species (Mora et al., 2011), Earth harbours a huge variety of living creatures. The resulting diversity in genes, traits and species, commonly called biodiversity, yields a wide range of benefits for humanity. These benefits are often termed ‘ecosystem services’, as they are considered as a service to society (Costanza et al., 1997).

Over the last decades, a steep global decline in biodiversity has been observed, which led to the conclusion that a sixth mass-extinction is occurring (Ceballos et al., 2015). Various, mainly anthropogenic drivers contribute to the current loss in biodiversity, including habitat destruction, climate change and invasive species (Brook et al., 2008). A decline in biodiversity often leads to a loss of ecosystem services (Cardinale et al., 2012) and can be a threat to food security (Thrupp, 2000), protection against natural disasters (Costanza et al., 2008) and human health (Sandifer et al., 2015).

2. Importance of pollinators

Insect pollination is an extremely important regulating ecosystem service, with 35% of the global crop production (Klein et al., 2007) and 90% of all flowering plant species (Nabhan and Buchmann, 1997) depending on it. Estimation of the economical importance of insect pollination is hard, but research indicates that the total global value of pollination runs in the hundred of billions of Euros per year (Gallai et al., 2009). Several crops, such as watermelon (Winfree et al., 2008) and squash (Hoehn et al., 2008) completely depend on insect pollination, while the yield of others, is strongly improved, both qualitatively (Bommarco et al., 2012; Garratt et al., 2014) and quantitatively (Bommarco et al., 2012; Garibaldi et al., 2013).

In addition to the economical importance of insect pollination, it also plays a key role in ecosystem functioning. In most terrestrial ecosystems, plants and insects interact in complex plant-pollinator networks. Throughout time, these networks may change. Newly introduced species of plants (Bartomeus et al., 2008) or pollinators (Aizen et al., 2008) enter the network, or species and interactions disappear due to species declines or local extirpation (Burkle et al., 2013) or phenological mismatch between plants and pollinators due to differential responses to climate change (Burkle et al., 2013). In this context, biodiversity loss may lead to serious disturbances in plant-pollinator interactions, in which extirpation of a pollinator may lead to a decline or disappearance of plant populations or vice versa (Rezende et al., 2007).

A third reason to conserve insect pollinators is simply the conservation of biodiversity. In addition to conserving economical benefits associated with biodiversity and conserving ecosystem stability, there are moral and aesthetic reasons to conserve biodiversity: it can be argued that letting species go extinct as a side-effect of our lifestyle is unethical (Caro et al., 2011). Additionally, many people appreciate the aesthetics associated with biodiversity (Longton and Hedderson, 2000), sometimes even at the level of smaller, less conspicuous life-forms.

3. Ecology of pollinators

In tropical regions, several vertebrates can act as important pollinators, such as birds (Ford, 1985), bats (Hodgkinson et al., 2003) or even primates (Kress, 1993) and lizards (Godínez-Álvarez, 2004). However, the most important pollinators are insects. While the honey bee, which has been managed for thousands of years (Roffet-salque et al., 2015), is the most well-known pollinator, various insect taxa play an important ecological role as pollinators. Concerning pollination, bees, with more than 16,000 described species (Danforth et al., 2006), of which 360 occur in Belgium (Rasmont et al., 2005) are the best studied taxon. However, several other insect taxa play an important role as pollinators (Rader et al., 2015), such as hoverflies (Jauker and Wolters, 2008), non-syrphid flies (Orford et al., 2015), butterflies (Jennersten, 1984) and beetles (Bernhardt, 2000).

Taxonomical differences between pollinators go along with strong differences in ecological requirements. In this dissertation, we focused on bees and hoverflies, as these are the best studied, and arguably the most important taxa of pollinators in the temperate region (Klein et al., 2007; Kremen et al., 2007). While both taxa play an important role in the ecosystem, their ecology can be very different.

3.1. Bees

Most bees build nests to lay their eggs. Females actively collect pollen, which serves as food source for larvae. Various nesting strategies exist. First, different degrees of sociality exist, ranging from solitary, individually nesting species to true eusocial bees, such as the honey bee. While solitary bees build nests on their own, truly eusocial bees have (a) individuals of the same species that co-operate in raising the next generation, (b) a division of work with sterile individuals working for reproducing individuals and (c) at least two overlapping generations working in the colony, where the second generation assists the parents (Wilson and Hölldobler, 2005). In between, a wide gradient in sociality exists, ranging from communal species that use common nests (e.g. some *Andrena* spp.), to semisocial species (e.g. several *Halictus* spp.), with individuals co-operating and specializing in different tasks, to primitively eusocial species (e.g. *Bombus* spp.). The latter differ from truly eusocial bees by the lack of big morphological differences between workers and queens (Michener, 1974).

Many bee species dig their nests in the soil, while others use existing cavities in dead wood, hollow plant stalks or walls. Some taxa, such as *Xylocopa* spp., chew their own nesting cavities in dead wood, while bumblebees can use old rodent burrows or bird nest boxes. Above-ground nesting bees often seal their nest cavities with mud, resins or hair (Peeters et al., 2012). This variety of nesting strategies results in different resources being used. Some kleptoparasitic species do not actively collect pollen, but lay their eggs in nests of other species. These kleptoparasite-host relations can be very strict, and presence of cuckoo bees is considered as a sign of a healthy bee population, making them good indicator species (Sheffield et al., 2013).

For survival and successful reproduction, bees depend on both pollen and nectar. Nectar, which is rich in sugar content, is used as an energy source, while pollen, containing proteins, is necessary for reproduction (Potts et al., 2003). Specialization in food sources differs strongly between species, varying from polylectic species, which forage on various plant families (Cane and Sipes, 2006), sometimes even on wind-pollinated plants such as corn and wild grass species (Malerbo-souza, 2011; Rivernider et al., 2017), to oligolectic species, which forage exclusively on specific plant families or genera (e. g. *Andrena vaga* on *Salix* spp.). Monolectic species strictly collect pollen from one or few closely related plant species, such as *Macropis europaeus* on *Lysimachia vulgaris* (Bassin et al., 2011).

As bees have to return to their nests after each foraging trip, the term ‘central place foragers’ has been coined (Westrich, 1996). The specific nesting requirements and pollen or nectar sources are often not present in the same area. Therefore, nesting habitat and foraging habitat are often considered as ‘partial habitats’ (Westrich, 1996). As foraging habitat should be present within a short distance from the nest, bees are very sensitive to habitat degradation (Winfree et al., 2011).

3.2. Hoverflies

While hoverflies visit flowers and consume nectar and pollen, they do not actively collect it, as larvae generally feed on other sources. Most hoverfly species are polylectic, showing no relationship with specific plant taxa, although exceptions exist (Branquart and Hemptinne, 2000a). Some species do not visit flowers but collect anemophilous pollen from leaf surfaces (e.g. *Xylota* spp.) (Ssymank and Gilbert, 1993).

Hoverflies do not build nests, but rather deposit their eggs in specific habitats, depending on the larval ecology, which is very diverse. Therefore, in contrast to bees, no sociality exists in hoverflies. Many species have larvae that feed on aphids (e.g. *Episyrphus balteatus*) and often thrive in agricultural landscapes, which raises interests in their use as biological control agents (Martínez-uña et al., 2013). Other species develop in dung (e.g. *Rhingia campestris*), mud (e.g. *Eristalis spp.*), dead wood or rotting holes in trees (e.g. *Xylota segnis*), sap streams (e.g. *Brachyopa* spp.) or social insect nests (e.g. *Volucella bombylans*). Several species have larvae that live in plants, and which are sometimes considered as pest species (e.g. *Merodon equestris*) (Reemer et al., 2009; Speight et al., 2016). While some species are generalists and occur in various habitats, many are restricted to specific biotopes, such as forests, wetlands or heathland.

While bees have generally been considered as the major group of pollinators, hoverflies also play an important role as pollinators in agricultural and natural habitats (Jauker et al., 2012; Ssymank et al., 2008). As hoverflies are no central-place foragers, they are less sensitive to anthropogenic disturbances and several species are able to survive in intensively managed farmland (Jauker et al., 2009), interest in these pollinators has increased over the past years.

4. Evolution of agricultural landscapes in North-Western Europe

Forty-eight percent of the area of Europe has been converted to agricultural land. The largest share of farmland consists of fields (59%), grasslands (34%) and permanent crops, such as orchards (7%) (European Union, 2018). Some elements in agro-landscapes can support an abundant and diverse pollinator community, such as extensively managed agricultural land with species-rich grasslands (Öckinger and Smith, 2007), legumes as green manure (Goulson et al., 2005; Goulson and Darvill, 2004) and small landscape elements, such as hedgerows (Hannon and Sisk, 2009). However, these landscapes have undergone drastic modifications since the start of the last century. These changes, including landscape simplification, more intensive tilling, increased pesticide and fertilizer use and changes in agricultural crops generally have adverse effects on biodiversity (Benton et al., 2003; Robinson and Sutherland, 2002). Several pollinator taxa underwent strong declines, including bumblebees (Goulson et al., 2008; Kosior et al., 2007), solitary bees (Biesmeijer et al., 2006) and butterflies (Van Dyck et al., 2009), while other groups, such as hoverflies, did not show a clear trend, at least at country level (Biesmeijer et al., 2006).

5. Agricultural landscapes as habitat for pollinators

Intensively managed agricultural landscapes are generally an unfavourable environment for wild pollinators (Marini et al., 2012; Ricketts et al., 2008). Ground-nesting bees are negatively affected by disturbances such as soil tilling on fields (Shuler et al., 2005) and soil compaction on meadows, resulting from higher densities of cattle (Kimoto et al., 2012). The latter also reduces the amount of pollen and nectar sources, together with the disappearance of species-rich grasslands (Öckinger and Smith, 2007). Additionally, use of pesticides places an additional pressure on pollinators in agricultural landscapes (Brittain et al., 2010b).

On the other hand, agricultural landscapes may be used by pollinators as habitat. Insect-pollinated mass-flowering crops can have a beneficial effect on the pollinator community (Westphal et al., 2003). A special case are orchards, which do not only provide ample pollen and nectar sources for a short period, but also can provide nesting opportunities for bees, as soil disturbance is less strong than on cropland. Furthermore, organic or less intensively managed farms with a higher proportion of semi-natural habitat may harbour a relatively rich pollinator community and deliver better pollination services (Holzschuh et al., 2008; Kennedy et al., 2013; Power et al., 2012, but see Brittain et al., 2010a). Additionally, agro-environmental schemes sometimes include measures to increase pollinator abundance and diversity by creating nesting places or sowing flower-rich field edges (Albrecht et al., 2007; Scheper, 2015; Wood et al., 2015). However, the intended beneficial effects of these measures are not always achieved (Kleijn et al., 2001).

5.1. Importance of forest fragments for wild pollinators

Semi-natural habitat is a broad term used to describe relatively ‘natural’ areas that have a more permanent character than cropland, such as hedgerows, woodlands and permanent grasslands (Duflot et al., 2015). Since species-rich grasslands have quasi disappeared in European agricultural landscapes (Strijker, 2005) and small landscape elements have largely been lost due to scale increases (Tscharntke et al., 2005), woodland is often the most abundant type of semi-natural habitat in agricultural landscapes. Small forest fragments can range in size from less than a hectare to several dozens of hectares, and can strongly differ in age and tree species composition. While small and scattered, these forest fragments therefore form one of the most abundant types of semi-natural habitat in many European agro-landscapes. Although these forest fragments are often degraded by anthropogenic influences, such as eutrophication and invasive species, they are generally a more stable habitat than the agricultural land in between, and can therefore serve as refuges for organisms that cannot survive in intensively managed agricultural land (Decocq et al., 2016). These forest fragments still possess a relatively high biodiversity and offer several ecosystem services, including erosion control, water regulation, social and cultural services and biological pest control (Decocq et al., 2016).

Most studies on pollinators focus on species-rich grasslands (e.g. Hegland and Boeke, 2006; Hopfenmüller et al., 2014; Tscharntke et al., 2002), urban environments (e g. Ahrné et al., 2009; Fortel et al., 2014; Quistberg et al., 2016) or cropland (Bailey et al., 2014; Carrié et al., 2018; Kim et al., 2006). In forests, however, the pollinator community has largely been neglected in the temperate region, while the tropics have been investigated more thoroughly (e.g. Brosi et al., 2007; Liow et al., 2001; Tylianakis et al., 2017). Although several studies show a positive relationship between forest cover and pollinator abundance and diversity (Farwig et al., 2009; Joshi et al., 2016; Shackelford et al., 2013; Watson et al., 2011, but see Winfree et al., 2007), they mostly focus at the landscape scale. Additionally, some studies have looked at the effect of local site characteristics (Fuller et al., 2018; Larrieu et al., 2015; Williams and Winfree, 2013). However, research on this topic is very scarce and mostly limited to hoverflies.

Forest fragments have the potential to serve as foraging and reproduction habitat for pollinators. Below-ground nesting bees benefit by the presence of undisturbed, sun-exposed bare soil, especially in south-exposed forest edges. Cavity-nesting species may use holes in dead wood. Many hoverflies are associated with woodland (Speight et al., 2016), and lay their eggs in rot holes, sap streams or dead wood. Additionally, forest fragments are often rich in floral resources, with especially older forest patches containing a rich herb layer (Bossuyt et al., 1999), which, particularly in spring, may be an important foraging resource for pollinators. The canopy may also serve as an important, but understudied, source of pollen and nectar (Ulyshen et al., 2010), and of non-floral resources, such as honeydew (Van Rijn et al., 2013).

5.2. Processes influencing the pollinator community

As pollinators are dependent on both nesting and foraging resources, environmental factors that affect their availability have a strong influence on the pollinator community. These factors act on different scales, ranging from local forest characteristics, to landscape or large-scale biogeographical characteristics. The factors influencing the pollinator community and therefore pollination services are displayed in Figure 1.1. Landscape composition and local habitat quality may affect floral abundance and diversity, which is linked to both pollinator abundance and diversity, as different species use different food sources. Additionally, species-specific responses to availability of reproductive habitat depends on nesting or larval requirements. Furthermore, reproductive and foraging habitat may be present in different land use types (Westrich, 1996), leading to a complex relation between landscape configuration and the pollinator community. In addition to this, phenological changes in availability of food resources throughout the year within land use types, and phenology of pollinator species may further complicate the relation between environmental characteristics and the pollinator community.

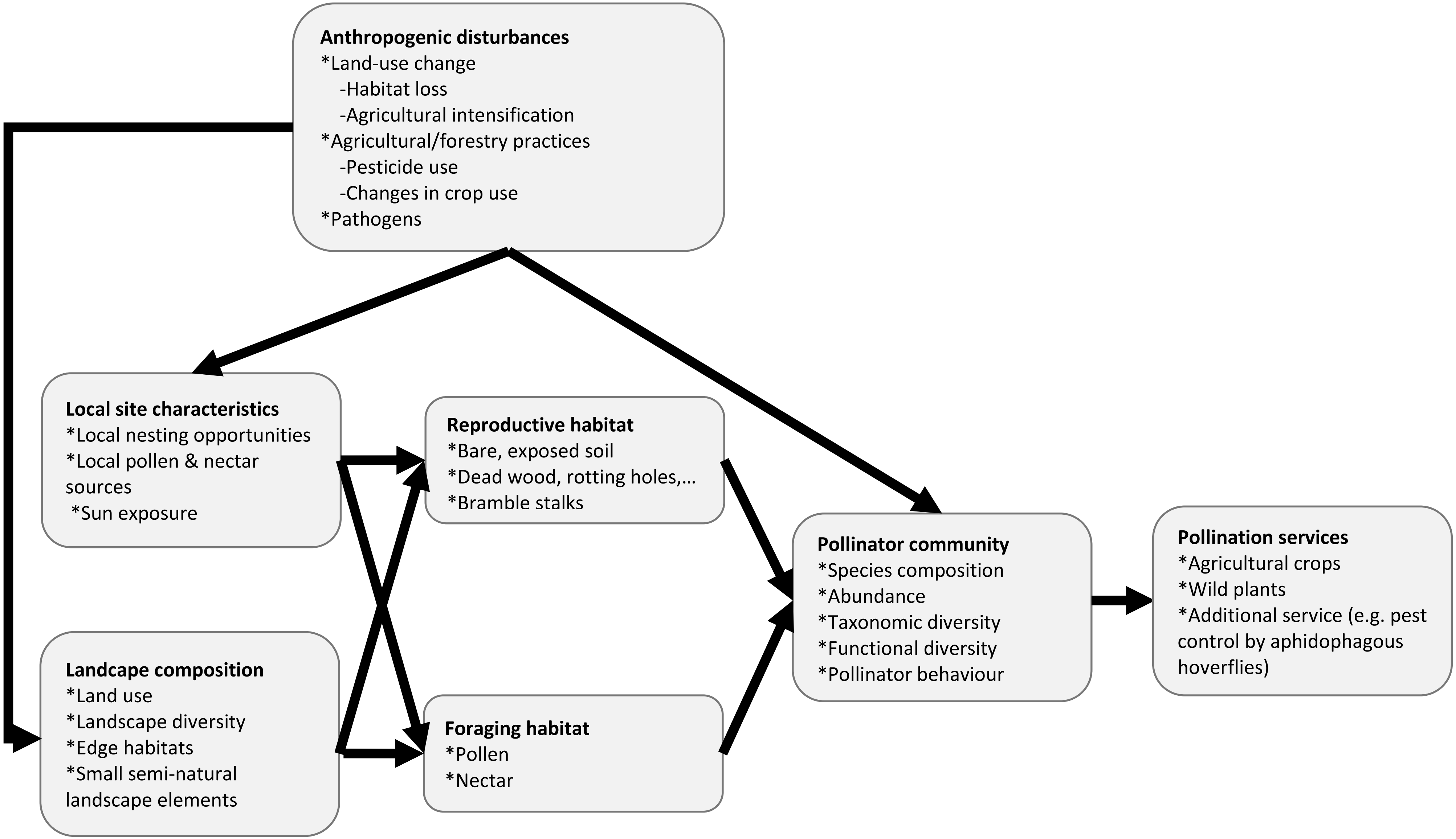

Figure 1.1.: Conceptual model of how anthropogenic disturbances and landscape and local site characteristics affect the pollinator community and pollinator community through influencing the quantity and quality of reproductive and foraging habitat.

6. Goals & Research questions

Woodland represents a high proportion of semi-natural habitat in agricultural landscapes. However, most of these forests are small and highly fragmented. Earlier studies (Decocq et al., 2016) have shown that these forest fragments often have a high ecological value and deliver important ecosystem services. However, research on pollinators in these small forest fragments is very scarce. While some species of hoverflies are strict forest specialists (Speight et al., 2016), most bees are generally more abundant in open landscapes (Grundel et al., 2010). However, given the adverse conditions in intensively managed agricultural land and the general absence of other types of semi-natural habitat in many agricultural landscapes, these forest fragments may act as refugia. Several species of bees, hoverflies and other pollinators may use forests as foraging or reproductive habitat. Both local and landscape characteristics are expected to structure the pollinator community in complex ways. We studied intensively managed agricultural landscapes with a large share of apple and pear orchards, where pollinators played an important role. We hypothesized that presence of abundant and diverse foraging, nesting (for bees) and larval (for hoverflies) habitat would lead to a more abundant and diverse pollinator community and that this would lead to better pollination services.

This leads to four main research questions, which we will address in this thesis:

Q1: How do local site characteristics and landscape composition affect the pollinator community in small forest patches in agricultural landscapes?

Q2: Does the pollinator community in small forest fragments respond differentially to environmental factors with season and taxonomical identity?

Q3: In what way does the surrounding landscape composition affect pollinator fitness in agricultural landscapes?

Q4: Do pollinator communities in more favourable habitat patches deliver better pollination services?

7. Thesis outline

Each of the research questions is answered in a distinct thesis chapter. While various insect taxa play a role as pollinators, it is impossible to study them all, given their huge ecological and taxonomical diversity. We focused on bees and hoverflies, as these are the best studied and arguably the most important taxa of wild pollinators. The ecology of both groups is well known and strongly different, which leads to other requirements for reproduction and survival, and possibly interesting differential responses to environmental drivers.

In **Chapter 2,** we treat the first research question (Q1). We used coloured pan traps to investigate the bee and hoverfly community in the edges of small forest fragments, at the interface between agricultural land and semi-natural habitat. We investigated the effects of local factors influencing the availability of foraging and reproductive habitat (e.g. floral abundance, availability of bare soil, presence of dead wood) and landscape composition (e.g. forest cover) on species richness, diversity and activity-abundance of bees and hoverflies. To extend the scope of this research, it was carried out in five 25 km^2 agricultural landscapes with varying land-use intensity ranging from the north of France to the south of Sweden.

Chapter 3 focuses on the differences between bees and hoverflies in their ecological requirements (Q2). Additionally, seasonal differences in responses, caused by seasonal habitat changes were investigated. This research was carried out in a single landscape in Glabbeek, Belgium, where pollinators were sampled with coloured pan traps and standardized transect walks for two consecutive years between March and August. Given the abundant presence of apple and pear orchards in this landscape, insect pollination is of substantial economical importance in the study region.

In addition to the responses of the community as a whole, we looked at the effect of landscape composition on the fitness of a single species (Q3). This is the subject of **Chapter 4**. Artificial *Bombus terrestris*-nests were placed in orchards during and after the bloom to assess the effect of semi-natural habitat both in presence and in absence of mass-flowering crops. Additionally, pollen was detached from foraging workers to determine the preferred foraging habitat.

While favourable conditions in forest fragments may lead to a richer and more abundant pollinator community, it is unclear whether this leads to improved pollination services. **Chapter 5** attempts to answer this research question (Q4). Phytometers were placed in the same forest fragments as chapter 3 to measure pollination. As different flowers attract different subsets of the pollinator community, two plants with morphologically strongly differing flowers – strawberry and blueberry – were used.

Chapter 6 synthesizes the results of the research described in the earlier chapters and summarizes the role that small forest fragments play in conserving the pollinator community in agricultural landscapes. We also propose guidelines to manage small forest fragments and agricultural landscapes to increase their value as pollinator habitat.

Chapter 2: Forest patches as pollinator habitat in agricultural landscapes

Adapted from:

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Abstract

Small forest fragments are often the most abundant type of semi-natural habitat in intensive agricultural landscapes. Wild pollinators can use these forest patches as nesting or foraging habitat. However, the importance of small forest fragments as pollinator habitat has been neglected so far. We evaluated the role of these forest patches as pollinator habitat, focusing on the effect of nesting and foraging resources, both at a local and at a landscape scale.

Pollinators were sampled with pan traps in 78 forest patches, spread over five study regions in Northwestern Europe. We evaluated effect of forest and landscape characteristics on bee and hoverfly species richness, diversity and activity-abundance.

We showed that the bee community is influenced by both microsite conditions and landscape characteristics. Species richness and activity-abundance were higher when suitable nesting resources, such as sloped terrain and bare soil were available. This suggests that forest edges are important in providing nesting sites, but that most species forage in different habitats. Hoverfly species richness was higher in old forest fragments. This relation was mainly caused by the presence of forest specialist hoverflies in old forest fragments.

Small forest fragments in agricultural landscapes can harbour a diverse pollinator community. Increasing the amount of nesting habitat, such as bare soil and sloped terrains is expected to have beneficial effects on the bee community, whereas older forest fragments should be conserved to sustain a rich hoverfly community.

1. Introduction

1.1. Pollinator declines

Insect pollinators provide important ecosystem services by pollinating about 87.5% of all known plant species (Ollerton et al., 2011), including 75% of all crop species. In total, 30% of agricultural production depends on insect pollination (Klein et al., 2007). However, there is increasing evidence for a decline in certain pollinators in Europe over the last decades. This has been assessed for bumblebees (Kosior et al., 2007) and solitary bees (Biesmeijer et al., 2006), whereas hoverflies show a less clear trend (Biesmeijer et al., 2006).

Northwestern European agricultural landscapes have undergone a thorough change during the last century. These changes often caused environmental damage and a decline in biodiversity (Stoate et al., 2009). Agricultural intensification, in particular through the conversion of semi-natural habitats (e.g. hedgerows, banks, grasslands, wetlands) into big parcels of arable lands and the heavy use of agrochemicals (e.g. fertilizers and pesticides), is widely acknowledged as the most important driver of this biodiversity loss (Butchart et al., 2010).

Although forest is generally not considered as the most important habitat type for most bee species (e.g. Grundel et al., 2010), in these intensively managed agricultural landscapes, forests often represent the most widespread remaining patches of semi-natural habitat. Both activity-abundance and species richness of wild bees has been shown to be higher in agricultural landscapes with a higher forest cover (Joshi et al., 2016; Watson et al., 2011) and near forest edges (Bailey et al., 2014). In this study, we focused on these forest fragments, since they may play an important role for pollinator conservation in agricultural landscapes.

1.2. Pollinator guilds

Several insect taxa play a role as pollinators. Bees and hoverflies are the most important pollinators in the temperate region (Larson et al., 2001) and their ecology is well studied. The ecology of these two groups differ strongly, which causes them to have differing habitat requirements and to respond differently to environmental features (Verboven et al., 2014).

Wild bees have several requirements for completing their life cycle and are dependent on ‘partial habitats’ (Westrich, 1996) as foraging or nesting habitat, that need to be close to each other. The specific requirements in nutrition and nesting opportunities depend on life history characteristics such as nesting behaviour, phenology and nutritional requirements.

In the first place, wild bees require sufficient floral resources (Scheper et al., 2014), both for nectar, which provides energy, and for pollen, which provides the protein necessary for reproduction. The second important factor is nesting habitat, which varies with the species’ life history. Based on nesting habitat, distinction can be made between ground-nesting bees and cavity-nesting bees

(Westrich, 1996). Presence of bare soil and sloped forest edges can serve as a proxy for nesting habitat for ground-nesting bees (Potts et al., 2005), whereas presence of dead wood is a proxy for cavity-nesting bees, the latter of which also contains species using hollow *Rubus*-stalks (Torné-Noguera et al. 2014). In addition to these two lifestyles, some bees are cleptoparasites (nest parasites). These species are often very host-specific and very sensitive to environmental disturbances and habitat changes. For this reason, they are sometimes considered as important indicator species to assess the environmental quality for pollinators and the state of the whole bee community (Sheffield et al., 2013).

Hoverflies are probably the best known dipteran pollinators (Jauker and Wolters 2008; Jauker et al. 2012). Although they seem to carry less pollen and are less efficient pollinators than bees, hoverflies can still provide an important contribution to pollination (e.g. Fontaine et al. 2006; Jauker & Wolters 2008). Ecologically they differ from bees in several ways, which affects their ecological requirements. As hoverfly larvae do not depend on pollen for their development, most species are less dependent on specific floral resources or on large pollen availability. In contrast to bees, hoverflies have more diverse larval requirements. Many species are not dependent on semi-natural habitat for nesting places as several species' larvae feed on aphids. These often occur abundantly in intensively managed cropland, which can serve as a habitat for these species. Therefore, the diversity and abundance of hoverflies is expected to be be less influenced by landscape and microsite characteristics. However, some species are true forest specialists (Speight et al., 2016). Many of these species have larvae that develop in dead wood, rotting holes or sap streams and are therefore strongly dependent on old forests with large amounts of dead wood.

1.3. Goal and research questions

The main goal of this study was to assess the effect of both landscape composition and microsite conditions on the pollinator community in south-facing forest edges of small forest patches embedded in agricultural landscapes. South-facing edges were selected to have an equal solar regime at each site and as this orientation was expected to be the most suitable for pollinators, being poikilothermous, and usually thermophilic animals. By replicating the research in five Western European regions, it was possible to make generalizations for this region.

Our main research goal was to assess how local and landscape conditions influenced the bee and hoverfly communities by affecting the presence of foraging and nesting resources. It was hypothesized that the pollinator community characteristics were strongly related to:

(1) Microsite conditions, which influence the availability of nesting and foraging resources in the forest edge. The pollinator community is expected to be more diverse and show higher activity-abundances in sun-exposed forest edges with sufficient nesting habitat, such as bare soil and dead wood, and foraging resources.

(2) The surrounding landscape: forests and hedgerows can provide nesting and foraging habitat. A high forest cover and a large amount of edge-habitat in the direct vicinity are therefore expected to increase diversity and activity-abundance of pollinators.

(3) We further hypothesized that hoverfly species richness and activity-abundance are less influenced by landscape characteristics and local microsite conditions, since they are not central place foragers and since the community as a whole is ecologically more diverse due to differences in larval ecology, leading to a higher diversity of potential nesting sites. However, species that specifically depend on forest habitat for survival and reproduction are expected to be more abundant in larger and older forest fragments.

2. Material & Methods

2.1. Study regions

The study was performed in five 5 x 5 km² study regions in Northwestern Europe (Figure 2.1.). The selected regions are typical Northwestern European rural landscapes. They are dominated by agriculture, with scattered small forest fragments. The land use varied from very intensive agriculture dominated by open cropland in the French study region, to a more diverse landscape, with orchards, fields and intensively managed meadows in Belgium and Sweden and less intensive agriculture in the West and East German regions, with a relatively large share of forest and extensively managed grassland respectively, but slightly larger parcel sizes in East Germany (Appendix 2.A.).

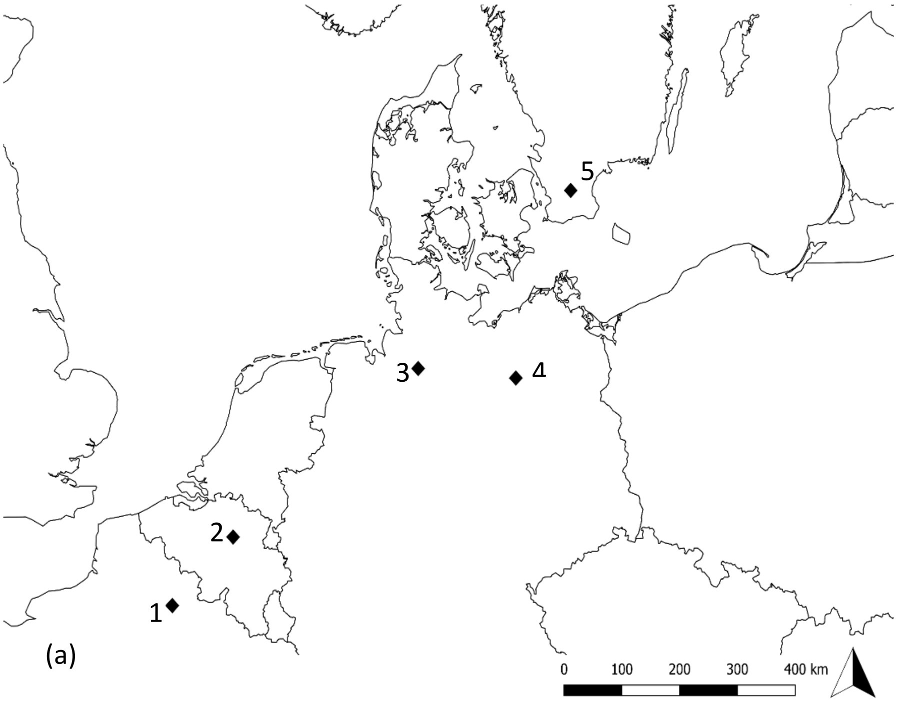
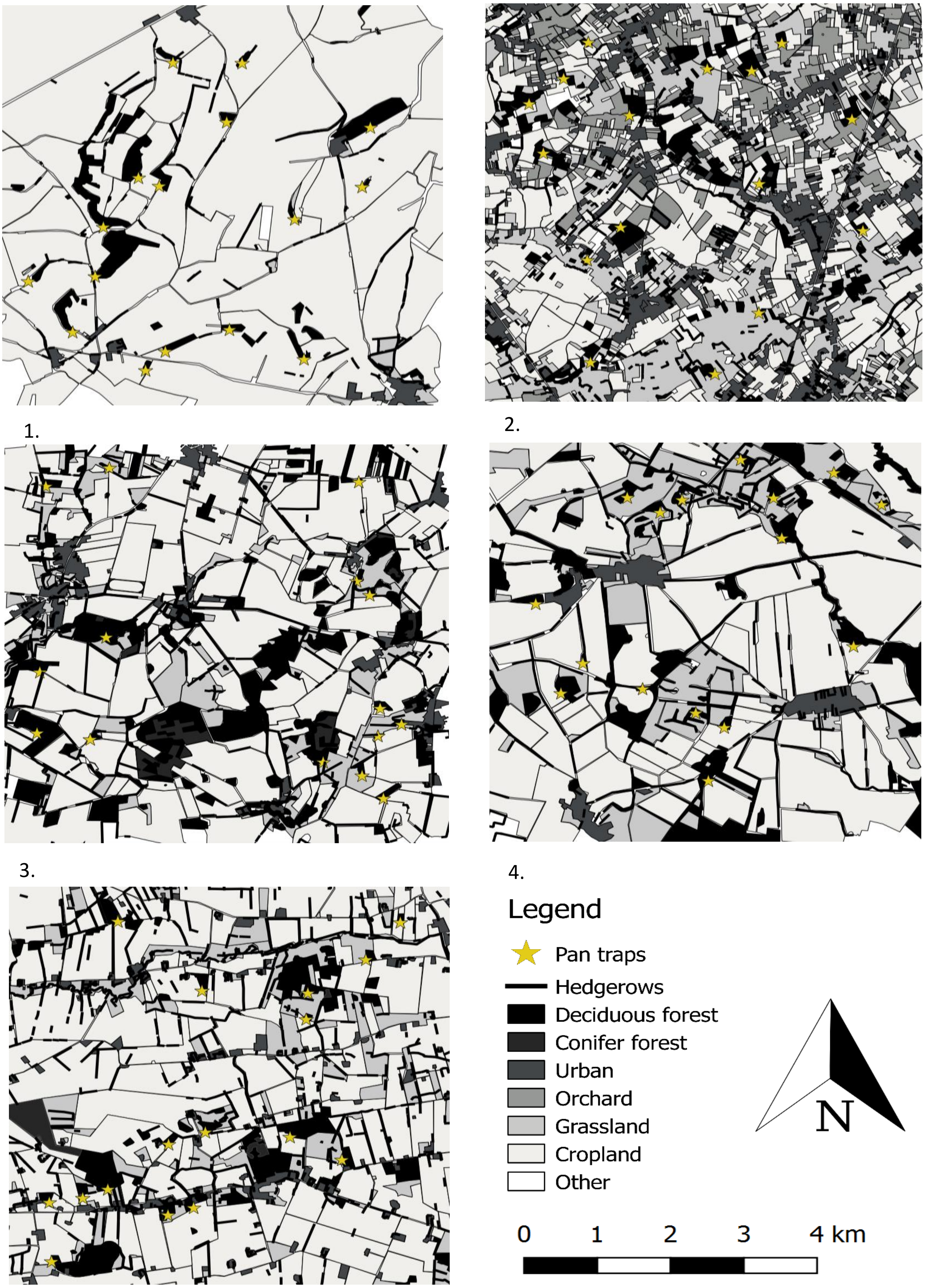


Figure 2.1.: (a) Overview of the five regions from this study and (b) maps of each study region.: 1. Vermandois (Fr); 2. Glabbeek (Be); 3.Zevener Geest (De); 4. Prignitz (De); 5. Sebbarp (Se)



(b)

Figure 2.1. (continued)

2.2. Site selection and pollinator sampling

In each region, 16 deciduous forest fragments (area: 0.30-28.1 ha) were selected to encompass a broad range in patch size and patch age in each region. Forest patches had a mixed tree species composition but were mostly dominated by ash (*Fraxinus excelsior* L.), beech (*Fagus sylvatica* L.), sessile oak (*Quercus robur* L.) or red oak (*Quercus rubra L.*). All selected forest patches had a closed canopy (canopy closure >80%). In West Germany and France, one forest fragment was omitted from analyses due to theft of the traps. In total, 78 forest patches were sampled for pollinators.

Pollinators were sampled in mid-April, at the end of May and in the beginning of July for two consecutive years (2015-2016) to compensate for yearly fluctuations of individual species (Garratt et al., 2014). Blue, yellow and white pan traps (Ø 20 cm, Motip® Fluor Blue, Motip® Fluor Yellow, Motip® High Gloss White) were placed in the south-facing forest edge in each selected fragment (Campbell and Hanula, 2007). The three traps were attached to the outer trees in the forest at 1.3 m above the ground to prevent disturbance by wild boar. The pan traps were filled with water and a drop of bio-degradable detergent to break the surface tension. The pan traps were placed at least three metres apart from each other to prevent interference (Droege et al., 2010).

The traps were set out for four days under suitable weather circumstances (cloud cover < 50%; wind speed < 5 m s^{-1}) and at temperatures representative for the time of the year. After emptying the traps, the animals were stored in 70% ethanol. In the lab, bees and hoverflies were sorted out, dried, pinned and identified. Voucher specimens were deposited in the collection of the Forest and Nature Lab, Dept. of Environment, Ghent University.

2.3. Explanatory variables

Forest patch and edge features

Forest and forest edge characteristics were measured in May 2016 in all five regions (Table 2.1., Figure 2.2.). Forest edge characteristics (cover bare soil, *Rubus* cover) were measured at five 1 m² squares, each spaced 10 metres apart. Slope length was measured at the same points over the whole width of the forest edge. Herb layer cover was determined in three 50 m long transects from forest edge to inner forest. On each transect, the herb layer cover was assessed in five equally spaced 5x5 m² plots. Presence of dead wood (diameter > 30 cm) was measured up to 50 m inside the forest. Forest age was calculated as the area-weighted average age of all stands within each forest patch (Appendix 2.A.2.).

Table 2.1.: Evaluated forest, forest edge and landscape characteristics. For forest edge characteristics, the area between the exterior row of trees and the beginning of other land uses was used.

Variable	**Explanation**		**Min.**	**Average**	**Max.**
FOREST (EDGE) CHARACTERISTICS					
Age	Area-weighted average age of all stands in the forest fragment, based on map data.		12	100	269
Bare soil	Bare, unvegetated soil in forest edge (% cover)		0	9	53
Dead wood	Dead Wood in forest edge, in 50m radius around traps (0=absent; 1 = 1-2 trunks present; 2 = over 2 trunks present		0	0.63	2
Edge width	Width of forest edge (m), defined as distance between final tree row at stem basis and start of other land use (meadow, field)		0.50	2.78	10.50
Flower index	Sum of Tansley-scores (0-5) of all insect-pollinated plant genera within 200m around the pan traps		14	33.9	52
Herb	Herb layer cover up to 50m inside forest fragment (% cover)		5	68	100
Rubus %	Cover of *Rubus* spp. in forest edge (% cover)		0	12	100
Slope	Length of sloped terrain in forest edge (m)		0.00	0.47	3.27
Sun exposure	Insolation of the forest edge, based on sun exposure at 10:00, 13:00 and 16:00. Categorical (0 = Shade; 1 = Sun)		-	-	-
LANDSCAPE CHARACTERISTICS					
Forest	Forest cover measured within 100, 200, 300, 400 m radius around the sampling point (ha)	100 m	0.23	1.04	2.25
		200 m	0.25	2.86	8.65
		300 m	0.57	4.81	15.84
		400 m	0.78	7.17	21.84
Forest edges	Total length of forest edges within 100, 200, 300, 400 m radius around the sampling point (m)	100 m	138	287	624
		200 m	230	754	2491
		300 m	357	1331	3852
		400 m	496	2060	4983
Hedgerows	Total length of hedgerows within 100, 200, 300, 400 m radius around the sampling point (m)	100 m	0	31	207
		200 m	0	214	1146
		300 m	0	503	1998
		400 m	0	978	3637

The sun exposure differed per location, as tree shadows reduced insolation of the forest edge at some sites. Sun exposure of the pan traps was assessed at three points during the day (10:00, 13:00 and 16:00). Trapping locations that were exposed to solar radiation at two or more points during the day were considered sun-exposed, whereas locations that were less exposed were considered as shaded.

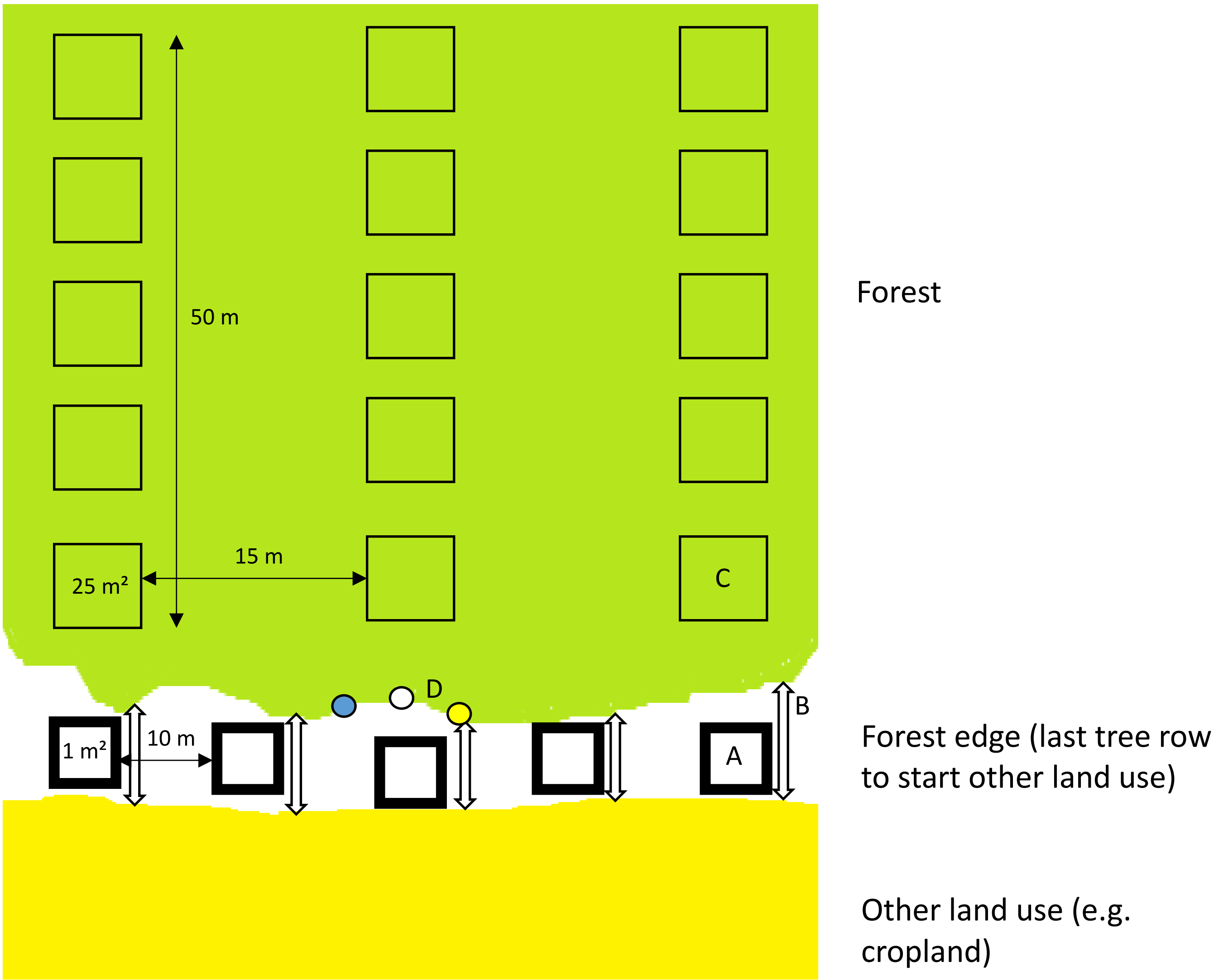


Figure 2.2.: Setup showing the assessment of the environmental variables used in the model. Within the thick squares (A), measuring 1m² in area, the cover of bare soil and Rubus*-cover were measured, while at the same place forest edge width and slope were measured along the full width of the forest edge (B). Herb layer cover was measured in 25m²-squares along three 50m transects from forest edge to forest interior (thin-lined squares, C). Amount of dead wood was measured within the complete 45x50m²-area bordered by the outer two herb-layer transects. The position of the pan traps is indicated by the yellow, blue and white circles (D). Sun exposure was measured here.*

The plant community was assessed in a 200m radius surrounding the pan traps. The plant community was surveyed in six 2 m wide and 200m long, radially oriented transects going outward from the trapping location. Insect pollinated plants were identified up to the genus level and cover was scored on a 0-5 Tansley scale (Alberdi et al. 2010) A flower-index, composed of the sum of the

Tansley scores of the plant taxa present ($Taxonsum = \sum_{taxon=1}^{taxon} tansley_i$) was considered as a measure for floral resource quality.

Landscape characteristics

The land cover type around each forest fragment was analyzed using QGIS 2.16 (QGIS Development Team, 2015). Based on aerial photographs and terrain visits, land use classes were determined within a radius of 100m, 200m, 300m and 400m around the traps. Land use was classified into six classes: deciduous forest, coniferous forest, cropland, grassland, urbanized area and orchards. Deciduous forest and cropland were the only land use classes with a comparable share in each region. As there were strong negative correlations between cropland and deciduous forest (r = -0.35 to r = -0.41, depending on spatial scale), deciduous forest was the only land use class used as an explanatory variable in the analyses. Additionally, the length of forest edges and hedgerows within a 100m, 200m, 300m and 400m radius were measured.

2.4. Data analysis

Bees and hoverflies were analysed separately. All specimens from each field campaign (*n*=6) were pooled per forest patch in further analyses. Because species accumulation curves did not show saturation, species richness was rarefied (Gotelli and Colwell, 2001). As explanatory variables were measured at different scales, they were standardized by subtracting the mean and dividing by their standard deviation, to allow comparison of effect sizes. Rarefied species richness, Shannon diversity and activity-abundance, represented by the number of specimens caught in each forest patch, were used as response variables.

First, models were run using forest cover, forest edge length and hedgerow length as explanatory variables at all analyzed scales, and species-richness, diversity and activity-abundance as response variables (Holland et al., 2004). Based on the R^2 of these models, the optimal scale was chosen to be 100 m.

To avoid multicollinearity, explanatory variables were analyzed using variance inflation factors (VIF). A VIF larger than three indicated multicollinearity. Highly correlated variables were removed from the models.

Statistical models were performed to assess the effect of the environmental variables (Table 2.1.) on species richness, Shannon diversity and activity-abundance of bees and hoverflies separately. Region was included as a random effect. Full random intercept models, random slope models and models without random term were compared based on their AICc-values, using restricted maximum likelihood. For models on bee and hoverfly species richness and diversity, adding region as a random effect did not improve the model fit, thus the random factor was removed from the model. General linear models were then used to assess the optimal fixed structure. We used AICc-optimization to select the optimal model. All models with a ΔAICc<2 compared to the optimal model were considered equivalent and are given in Appendix 2.B.

As the models on bee and hoverfly activity-abundance were overdispersed, a generalized linear mixed model using a negative binomial distribution was used. The optimal random structure was selected by AICc-comparison of models containing all fixed effects. For the models on bee species richness, we used a random slope, allowing the effects of sun exposure to differ per region, whereas for hoverfly species richness, the random intercept model fitted the data best. Inference of the optimal fixed structure was performed by AICc-optimization, using maximum likelihood. All models with a ΔAICc<2 compared to the optimal model were considered equivalent and are given in Appendix 2.B. Final model estimation was done using restricted maximum likelihood (Zuur et al., 2009).

Given the strong ecological differences between hoverfly species, these were divided in a group of 'forest specialist'-species and 'non-forest specialist' species based on the database of Speight et al. (2016). For models on forest specialist hoverflies, a generalized linear mixed model using a Poisson distribution with log-link function was used. Allowing the effect of forest cover to vary over the regions provided the best model fit. As the model on non-forest species was overdispersed, a generalized linear mixed model with negative binomial distribution was used. The random intercept model provided the best fit. Selection of the optimal fixed model structure was performed in the same way as for bee and hoverfly activity-abundance, with equivalent models displayed in Appendix 2.B.

3. Results

In total, 4867 pollinators were caught during the study, including 3376 bees belonging to 111 species and 1491 hoverflies belonging to 46 species (Table 2.2.). A detailed table is given in Appendices 2.C.1. and 2.C.2.

3.1. Bees

1995 individuals and 30 species belonging to the genus *Andrena* were caught, (59.1% of all bee specimens). The genus *Lasioglossum* was repesented by 766 individuals (22.7%) belonging to 28 species and *Bombus* by 420 individuals (12.4 %), belonging to 14 species. In total, 138 individuals (4.1%) belonged to cleptoparasitic taxa. The vast majority of all solitary bees, 2881 individuals (85.3%), were ground-nesting, solitary or communal species. Only 48 cavity-nesting solitary bees were caught (1.4%).

Bee species richness was significantly positively associated with the presence of hedgerows and the forest cover (Figure 2.3.; Table 2.3). The presence of sloped forest edges and herb layer cover had a marginally significant positive effect ($p < 0.10$). Additionally, there was a strong positive effect of sun exposure.

Shannon diversity of bees showed a significant positive relationship with the presence of hedgerows and sun exposure. Furthermore, presence of sloped terrain had a marginally significant positive effect on bee diversity.

The activity-abundance of bees in forest edges was significantly positively influenced by the amount of forest edge habitat present near the pan traps *Rubus*-cover, presence of bare soil and sun exposure of the forest edge.

Table 2.2.: Specimens and species number of hoverflies and bees caught in the five study regions.

Regions	**Specimens**			**Species**		
	Bees	**Hoverflies**	**Total**	**Bees**	**Hoverflies**	**Total**
1. Vermandois, Fr	1718	768	2486	62	24	86
2. Glabbeek, Be	344	284	631	45	25	70
3. Zevener Geest, De (W)	233	154	386	28	24	53
4. Prignitz, De (E)	491	111	601	38	16	54
5. Sebbarp, Se	590	174	764	47	23	70
Total	3376	1491	4867	111	46	156

3.2. Hoverflies

Among the 1491 hoverflies caught in this study, *Episyrphus balteatus* was by far the most common species, with 670 individuals caught (44.9% of total). Looking at larval ecology, the majority, representing 1018 specimens (68.3%) belonged to species with aphidophagous (aphid-eating) larvae. A second large group, represented by 251 specimens, had larvae developing in muddy habitats or in manure (16.8%). 205 individuals (13.7%) belonged to species with larvae developing in rotting wood. A very small share belonged to species with phytophagous larvae (7 specimens) or larvae living in social insect nests (10 specimens).

Hoverfly species richness and Shannon diversity were significantly higher in older forests, with higher herb cover and more bare soil in the forest edge (Figure. 2.3.; Table 2.4.). Sun exposure was the only variable that significantly influenced hoverfly activity-abundance. However, when only looking at species that depend on forest habitat, hoverfly activity-abundance was strongly linked with higher forest cover. Generalist species that did not depend on forest habitat were only positively affected by sun exposure and sloped terrain.

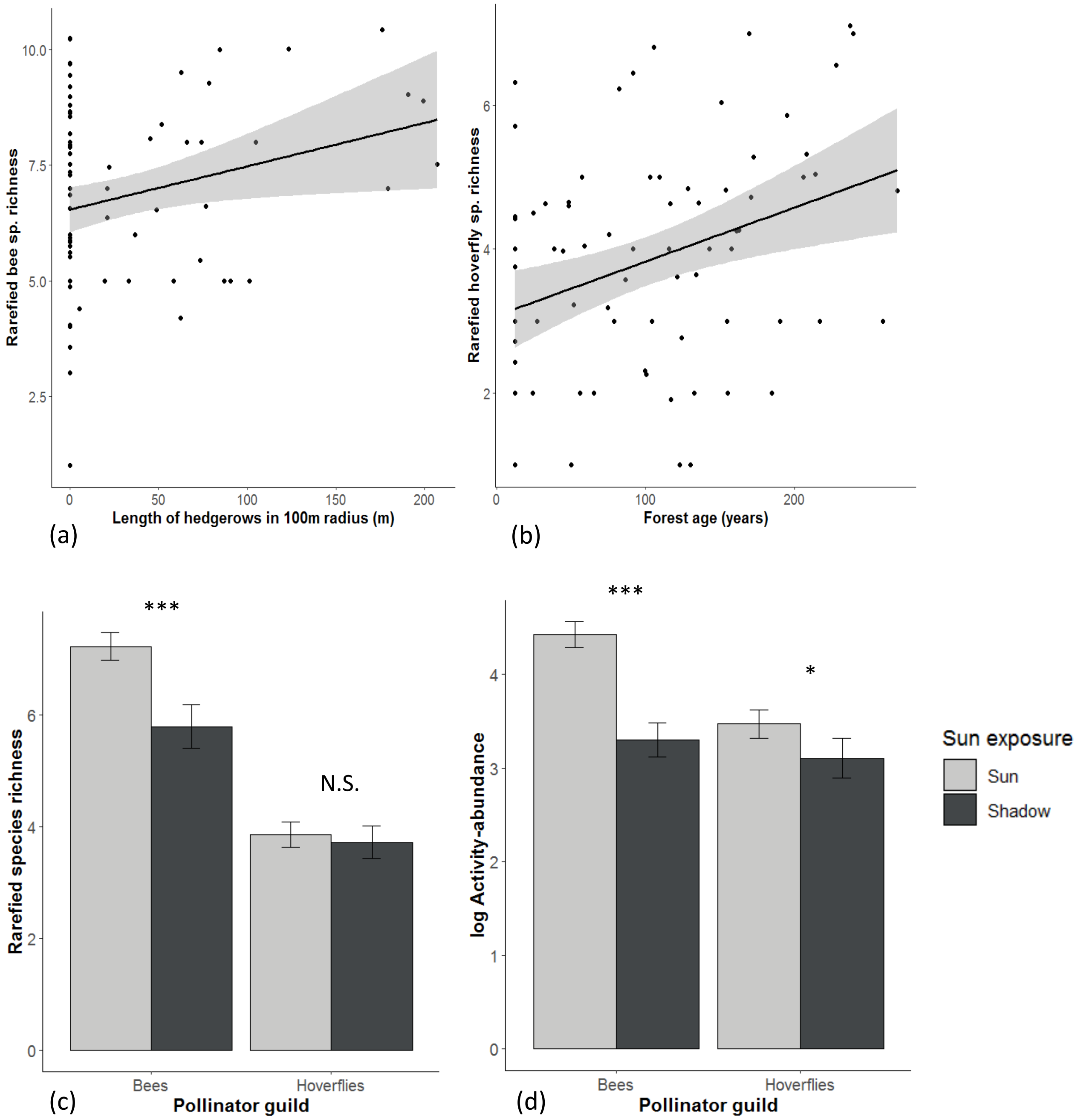


Figure 2.3.: Graphs showing the relation between the pollinator community and local and landscape characteristics: (a) relation between bee species richness and amount of hedgerows near the forest edge, (b) hoverfly species richness and age of the forest fragment, (c) effect of sun exposure on species richness and (d) effect of sun-exposure on pollinator activity-abundance.

Table 2.3.: Best models for bee species richness, diversity and activity-abundance. Effect size and SE are given; level of significance is indicated: · p<0.10; * p<0.05; ** p<0.01; *** p<0.001. *Presence of dead wood, weighted plant species richness, forest edge width and forest age were not significant in any model and were ommitted from the table*.

	Intercept	**Bare soil**	**Forest cover**	**Forest edge**	**Herb**	**Hedgerows**	**Rubus**	**Slope**	**Sun**	**Random effect**
Species richness	6.83*** ±0.19		0.48* ±0.21		0.35. ±0.20	0.66*** ±0.20		0.34. ±0.20	0.76*** ±0.20	-
Shannon diversity	1.83*** ±0.05		0.08. ±0.05			0.12* ± 0.05		0.08. ±0.05	0.19*** ±0.05	-
Act.-abundance	3.35*** ±0.29	0.19* ±0.08		0.17* ±0.08			0.22* ±0.09		0.57*** ±0.16	Sun|Region

Table 2.4.: Best models for hoverfly species richness, diversity and activity. Effect size and SE are given; level of significance is indicated: · p<0.1; * p<0.05; ** p<0.01; *** p<0.001. *Presence of dead wood, weighted plant species richness, sloped forest edge, hedgerows and forest edge length were not significant in any model and were ommitted from the table*.

	Intercept	**Forest age**	**Bare soil**	**Herb**	**Sun**	**Slope**	**Forest cover**	**Edge width**	**Random effect**
Species richness	3.83*** ±0.17	0.53* ±0.17	0.34* ±0.17	0.35* ±0.17					-
Shannon diversity	1.16*** ±0.06	0.16* ±0.06	0.12. ±0.06	0.10. ±0.16					-
Activity-abundance									
Total	2.69*** ±0.31				0.19* ±0.09				Region
Non-forest	2.10*** ±0.37				0.27** ±0.09	0.15 ±0.09			Region
Forest	0.99*** ±0.27						0.31** ±0.10	-0.16 ±0.09	For. cover|Region

4. Discussion

4.1. Differing effects of forest characteristics on pollinator guilds

4.1.1. Bee community

Presence of hedgerows and forest edges had a strong positive effect on bee species-richness and activity-abundance. These landscape features can harbour a diverse plant community (McCollin et al., 2000) and serve as a good indicator for foraging resources when looking at the bee community as a whole. However, as these edge habitats also play an important role as nesting habitat (Holzschuh et al., 2009), it is hard to disentangle the effect of both resource types on the bee community. Additionally, due to their spatial configuration, hedgerows are often used by bees as reference points to guide their foraging trips. Therefore, species that are more associated with other habitat types can be guided from the surrounding landscape to forest edges by following hedgerows (Cranmer et al., 2012), increasing the total species pool in the forest edge.

Local forest and forest edge features such as presence of bare soil, *Rubus*-cover and presence of sloped forest edges had a positive effect on bee species richness, diversity and activity-abundance. These variables are considered as a proxy of nesting site quality (Potts et al., 2005), indicating the importance of forest edges as nesting place for bees in intensive agricultural landscapes. Sun exposure also had a very strong positive effect on the bee community. While this may partially be a technical effect due to pan traps being more exposed, an thus more attractive to bees, being thermophilic species, ground-nesting bees, which made up the majority of the bee community in the forest edges, are expected to benefit from sun-exposed, bare soil in sloped, south-oriented forest edges.

We detected a positive effect of forest cover on bee species richness. A larger area of forest within short range can increase the amount and diversity of nesting and – in spring, during the flowering period of most forest herbs – foraging habitat, as a larger forest area is correlated with higher habitat heterogeneity (Ouin et al., 2006). Especially less mobile species that nest in the forest edge may benefit from a higher forest cover (Taki et al., 2007).

Presence of nesting resources has a strong influence on bee species richness, diversity and activity-abundance in our study. In general, the importance of nesting habitat is poorly known (Murray et al., 2009; Roulston and Goodell, 2011) and most studies consider pollen and nectar availability as primary drivers in the pollinator community (Potts et al., 2004, 2003; Schaffers et al., 2008; Torné-Noguera et al., 2014). However, these studies focus on other habitat types, such as grasslands and mediterranean shrubland, where nesting habitat may be more abundant and more uniformly distributed. In intensive agricultural habitats, nesting habitat is often limited to small areas of semi-natural habitat, while cropland can often still provide pollen and nectar.

Most bees in our study belonged to ground-nesting species, whereas cavity-nesting species were found in very low numbers. Cavity-nesting species may have been overlooked as they may be more abundant in the canopy (Ulyshen et al., 2010), or they may actually be less abundant in forest habitat (Sobek et al., 2009). However, even keeping this in mind, the numbers of cavity-nesters were very low. Many above-ground nesting species use holes in dead wood, which is scarce in most forests in the study region (Vandekerkhove et al., 2011).

4.1.2. Hoverfly community

Hoverfly species richness and diversity were positively affected by the age of the forest fragments. Additionally, herb layer cover and presence of bare soil in the forest edge had a positive effect on species richness. Other local and landscape characteristics did not have a significant effect. As several generalist species thrive in intensive agricultural land (Cowgill, Sotheron and Wratten 1993) and are present throughout the landscape, the community as a whole is less influenced by forest characteristics than the bee community. Many aphidophagous species, which represent more than two-thirds of all individuals caught, are generalist species and can complete their lifecycles in cropland, being less dependent on semi-natural habitat. However, several species are forest specialists, often requiring rotting wood for larval development (Speight et al., 2016). These species, which showed a higher activity-abundance at sites with a high forest cover, mainly occur in older forests, increasing the total species richness in the forest edge community and making these old forests more diverse and species rich.

A similarly low sensitivity of hoverflies to landscape context was found by Jauker et al. (2009). Hoverflies do not build nests and environmental requirements for egg-deposition and larval development are much more diverse (Reemer et al., 2009). Therefore, southern forest edges are generally less important as habitat for hoverflies in agricultural landscapes than the forest itself, which serves as a necessary habitat for several forest-associated species.

4.2. Ecological significance of forest fragments for the pollinator community

The positive effect of forest fragments on pollinators and pollination in the agricultural matrix is well studied in the temperate region (e.g. Farwig et al. 2009; Schüepp et al. 2011; Bailey et al. 2014). However, these studies focused either on pollination services or on the pollinator community inside the agricultural matrix, whereas we investigated the communities in the forest edge and explored the effects of specific forest characteristics.

Although both the bee and hoverfly community were positively affected by local environmental characteristics, their responses were clearly different. Bee species richness, diversity and activity-abundance was strongly linked with forest edge and local landscape features, especially the amount of edge habitat and the quality of the nesting habitat for ground-nesting bees. Hoverflies, on the other hand, were far less affected by these factors, with the hoverfly community mainly showing a positive trend with forest age.

The bee community was ecologically relatively homogenous, consisting mostly of solitary or communal, ground-nesting species with similar nesting requirements. All bee larvae depend on pollen for development, which makes the community ecologically less diverse than the hoverfly, therefore leading to a more uniform response of the whole community to the examined variables. In agricultural landscapes, nesting habitat for ground-nesting bees is often rare, as semi-natural habitat is very fragmented and scarce. Soil tilling usually destroys nests built in cropland (Shuler et al., 2005). As many species are thermophilic, south-oriented forest edges with sun-exposed, open, undisturbed soil can provide an important share of nesting habitat in these landscapes.

Our results indicate that the bee community benefits from forest edges with good nesting habitat. However, the relation between the bee community and the forest itself was less clear. A larger forest cover led to a more species-rich community but a lower bee activity-abundance. Large forest patches with more edge habitat seems to support a more diverse bee community by having a larger variety of nesting resources, whereas bee activity-abundance is lower as forest itself may be less suitable as foraging habitat (Heneberg et al., 2013; Winfree et al., 2007). Most species in our research are polylectic species, and are able to forage on crops and herbs in the agricultural matrix.

Hoverflies are ecologically far more diverse, with several species surviving in intensive agricultural habitat. Individuals belonging to these generalist species made up the majority of the hoverfly community in our study. These species do not depend on forests and forest edges to sustain a stable population. However, a large share of hoverflies in our study were forest specialists, such as *Ferdinandea cuprea*, which was one of the most abundant species in our samples (Speight et al., 2016). Especially older forests can harbour these typical forest species that do not occur in any other habitat type in this kind of landscapes, therefore contributing to a more diverse hoverfly community.

4.3. Management implications

In intensively managed agricultural landscapes, semi-natural habitat is often very scarce. However, small forest fragments harbour a diverse pollinator community. For bees, forest patches have the potential to play an important role in providing nesting habitat, increasing the total species richness on a small scale, which makes even small forest fragments potentially important for pollinator conservation. Based on the results of this study, guidelines for conserving pollinator diversity are proposed.

First of all, conservation of these forest fragments is important for maintaining pollinator species associated with the forest edges and the forest itself. Especially the preservation of older forest fragments is important to conserve a diverse hoverfly community. The effect of forest cover on bee species richness was strongest when using a 100m radius. This indicates that the effect of forest fragments on the bee community acts on a very local scale. This implies that even small, scattered forest patches can locally increase bee species richness and should therefore be conserved.

Secondly, forest edges can be made more suitable for bees by improving the site conditions for nesting. Sloped, south-oriented forest edges have a high potential as nesting place for ground-nesting bees. Management aimed at improving this potential nesting habitat by creating more exposed forest edges with plenty of bare soil will yield a more species rich bee community and lead to a higher activity-abundance of bees in the forest edges.

Finally, increasing the amount of edge habitats, such as hedgerows, is expected to benefit the bee community. Conserving forests and hedgerows, thereby increasing the amount of edge habitat, is necessary to increase the species richness, diversity and abundance of bees.

5. Acknowledgements

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Appendix 2

Appendix 2.A.: Study landscapes

Appendix 2.A.1.: Land use cover in the five 5x5 km study landscapes (% of total). Category 'others' include roads, ditches, unpaved terrains.

Region	Decid. forest	Conif. forest	Cropland	Grassland	Urban	Orchard	Others
1. Vermandois, Fr	5.5	0	88.9	0.5	0.5	0	4.6
2. Glabbeek, Be	7.4	0	37.9	27.5	14.6	11.26	1.4
3. Zevener Geest, De	14.1	1.9	63.5	11.1	3	0	6.4
4. Prignitz, De	9.6	0	63.4	16.7	2.8	0	7.5
5. Sebbarp, Se	6.0	0.9	73.0	12.8	4.1	0	3.0

Appendix 2.A.2.: Dates of maps used to estimate forest age per region..

N-France: 1760: 1880, 1950, 2000

Belgium: 1770, 1850, 1910, 2000

W-Germany: 1770, 1900, 1955, 2000

E-Germany: 1780, 1880, 1980, 2000

Sweden: 1721, 1769, 1820, 1915, 2000

Appendix 2.B.: Best model estimates

Appendix 2.B.1. Parameter estimates of best models on bee species richness

Model	Intercept	Edge Width	Hedgerows	Slope	Herb	Forest cover	Bare soil	Rubus	Sun	Flower richness	AICc
1	6.83		0.66	0.35	0.35	0.48			0.76		314.4
2	6.83	-0.30	0.64	0.42	0.35	0.49			0.84		314.5
3	6.83		0.60		0.32	0.47			0.77		315.2
4	6.83		0.62	0.31		0.42			0.79		315.2
5	6.83	-0.31	0.60	0.39		0.44			0.86		315.3
6	6.83		0.57			0.42			0.79		315.4
7	6.83		0.64	0.32	0.41	0.51			0.75	-0.23	315.5
8	6.83		0.63		0.39	0.48	0.26		0.72		315.8
9	6.83		0.67	0.35	0.35	0.44		0.20	0.80		315.8
10	6.83		0.59		0.38	0.51			0.75	-0.26	315.9

Appendix 2.B.2. Parameter estimates of best models on bee Shannon diversity

Model	Intercept	Width	Hedgerows	Slope	Herb	Forest cover	Bare soil	Rubus	Sun	Flower richness	AICc
1	1.83		0.12	0.08		0.08			0.19		92.8
2	1.83		0.12	0.09				0.07	0.19		93.1
3	1.83		0.12	0.08					0.17		93.2
4	1.83	-0.06	0.12	0.10		0.08			0.21		93.5
5	1.83		0.13	0.09		0.07		0.06	0.20		93.6
6	1.83		0.11			0.08			0.19		93.6
7	1.83		0.12			0.08	0.07		0.18		93.6
8	1.83		0.11				0.07		0.16		93.8
9	1.83		0.1						0.17		93.9
10	1.83		0.11					0.07	0.19		94.0
11	1.83	-0.06	0.11	0.10					0.18		94.1
12	1.83		0.13	0.09	0.05	0.09			0.19		94.2
13	1.83		0.11				0.07	0.07	0.17		94.2

14	1.83		0.12		0.07	0.09	0.09		0.18		94.3
15	1.83		0.11			0.07		0.06	0.20		94.5
16	1.83	-0.05	0.12	0.10				0.07	0.19		94.5
17	1.83		0.12	0.08		0.08			0.19	-0.03	94.8
18	1.83		0.12			0.07	0.07	0.05	0.19		94.8
19	1.83	-0.055	0.12	0.10		0.07		0.05	0.21		94.8

Appendix 2.B.3. Parameter estimates of best models on bee activity-abundance

Model	Intercept	Age	Forest edge	Bare soil	Rubus	Sun	Flower richness	AICc
1	3.35		0.17	0.19	0.22	0.57		685.8
2	3.35	-0.084	0.15	0.19	0.22	0.55		687.4
3	3.35		0.18	0.21	0.23	0.57	0.071	687.7

Appendix 2.B.4. Parameter estimates of best models on hoverfly species richness

Model	Intercept	Age	Forest edge	Hedgerows	Herb	Forest cover	Bare soil	Rubus	Flower richness	AICc
1	3.83	0.53			0.36		0.34			287.7
2	3.83	0.58	0.22		0.36		0.36			288.2
3	3.83	0.51			0.36		0.34	0.22		288.2
4	3.83	0.55	0.24		0.36		0.35	0.23		288.5
5	3.83	0.47			0.39	0.19	0.36			288.8
6	3.83	0.52		-0.15	0.34		0.33			289.2
7	3.83	0.55			0.38		0.32		-0.14	289.3
8	3.83	0.55			0.27					289.5
9	3.83	0.52	0.21		0.39	0.17	0.37			289.6

Appendix 2.B.5. Parameter estimates of best models on hoverfly Shannon diversity

Model	Intercept	Age	Forest edge	Edge width	Hedgerows	Herb	Forest cover	Bare soil	Rubus	Flower richness	AICc
1	1.16	0.16				0.10		0.12			124.2
2	1.16	0.16						0.10			124.6
3	1.16	0.15				0.10		0.12	0.07		125.0
4	1.16	0.16									125.2
5	1.16	0.15						0.10	0.07		125.3
6	1.16	0.17	0.06			0.10		0.13			125.7
7	1.16	0.15							0.08		125.8
8	1.16	0.14				0.11	0.053	0.13			125.8
9	1.16	0.15			-0.05			0.10			126.0
10	1.16	0.15			-0.04	0.09		0.12			126.0
11	1.16	0.17	0.05					0.10			126.0
12	1.16	0.16				0.07					126.1
13	1.16	0.16				0.10		0.11			126.1
14	1.16	0.16		-0.04		0.10		0.13		-0.04	126.1

Appendix 2.B.6. Parameter estimates of best models on hoverfly activity-abundance

Model	Intercept	Age	Slope	Herb	Forest cover	Sun	AICc
1	2.68					0.19	587.0
2	2.67		0.11			0.20	587.5
3	2.67	0.09				0.21	588.2
4	2.67			0.08		0.20	588.7
5	2.68				0.05	0.21	588.9

Appendix 2.B.7. Parameter estimates of best models on activity-abundance of forest specialist hoverflies

Model	Intercept	Age	Forest edges	Edge width	Herb layer	Forest cover	Bare soil	Rubus	Sun	Flower richness	AICc
1	0.99			-0.16		0.31					454.2
2	0.99		0.10	-0.18		0.31					454.6
3	0.99			-0.18		0.33			0.09		454.8
4	1.00					0.32					455.1
5	0.99		0.09	-0.19		0.33			0.08		455.4
6	0.99	0.10	0.12	-0.18		0.27					455.5
7	0.99			-0.16	-0.06	0.30					455.6
8	0.99	0.07		-0.16		0.28					455.8
9	0.99	0.12	0.12	-0.20		0.28			0.10		455.8
10	1.00		0.08			0.32					455.9
11	0.99			-0.16		0.32				0.05	455.9
12	0.99			-0.16		0.30	-0.05				456.0
13	0.99	0.09		-0.18		0.30			0.10		456.0
14	1.00				-0.07	0.31					456.1
15	0.99			-0.16		0.30		0.04			456.2
16	0.99			-0.17	-0.06	0.32			0.09		456.2

Appendix 2.B.8. Parameter estimates of best models on activity-abundance of non-forest hoverflies

Model	Intercept	Age	Slope	Herb	Forest cover	Rubus	Sun	AICc
1	2.10		0.15				0.27	505.3
2	2.11						0.27	505.7
3	2.09		0.15	0.11			0.27	506.2
4	2.10	0.11					0.30	506.6
5	2.09	0.09	0.13				0.29	506.9
6	2.10			0.09			0.27	506.9
7	2.10		0.15			0.08	0.29	507.0
8	2.10		0.14		0.07		0.28	507.1

Appendix 2.C.: Species lists

Appendix 2.C.1: Detailed table of all bees encountered in the study per species and per window

Species	**1. Vermandois, Fr**	**2. Glabbeek, Be**	**3. Zevener Geest, De**	**4.Prignitz, De**	**5. Sebbarp, Se**	**Total**
Andrena alfkenella					1	**1**
Andrena angustior	11		39	97		**147**
Andrena barbilabris			1			**1**
Andrena bicolor	19	68			4	**91**
Andrena caranthonica	10			1	1	**12**
Andrena cineraria	14		5	5	2	**26**
Andrena clarkella	1		2		1	**4**
Andrena combinata	1					**1**
Andrena dorsata	2	2				**4**
Andrena flavipes	3	4	2			**9**
Andrena fucata	5	3	3	18	35	**64**
Andrena fulva	12	4		3	15	**34**
Andrena fulvago		8				**8**
Andrena fulvata	19	9				**28**
Andrena gravida	1					**1**
Andrena haemorrhoa	536	45	57	78	58	**774**
Andrena helvola	182	3	7	78	277	**547**
Andrena lapponica				2		**2**
Andrena minutula	44	13			3	**60**
Andrena minutuloides		1			2	**3**
Andrena mitis				1		**1**
Andrena nigroaenea	43		4	13	6	**66**
Andrena nitida	7		2	10		**19**
Andrena praecox					2	**2**
Andrena spinigera	13					**13**
Andrena subopaca	41	2	5	7	11	**66**
Andrena synadelpha	1				2	**3**
Andrena vaga	1	5				**6**
Andrena varians					1	**1**
Andrena wilkella		1				**1**
Anthophora furcata	1					**1**
Anthophora plumipes		1		2		**3**
Apis mellifera	4	9	10	2	7	**32**
Bombus hortorum	7			2	11	**20**
Bombus hypnorum	2	5	3	3	5	**18**
Bombus lapidarius	15			14	5	**34**
Bombus pascuorum	34	28	18	18	42	**140**
Bombus pratorum	11	12	15	15	18	**71**
Bombus ruderarius					8	**8**
Bombus sylvarum				1		**1**
Bombus terrestris s.l.	17	21	24	16	20	**98**
Ceratina cyanea	1					**1**
Chelostoma campanularum		1		1	2	**4**
Chelostoma florisomne			1		1	**2**
Chelostoma rapunculi		1				**1**
Coelioxys inermis		1				**1**
Dasypoda hirtipes				3		**3**

Halictus langobardicus	1					**1**
Halictus rubicundus	3					**3**
Halictus scabiosae	1					**1**
Halictus sexcinctus				1		**1**
Halictus tumulorum		1				**1**
Halictus tumumlorum	2					**2**
Heriades truncorum					1	**1**
Hylaeus communis			4	2	7	**13**
Hylaeus confusus		1	1			**2**
Hylaeus signatus					1	**1**
Lasioglossum albipes	1			4		**5**
Lasioglossum calceatum	39	9	15	56	4	**123**
Lasioglossum costulatum				1		**1**
Lasioglossum fratellum			1			**1**
Lasioglossum fulvicorne		2				**2**
Lasioglossum laticeps	2	4				**6**
Lasioglossum lativentre	1	2			2	**5**
Lasioglossum leucopus		2	1			**3**
Lasioglossum leucozonium				3	1	**4**
Lasioglossum majus	2					**2**
Lasioglossum malachurum	2	3				**5**
Lasioglossum minutissimum	4	1				**5**
Lasioglossum morio	303	20	2		3	**328**
Lasioglossum nigripes				2		**2**
Lasioglossum nitidiusculum	6					**6**
Lasioglossum nitidulum					1	**1**
Lasioglossum parvulum	169	4	4	12	2	**191**
Lasioglossum pauperatum			1			**1**
Lasioglossum pauxillum	14	10				**24**
Lasioglossum punctatissimum		6				**6**
Lasioglossum pygmaeum	1					**1**
Lasioglossum quadrinotatum				3		**3**
Lasioglossum rufitarse	3		1		6	**10**
Lasioglossum sabulosum			1	2		**3**
Lasioglossum sexnotatum		1		3		**4**
Lasioglossum sexstrigatum	2	5				**7**
Lasioglossum villosulum		1				**1**
Lasioglossum zonulum		11		4		**15**
Macropis europaeus				3	1	**4**
Nomada fabriciana	8	1				**9**
Nomada ferruginata			1			**1**
Nomada flava	30	1			1	**32**
Nomada flavoguttata	17			1	1	**19**
Nomada fulvicornis	2					**2**
Nomada goodeniana	4					**4**
Nomada lathburiana	4					**4**
Nomada panzeri	14		1		9	**24**
Nomada ruficornis	1	1				**2**
Nomada striata				1		**1**
Osmia bicolor	3					**3**
Osmia bicornis		6			3	**9**

Osmia leiana					1	**1**
Psithyrus barbutellus	1					**1**
Psithyrus bohemicus	1			3	1	**5**
Psithyrus campestris					1	**1**
Psithyrus rupestris	4				1	**5**
Psithyrus sylvestris	2	4	1			**7**
Psithyrus vestalis	10				1	**11**
Sphecodes crassus	1					**1**
Sphecodes ephippius		1				**1**
Sphecodes monilicornis					1	**1**
Sphecodes pellucidus	1					**1**
Sphecodes rubicundus	1				1	**2**
Stelis phaeoptera			1			**1**
Total	1718	344	233	491	590	**3376**

Appendix 2.B.2 Detailed table of all hoverflies encountered in the study per species and per window

Species	**1. Vermandois, Fr**	**2. Glabbeek, Be**	**3. Zevener Geest, De**	**4. Prignitz, De**	**5. Sebbarp, Se**	**Total**
Baccha elongata	1		1		1	**3**
Brachypalpoides lentus		2	1	1	1	**5**
Chalcosyrphus nemorum		4	1	2		**7**
Cheilosia pagana		1		2		**3**
Chrysogaster solstitialis					2	**2**
Chrysotoxum bicinctum			1			**1**
Criorhina ranunculi	1				1	**2**
Dasysyrphus albostriatus		3	1			**4**
Dasysyrphus venustus		1				**1**
Episyrphus balteatus	478	25	67	58	42	**670**
Eristalis horticola		1				**1**
Eristalis pertinax	1	5	1	1	1	**9**
Eristalis similis			1			**1**
Eristalis tenax	2		1			**3**
Eumerus strigatus	3				1	**4**
Eupeodes corollae	29	5	2	8	5	**49**
Ferdinandea cuprea	71	10	20	5	7	**113**
Helophilus pendulus		3				**3**
Heringia vitripennis		2				**2**
Melangyna cincta					2	**2**
Melanogaster hirtella					1	**1**
Melanostoma mellinum	13	12	5	4	24	**58**
Melanostoma scalare	39	20	27	2	10	**98**
Meliscaeva auricollis	2	1	3			**6**
Myathropa florea	7	7	5	10	3	**32**
Neoascia podagrica	1	7	3	8	23	**42**
Platycheirus albimanus	39	12		3	2	**56**
Platycheirus manicatus	5					**5**
Platycheirus peltatus	17		1		3	**21**
Platycheirus scutatus	10	1	1			**12**
Pyrophaena rosarum			1			**1**
Rhingia campestris	7	135	6	2	38	**188**
Riponnensia splendens		1				**1**
Sphaerophoria scripta	15			1		**16**
Syritta pipiens					1	**1**
Syrphus ribesi	2	3	1		1	**7**
Syrphus torvus			1			**1**
Syrphus vitripennis			1		1	**2**
Temnostoma apiforme			2			**2**
Temnostoma vespiforme				2		**2**
Volucella bombylans	3	4		2		**9**
Volucella pellucens	1					**1**
Xanthogramma pedissequum	1					**1**
Xanthogramma stackelbergi					1	**1**
Xylota segnis	20	17			3	**40**
Xylota sylvarum		2				**2**
Total	768	284	154	111	174	**1491**

Chapter 3: Importance of forest fragments as pollinator habitat varies with season and guild

Adapted from:
Proesmans, W.; D. Bonte; G. Smagghe; I. Meeus & K. Verheyen (2019). Importance of forest fragments as pollinator habitat varies with season and guild. *Basic and Applied Ecology* 34:95-107.

Abstract

Large areas of Western Europe are covered with intensively managed agricultural land. In these landscapes, wild pollinators depend on fragments of semi-natural habitat for foraging or reproduction. Small forest patches are often the most abundant type of semi-natural habitat in these agricultural landscapes. We investigated the role these patches play in conserving the pollinator community in intensively managed agricultural landscapes.

Our survey of the pollinator community in 16 forest fragments showed that the pollinator community in the edges of small forest fragments is strongly influenced by forest and forest edge characteristics. Old forest fragments with a well-developed herb layer had more diverse bee communities than recent forests or old forests without a herb layer, but overall lower activity-abundances, while sun exposure of the forest edges had a strong positive effect on pollinator activity-abundance in general. The hoverfly community had higher activity-abundances in forest edges with a higher flower-index, while saproxylic hoverflies were caught in higher numbers in sites with a higher forest cover in the surrounding landscape.

We also detected a strong seasonal effect. The effects of herb layer cover on bee species richness and activity-abundance were much stronger in spring than in summer, while bee species richness was also strongly positively correlated with forest age in spring. A strong positive correlation between pollinator species richness and sun exposure was found in summer, after canopy closure.

While the sampled forest edges harbour a rich and diverse pollinator community, cavity-nesting bees were very scarce. This is probably caused by the low amount of dead wood in the studied forest fragments.

We conclude that small forest fragments can play an important role in conserving the pollinator community, especially bees and saproxylic hoverflies. The importance of these forest fragments is strongest in spring, when the herb layer provides foraging resources.

1. Introduction

1.1. Effect of agricultural intensification on pollinator community

Europe is largely covered by agricultural land. During the last century, Western European agricultural landscapes have undergone some drastic modifications. Agricultural intensification, both on a local and a landscape scale, have led to biodiversity loss (Tscharntke et al., 2005; Butchart et al., 2010). While some aspects, such as the presence of mass-flowering crops, seem to have a positive influence, at least on generalist species (Diekötter et al., 2014), other changes have an adverse effect (Le Féon et al., 2010). Decreased pollen and nectar sources due to herbicide use (Kearns et al., 1998), disturbance of nesting habitat due to soil tilling (Shulere et al. 2005) and large monocultures of non-insect pollinated crops (Pywell et al., 2005) have made agricultural land largely unsuitable for pollinators (Ollerton et al., 2014). Many species therefore depend on fragments of semi-natural habitat (SNH) in these agricultural landscapes. These semi-natural habitats include forests and extensively managed permanent grasslands, as well as other open habitats, such as marches and heathlands. Several studies show an increase in pollinator abundance and biodiversity with increasing SNH (e.g. Carvalheiro et al., 2010; Kim et al., 2006; Le Féon et al., 2010; Öckinger & Smith, 2007; Sydenham et al., 2014), highlighting their importance in supporting a diverse pollinator community in agricultural landscapes.

1.2. Pollinator guilds

The precise ecological requirements of pollinators are often species- or guild-specific. Most studies investigating pollinator community structure focus solely on solitary bees (Williams and Kremen, 2007), bumblebees (Carvell et al., 2011), hoverflies (Haenke et al., 2014) or other pollinators (Rundlöf et al., 2008). However, the responses to environmental factors may differ strongly between these guilds (Steffan-Dewenter et al., 2002). Bees, as central place foragers (Westrich, 1996), require nesting and foraging habitat within close range, given their short activity radius (up to a few hundreds of metres; Gathmann & Tscharntke, 2002; Greenleaf et al., 2007). Hoverflies, on the other hand, do not build nests and can forage independently from egg-deposition sites. Within these guilds, parts of the community may also respond differently to environmental drivers, depending on their life history characteristics. Several generalist aphidophagous species, such as *Episyrphus balteatus*, thrive in agricultural habitat (Jauker et al., 2009), while saproxylic hoverflies are strongly linked to forests.

1.3. Forest fragments as pollinator habitat in agricultural landscapes

In many intensively managed agricultural landscapes, small forest fragments represent the largest share of semi-natural habitat. In general, the role of these patches in conserving the pollinator community is not clear (but see Ouin et al., 2006; Rubene et al., 2015). While several studies show an increase in pollinator abundance and diversity with increasing forest cover (Farwig et al., 2009; Watson et al. 2011), others show a decrease (Winfree et al. 2007). Within these landscapes, forest fragments serve as islands that are largely spared from disturbances associated with agricultural habitats. Forests can be sources of nectar and pollen, both in the herb layer (Banaszak and Jaroszewicz, 2009) and in the tree or shrub layer (Batra, 1985). Additionally, they may serve as nesting habitat for bees. Species nesting above ground use cavities in dead wood (Sydenham et al., 2016) or pithy stems (Potts et al., 2005), while ground-nesting species prefer sun-exposed terrains with bare soil to dig their nests, especially in the south-exposed forest edge (Everaars et al., 2011). Saproxylic hoverflies are also usually strongly linked with forests, requiring dead wood for egg deposition (Speight et al., 2016). Forests differ among each other. Herb layer composition, indirectly influenced by forest age (Bossuyt et al., 1999), has a strong influence on food availability. Furthermore, suitable nesting or egg-laying habitat may be present in varying degrees. Availability of nesting habitat can depend on presence of dead wood, pithy stems or sun-exposed open soil, depending on the specific nesting requirements of the species.

The role of the forest and the forest edge can differ strongly throughout the year. Forests in spring and in summer differ strongly in light exposure and pollen and nectar availability and can almost be considered as two different ecosystems (Taki et al., 2007). During early spring, before canopy closure, the forest floor is much more exposed to sun, which is linked with the flowering of most understorey plants. Furthermore, the phenology of each plant species limits its temporal availability as a pollen and nectar source, which may in turn cause temporal mismatches with species that depend on specific pollen sources (Forrest, 2015).

Goal and research questions

Very few studies investigated the influence of forest and forest edge characteristics on the pollinator community. Furthermore, the variation in season- and guild-specific responses is also largely unknown. In our study we hypothesize (a) increasing pollinator activity-abundance and species richness in old forests with a rich herb layer, which provide more nesting and foraging habitat, (b) a strong difference between the effect of forest characteristics in spring and in summer, including a stronger effect of the herb layer in providing floral resources in spring and a stronger effect of sun exposure on the pollinator community in summer and (c) differential responses between bees and hoverflies caused by differing requirements in nesting and foraging habitat, with bees being more strongly influenced by the amount of flowering resources and nesting habitat.

2. Material & methods

2.1. Study landscape

The study landscape was a 25 km² area in Glabbeek, Belgium. The landscape is a typical intensive agricultural landscape for the region, mostly consisting of cropland (37.9%), grassland (27.5%), houses and gardens (14.6%) and intensively managed apple and pear orchards (11.3%). The forest cover is 7.4%. As in many agricultural landscapes in the region, most grasslands are heavily fertilized and frequently mowed or grazed, reducing their value as pollinator habitat. Additionally, linear elements such as hedgerows are very scarce.

Figure 3.1.: Overview map of the study landscape. The 16 locations of the pan traps are indicated by stars. The location of the study area within Belgium is indicated on the overview map at the right-bottom side.

2.2. Site selection and sampling

16 deciduous forest fragments, ranging in size from 0.4 to 11.7 ha were selected within the landscape (Figure 3.1.). The age of these forest patches varies from old forests, present since at least 1775 to forests that were planted at the end of the last century. The forests had a mixed tree species composition and were dominated by ash (*Fraxinus excelsior* L.), sessile oak (*Quercus robur* L.) or red oak (*Quercus rubra L.*). The old forest fragments had a mixed tree age distribution, while recent forest fragments were even-aged. All forests had a closed canopy (canopy closure > 80%).

Pollinator sampling was performed in the southern forest edge during five periods (mid-March, mid-April, mid-May, mid-July, mid-August) for two consecutive years (2015-2016) to account for inter-annual variation (Oertli et al., 2005). The sampling was carried out during periods without rain, with sunny weather (cloud cover < 50%, wind speed < 5 m s^{-1}) and with temperatures representative for the time of the year (day temperature range: 13 °C-27 °C). At each location, blue, yellow and white pan traps (Ø 20 cm, Motip® Fluor Blue, Motip® Fluor Yellow, Motip® High Gloss White) were attached to trees in the outer tree row at a height of 1.3 m. The pan traps were filled with water and a drop of biodegradable soap to break surface tension. The pan traps were placed at least three metres apart from each other to prevent interference (Droege et al., 2010). After 96 hours, the pan traps were removed and all bees and hoverflies were transferred to 70% ethanol.

Additionally, during each sampling period, a transect walk of 15 minutes was carried out along the southern forest edge, adding up to a total of 150 minutes of transect walks in each forest edge. During each transect walk, a distance of 100 m was walked and any bees and hoverflies that were observed flying or foraging within 2 m of the observer were caught. Specimens that could not be identified in the field were killed and stored in 70% ethanol. In the lab, all specimens were sorted out, dried, pinned and identified.

2.3. Forest and landscape variables

In each forest fragment, local site characteristics considered potentially important for the occurrence of wild pollinators were measured in May 2015. More data on how these variables were defined and measured is given in Table 3.1. and Appendix 3.B.1. Ground-nesting bees are known to benefit from exposed bare soil on sloped terrains (Potts et al., 2005), while stalks of *Rubus* spp. can serve as nesting habitat for certain cavity nesting bee species. Other cavity nesters and saproxylic hoverflies, respectively use holes in dead wood or rotting wood as nests or habitat for egg deposition. In each forest edge, variables BARESOIL and RUBUS were measured at five 1 x 1 m² squares, each spaced 10 m apart, while WIDTH and SLOPE were measured at the level of these squares. DW was measured from the edge, up to 50 m inside the forest. HERB was determined in three 50 m transects from forest edge to inner forest. On each transect, the herb layer cover was measured in five equally spaced 5 x 5 m² plots. Sun exposure (SUN) was measured at the pan traps at three times during the day (10:00, 13:00 and 16:00). Locations that were exposed to solar radiation less than two times were classified as shady (SUN = 0).

Additionally, the plant community was assessed within a 200 m radius around the traps by surveying the plant community in six 2 m wide and 200 m long, radially oriented transects going outward from the location where the pan traps were deployed. All insect pollinated plants were identified to genus, their cover was measured and scored on a 0-5 Tansley scale (Alberdi et al., 2010). A weighted sum of the plant taxa present ($FLOWER = \sum_{taxon=1}^{n} Tansley_{taxon}$, with 'Tansley' being the score on the Tansley scale for the plant taxon), was calculated. This index was used as a measure of floral resource abundance.

The total cover of deciduous forest (FOREST) and edge habitat, including forest edges and hedgerows (EDGE) around each group of pan traps within a 400 m perimeter were calculated using QGIS 2.16 (QGIS Development Team 2015).

Table 3.1. Evaluated forest and landscape characteristics. For forest edge characteristics, the area between the exterior row of trees and the beginning of other land uses was used. Variables indicated with an asterisk (*) were not included in the models of species richness and activity-abundance due to multicollinearity (r>0.5).

Value	**Explanation**
FOREST	
AGE	Area-weighted average age of all stands in the forest fragment, based on map data from 1775, 1850, 1910 and 2000.
BARESOIL	Bare, unvegetated soil in forest edge (% cover; range = 0-53%)
*DW**	Categorical quantification of presence of standing and lying dead wood in forest edge, up to 50 m in forest (0 = absent, 1 = 1-4 trunks present; 2 = >4 trunks present)
HERB	Herb layer cover in forest edge, up to 50 m in forest (% cover; range = 10-100%)
*RUBUS**	Cover of *Rubus* spp. in forest edge (% cover; range = 0-100%).
SLOPE*	Length of sloped terrain (>10°) in forest edge (m; range = 0.00-3.27 m)
SUN	Insolation of the forest edge, based on sun exposure at 10:00, 13:00 and 16:00. Categorical (0 = Shade; 1 = Sun)
WIDTH	Width of forest edge, defined as distance between final tree row at stem basis and start of other land use (meadow, field, orchard) (m, range = 0.87-5.93 m)
LANDSCAPE	
*EDGE**	Total length of edge habitat within a 400 m radius (m, range = 1192-4706 m)
FLOWER	Flower abundance index (range = 14-51)
FOREST	Forest cover within a 400 m radius around the pan traps (hectares, range = 1.20-15.78 ha)

BOX: Trapping techniques: The effect of colour and pan trapping vs. transect walks

Sampling the pollinator community is an essential procedure for various kinds of research, ranging from simple faunistic surveys to large-scale ecological experiments. However, many different sampling methods exist, each with their own merits and pitfalls. It is important to notice that, as most technique measure activity rather than abundance, it is next to impossible to get an unbiased image of the complete pollinator community. Each sampling technique will over- or underestimate certain subsets of the pollinator community. During standardized transect walks, numbers of bigger, more conspicuous species are caught relatively more frequently (Westphal et al., 2008), while taxa that do not collect pollen, such as the cleptoparasitic *Nomada* and *Sphecodes*, are often less attracted to pan traps (Wilson et al., 2008). Additionally, large-bodied taxa, such as bumble bees, are sometimes able to escape pan traps, which leads to a bias to small-bodied species (Nielsen et al., 2011). Additionally, many pollinator species have a clear preference for certain colours, depending on the plant species that they generally visit. Therefore, differently coloured pan traps may attract a different subset of the pollinator community, and using only a single colour may lead to underestimation of species diversity (Leong and Thorp, 1999).

Effect of pan trap colour on sampling results

To assess the quantitative and qualitative effects of pan trap colour on the yield, we used pan trapping data from France, West- and East-Germany and Sweden **(Chapter 2)** and Belgium **(Chapter 3)**, representing 78 sites in five regions (Appendix 2.A.1.). Blue, white and yellow pan traps were used to catch bees and hoverflies. For each colour of pan trap per site, all trapping periods were pooled for further analysis. General linear mixed models were used to assess the effect of pan trap colour on catch rates, with pan trap colour as fixed variable and site identity nested in region as random effect. The number of individuals caught was log-transformed to achieve normality and used as response variable. This procedure was carried out separately for bees and hoverflies, and for two abundant, and ecologically strongly different bee genera (*Bombus* and *Andrena*).

We found significant differences in numbers of pollinators caught between the three colours of pan traps. This effect differed strongly between taxonomic groups: while hoverflies were more attracted to blue pan traps than to yellow ones, bees showed an opposite response. However, even within the bee community, strong differences were notable: blue pan traps caught about four times as much bumble bees than white or yellow pan traps, while bees belonging to the genus *Andrena* were 3-4 times more attracted to yellow pans than to blue or white ones (Table B.1.).

Table B.1.: Retransformed least- square means of the number of pollinators caught in each colour of pan traps. 95% confidence limits are indicated between brackets. Letters in superscript indicate significant differences between colours.

	Blue	White	Yellow
Hoverflies	6.55 [3.60, 11.82]^{a}	5.87 [3.22, 10.70]^{ab}	3.13 [1.67, 5.93]^{b}
Bees	5.05 [2.69, 9.49] ^{a}	8.50 [4.81, 15.03] ^{ab}	13.20 [7.69, 22.42] ^{b}
Bombus spp.	4.90 [4.14, 5.87] ^{a}	1.35 [1.06, 0.73] ^{b}	1.03 [0.77, 1.37] ^{b}
Andrena spp.	2.16 [1.20, 3.86] ^{a}	3.22 [1.86, 5.53] ^{a}	8.33 [5.05, 13.74] ^{b}

Trapping methodology: pan traps vs standardized transect walks

The qualitative difference between subsets of the pollinator community caught by pan trapping and by standardized transect walks was assessed by using the dataset from **Chapter 3**. No quantitative analysis was carried out, as sampling intensity for transect walks and pan traps are hard to compare quantitatively and pan trap yield increases with trap size and design modifications (Wilson et al., 2016). For both trapping techniques, pollinators from all sampling periods were pooled per site. The pollinator community was analyzed at the genus level. The species-matrix was squareroot-transformed to reduce the effect of dominant taxa. A PCA was carried out to assess the difference between sampling techniques and sites. To assess whether the effects of trapping method and site identity were significant, a permutational analysis of variance (PERMANOVA) was carried out on a Bray-Curtis matrix between sites, using 9999 permutations.

The PCA (Figure B.1.) showed a clear separation between both sampling techniques, with one outlier for the netting data, which was caused by the presence of a large nesting aggregation of *Andrena vaga* at this site. Both sampling techniques yielded a significantly different subset of the pollinator community ($F = 7.66$, $df = 1$, $p < 0.0001$, $R^2 = 0.17$), which is clearly visible at the first PCA-axis, while the significant effect of site identity ($F = 1.42$, $df = 15$, $p = 0.012$, $R^2 = 0.49$) was visible on the second axis.

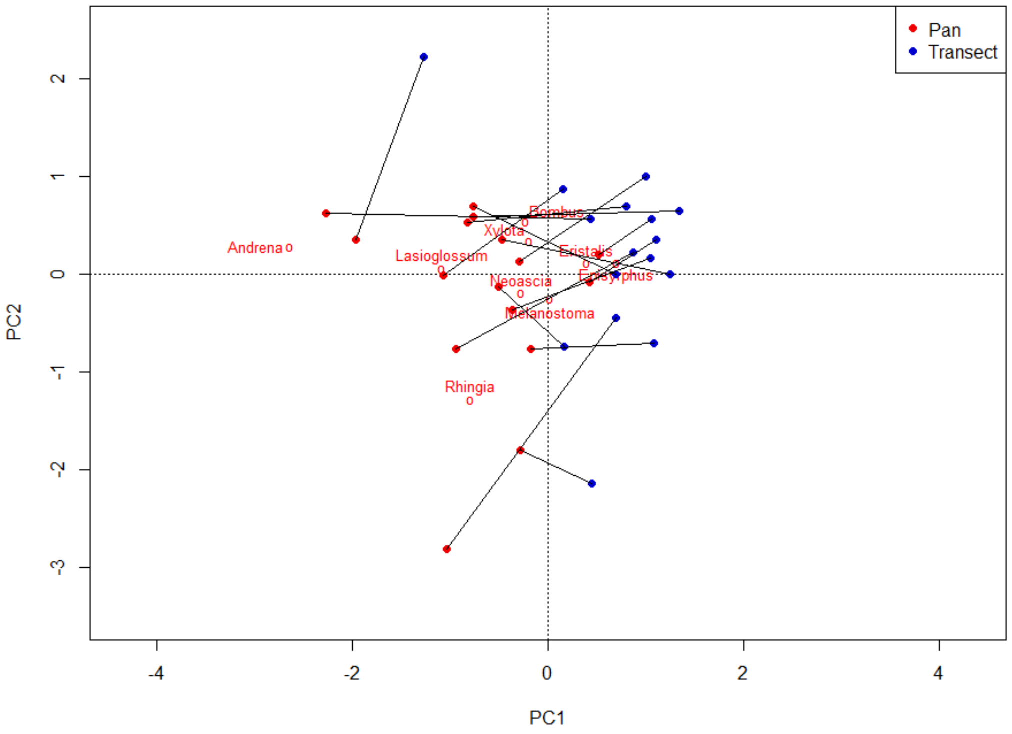


Figure B.1.: Biplot of the first two PCA-axes of the pollinator community in forest edges in Glabbeek (Belgium). Each point indicates a subset of the pollinator community at a site sampled by pan trapping (red) or standardized transect walks (blue). Samples taken at the same sites are linked by black lines. Bee and hoverfly genera that represented more than 2% of the community are displayed in red text.

Implications for pollination research

Pan traps lure foraging pollinators by imitating flowers. However, as different pollinator taxa have preferences for different types of flowers, and vary in their ability to perceive colour (Briscoe and Chittka, 2001), using multiple colours of pan traps will yield a more complete image of the pollinator community, while using only one colour will lead to an underestimation of species diversity. In the same way, pan trapping and standardized transect walks are complementary. Smaller, inconspicuous bee taxa are relatively more represented in samples from pan traps than from transect walks. However, while these methods yield a completely different subset of the pollinator community, a consistent and significant site effect was present in our dataset.

We therefore strongly recommend that, whenever feasible, both pan trapping and standardized transect walks shoud be performed to have a more complete image of the pollinator community. When using pan traps, using multiple colours is essential when the goal is to sample over the complete diversity of the pollinator community. When the research subject is a specific subset of the pollinator community, e.g. bumble bees, it might be appropriate to use one single colour that is preferred by this specific group.

To test for multicollinearity, a correlation matrix was composed (see Appendix 3.B.2.) and for variable pairs with a correlation coefficient > 0.5, only one variable was retained for further analyses. Variables DW, RUBUS, SLOPE and EDGE were excluded from the analyses in this way.

2.4. Statistical analysis

Data from all ten sampling periods were pooled per forest fragment and records of *Apis mellifera* Linnaeus, 1758 were removed from the dataset, as presence of this species is strongly related to the presence of beehives (Winfree et al., 2007a), which were present in large densities in fruit orchards in the study area. As explanatory variables (Table 1) were measured at different scales, these were standardized by subtracting the mean and dividing by their standard deviation to allow better comparison between the effects of the explanatory variables. To account for spatial autocorrelation, we used Moran's eigenvector mapping (MEM) (Borcard et al., 2011). Spatial variability was decomposed in broad and fine scales and positive MEM eigenvectors were used for further analysis (Borcard & Legendre, 2002; Dray et al., 2006). Six positive eigenvectors were retained (see Appendix 3.B.3.).

To assess relations between the environmental variables and the species composition, ordinations were performed on both the hoverfly community and the bee community. Species activity-abundance was square root transformed. For both communities, a detrended correspondence analysis (DCA) was carried out to see whether unimodal or linear ordination methods were appropriate (Lepš and Šmilauer, 2003). Based on this data, a redundancy analysis (RDA) was carried out on both communities. Environmental variables were backward selected ($p<0.05$) using the 'ordistep' function. A Monte Carlo permutation test with 9999 iterations was carried out to assess the significance of the ordination.

The species accumulation curves for bees and hoverflies did not show saturation. Therefore, the species richness at each site was interpolated using sample-based rarefaction (Gotelli and Colwell, 2001). The effect of the selected environmental variables on the rarefied bee and hoverfly species richness was analysed using general linear mixed models. As the herb layer composition in the forest fragments was strongly dependent on forest age, with young forests being dominated by graminoids and stinging nettles, while old forests had a herb layer consisting of insect-pollinated species, an interaction term HERB*AGE was included in the models. To account for differences between guild and season, a categorical variable GUILD.SEASON was created with four levels: ‘Bee spring’, ‘Bee summer’, ‘Hoverfly spring’ and ‘Hoverfly summer’. This variable was included in the model as a random factor. Interactions between GUILD.SEASON and environmental variables were included in the starting model. To account for pseudoreplication, site identity was included as a random effect. We used backwards model selection, dropping the least significant variable and keeping explanatory variables with a p-value < 0.05.

For the effect on activity-abundance, expressed as the number of bee and hoverfly individuals caught, Poisson regression was performed. To account for overdispersion, the Poisson variance was inflated by an unknown factor and quasi-likelihood was used for parameter estimation (McCullagh and Nelder, 1989). Penalized quasi-likelihood was used to estimate significance of the variables (Ver Hoef and Boveng, 2007), using the glmmPQL function in the MASS-package (Ripley and Venables, 2002).

As the hoverfly community was dominated by generalist species, a separate analysis was carried out on the activity-abundance of species with larvae developing in dead wood, as this group was expected to respond more strongly to forest characteristics than the full hoverfly community (Speight et al., 2016). Poisson regression was used to model the activity-abundance of saproxylic hoverfly species. The best model was selected by backwards model selection, while retaining all explanatory variables with a p-value below 0.05.

3. Results

3.1. General results and species composition

Over the total sampling period, 1161 bees were caught, belonging to 70 different species. 45 species of hoverflies were found, accounting for 931 individuals. Pan trapping yielded 750 bees (61 species) and 397 hoverflies (34 species), while the transect walks yielded 411 bees (44 species) and 534 hoverflies (39 species). A list with all recorded species is shown in Appendix 3.A.1.

Fifty bees (4.3%) were honeybees (*A. mellifera*) and were omitted from the analyses. The most abundant genera were *Andrena* (514 individuals, 44.4%), *Bombus* (338 individuals, 29.2%) and

Lasioglossum (141 individuals, 12.2%). The majority of the bee community consisted of non-parasitic solitary ground-nesting species (687 individuals, 59.1%). Kleptoparasites (66 individuals, 5.7%) were present in relatively low numbers. Cavity-nesting species were very rare in our study (21 individuals, 1.8%).

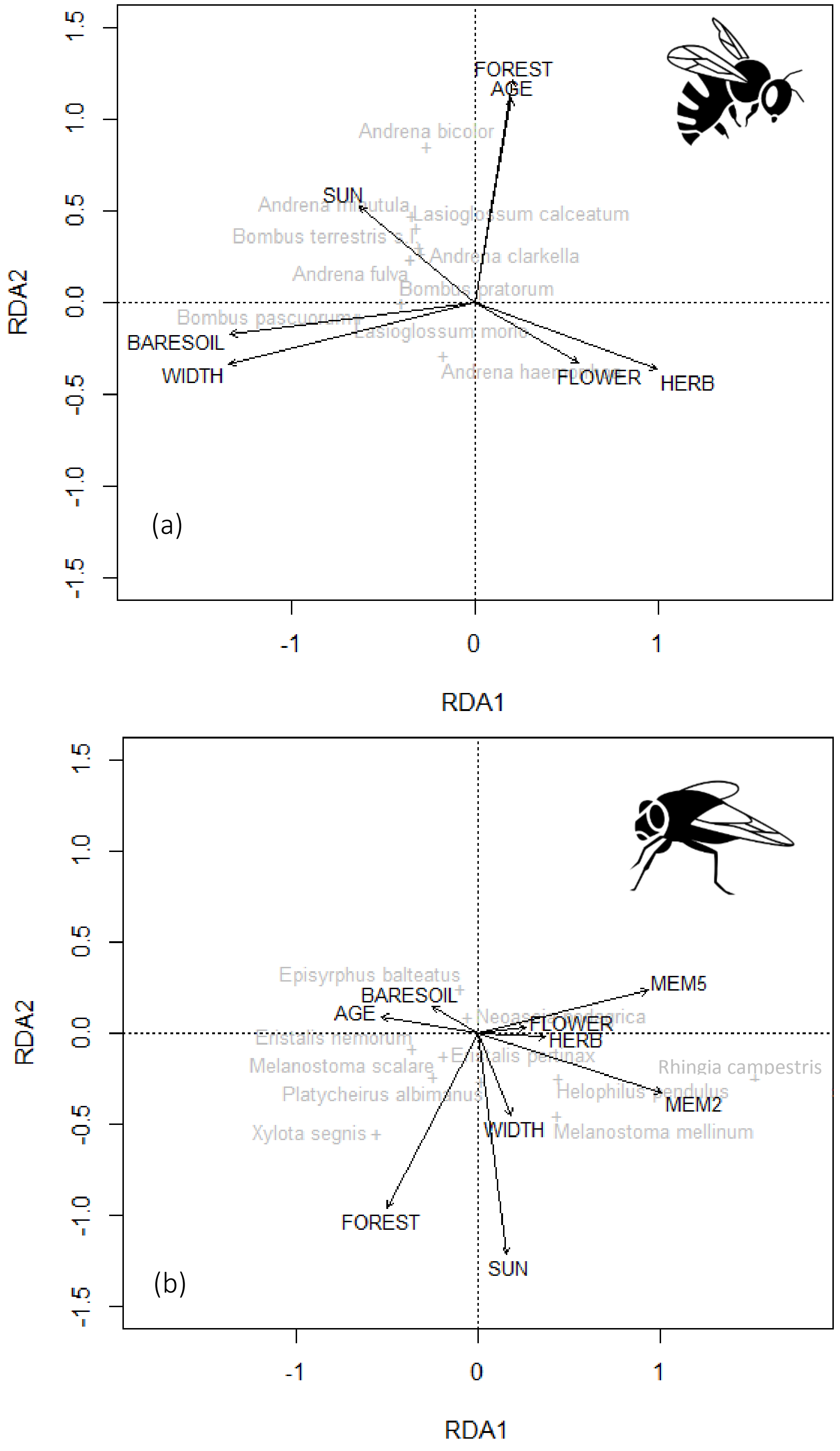


Figure 3.2.: Bee (a) and hoverfly (b) RDA-biplots showing correlation between species (in light grey) and environmental variables (black arrows). Only species that represented more than 2% of the total community are displayed on the plots. For explanation of the variables, see Table 3.1. Pictograms "bee" and "fly" by Parkjisun from the noun project (thenounproject.com).

The three most common hoverfly species accounted for almost half of the total number of specimens caught. These species were *Rhingia campestris* (182 individuals, 19.5%), with larvae that develop in dung and the generalist *Episyrphus balteatus* (177 individuals, 19.0%) and *Melanostoma mellinum* (92 individuals, 9.9%), both with aphidophagous larvae.

3.2. Community composition

The DCAs of bee and hoverfly communities yielded a gradient length of 2.15 and 1.33 respectively, indicating that RDA was an appropriate ordination method. No Moran's eigenvectors were significantly correlated with the bee community. However, the second and the fifth eigenvector were significantly correlated with the hoverfly community and were included in the ordination (Figure 3.2.).

The global Monte Carlo permutation test indicated that the bee community was significantly influenced by the measured environmental variables ($p = 0.019$). SUN, HERB and FOREST had a significant effect on bee community composition.

Hoverfly community composition was not significantly influenced by the measured environmental variables ($p = 0.15$). Except for the two significant Moran's eigenvectors (MEM2 and MEM5, see Appendix 3.B.3.), none of the environmental variables had a significant effect on community composition.

3.3. Species richness and activity-abundance of pollinator community

Parameter estimates of the models on species richness and activity-abundance are given in Tables 3.2. and 3.3. A three-way interaction between pollinator species richness, herb layer cover and forest age was detected. For bees, species richness was higher in older forests, although in spring, this effect was only observed in forests with an extensive herb layer (Figure 3.3.), while hoverflies were slightly more species-rich in old forests with a lower herb layer cover than in other forest fragments. Additionally, a positive effect of sun exposure was found for both hoverflies and bees, but only in summer (Figure 3.4.). Presence of bare soil in the forest edges had a marginally significant positive effect on bee species richness ($p = 0.06$), but was not included in the final model.

Activity-abundance was strongly positively correlated with sun exposure for both bees and hoverflies in spring and in summer. Hoverflies additionally showed a positive correlation with the flower index, especially in summer. Additionally, bees had a lower activity-abundance in forests with a higher herb layer cover.

Saproxylic hoverfly activity-abundance was positively correlated with forest cover ($\beta = 0.54 \pm 0.10$; $p < 0.001$), sun exposure ($\beta = 0.52 \pm 0.16$; $p = 0.001$) and flower index ($\beta = 0.27 \pm 0.13$; $p = 0.04$) (model adjusted $R^2 = 0.59$) (Figure 3.5.).

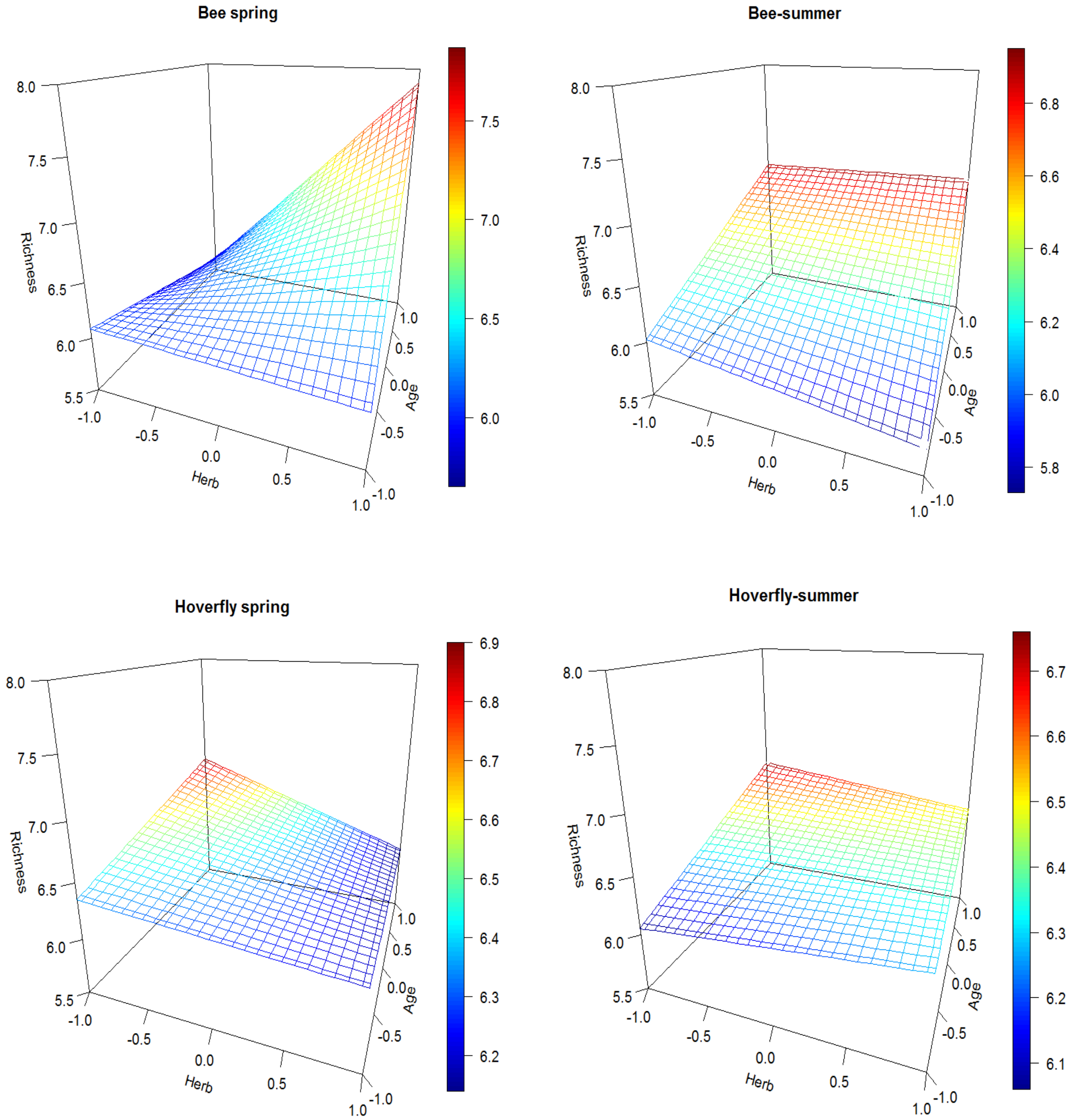


Figure 3.3.: Plot showing the intereaction effect between HERB, AGE and Guild.season. For each pollinator guild, a distinct graph was made in spring and in summer.

Table 3.2.: Standardized coefficient estimates for rarefied species richness. Parameters with p > 0.05 were not included in the model and are not displayed. Interaction terms of measured variables and guilds per season are grouped together.

	Rarefied species richness		
	Estimates (CI)	*Standard error*	*p*
Fixed Parts			
Intercept	6.40 (6.05 – 6.75)	0.18	**<0.001**
AGE	0.36 (-0.01 – 0.74)	0.19	0.055
HERB	0.53 (0.17 – 0.89)	0.18	**0.004**
SUN	-0.29 (-0.65 – 0.06)	0.18	0.109
AGE*HERB	0.58 (0.17 – 1.00)	0.21	**0.006**
SUN*Guild.season			
Bee summer	0.72 (0.22 – 1.22)	0.25	**0.005**
Hoverfly spring	0.31 (-0.19 – 0.81)	0.25	0.231
Hoverfly summer	0.82 (0.32 – 1.32)	0.25	**0.001**
AGE*Guild.season			
Bee summer	0.16 (-0.37 – 0.68)	0.27	0.559
Hoverfly spring	-0.24 (-0.76 – 0.28)	0.27	0.369
Hoverfly summer	-0.13 (-0.65 – 0.39)	0.27	0.622
HERB*Guild.season			
Bee summer	-0.59 (-1.09 – -0.08)	0.26	**0.023**
Hoverfly spring	-0.76 (-1.26 – -0.25)	0.26	**0.004**
Hoverfly summer	-0.54 (-1.05 – -0.04)	0.26	**0.036**
AGE*HERB*Guild.season			
Bee summer	-0.49 (-1.07 – 0.10)	0.30	0.102
Hoverfly spring	-0.73 (-1.31 – -0.15)	0.30	**0.014**
Hoverfly summer	-0.70 (-1.28 – -0.12)	0.30	**0.019**

Table 3.3.: Standardized coefficient estimates for pollinator activity-abundance. Parameters with p > 0.05 were not included in the model and are not displayed. Interaction terms of measured variables and guilds per season are grouped together.

	Activity-abundance		
	Estimates (95% CI)	*Standard error*	*p-values*
Intercept	3.74 (3.52 – 3.95)	0.11	**<0.001**
HERB	-0.44 (-0.61 – -0.27)	0.08	**<0.001**
FLOWER	-0.15 (-0.36 – 0.06)	0.11	0.167
SUN	0.30 (0.16– 0.45)	0.07	**<0.001**
FLOWER*Guild.season			
*FLOWER*Bee summer*	0.06 (-0.33 – 0.45)	0.19	0.768
*FLOWER*Hoverfly spring*	0.40 (0.03 – 0.76)	0.18	**0.035**
*FLOWER*Hoverfly summer*	0.52 (0.16 – 0.88)	0.18	**0.005**
HERB*Guild.season			
*HERB*Bee summer*	0.08 (-0.24 – 0.39)	0.16	0.628
*HERB*Hoverfly spring*	0.48 (0.15 – 0.82)	0.17	**0.005**
*HERB*Hoverfly summer*	0.31 (0.01 – 0.60)	0.15	**0.044**

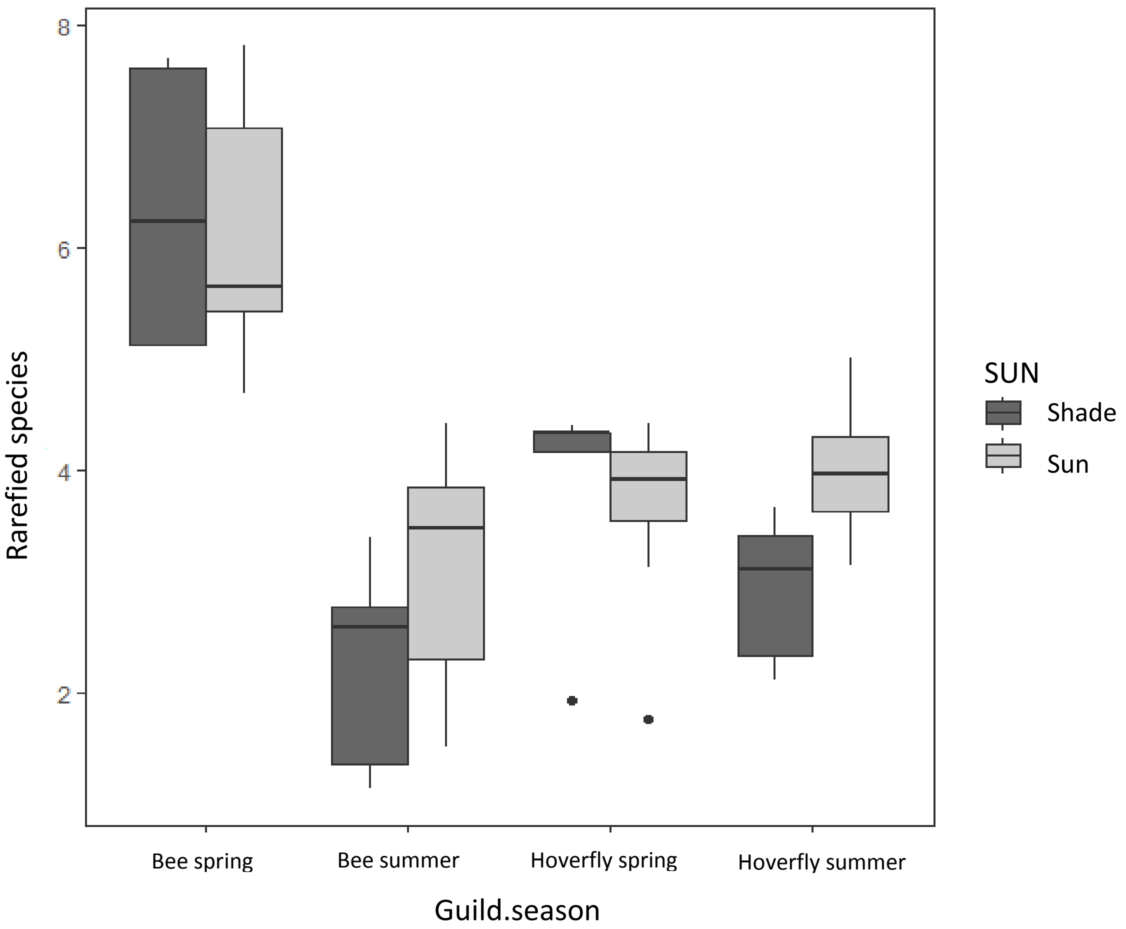


Figure 3.4.: Effect of sun exposure on rarefied species richness in different seasons for bees and hoverflies. While In spring sun exposure has no significant effect on species richness, in summer species richness is significantly higher at sites with high sun exposure.

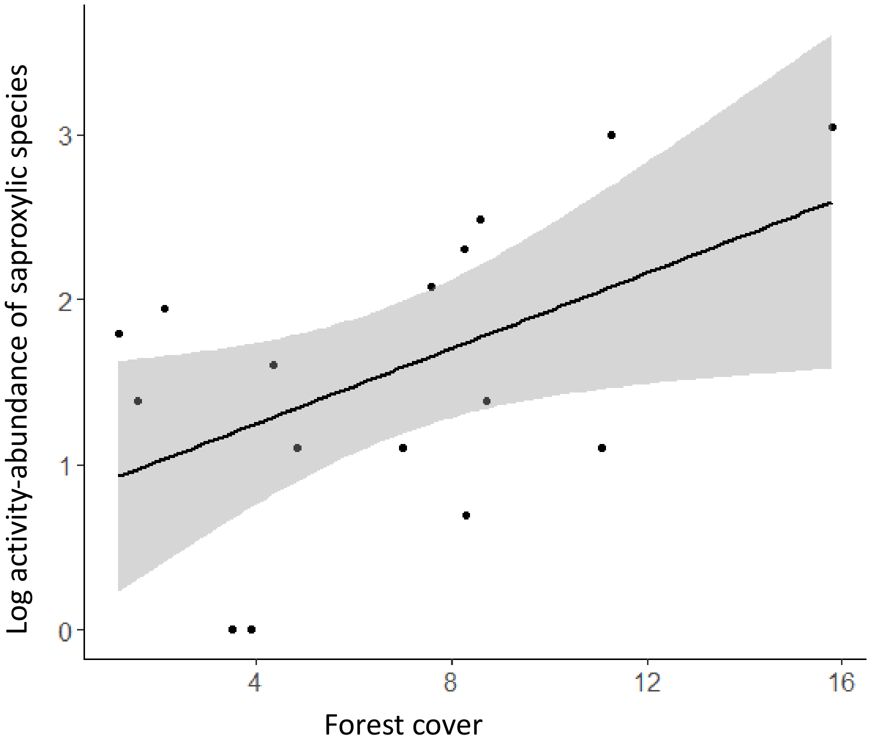


Figure 3.5.: Effect of forest cover within a 200 m radius on saproxylic hoverfly activity-abundance. Grey fill indicates the 95% confidence limit.

4. Discussion

4.1. Forests as pollinator habitat

The potential value of forest fragments as pollinator habitat in agricultural landscapes is strongly influenced by the specific characteristics of the forest fragments and edges. Additionally, responses strongly depend on the guild and the time of the year. The most important factors in our study were sun exposure, forest age and herb layer cover. In older forests, more diverse types of larval habitat may be present, increasing the total pollinator species richness (Reemer, 2005). The herb layer often contains several insect-pollinated plant species that can serve as pollen and nectar sources (Dailey and Scott, 2006). The herb layer of old forests is generally more species-rich and can serve as an important pollen and nectar source in otherwise poor intensive agricultural landscapes. However, composition, and therefore the importance of the herb layer to pollinators, strongly depends on forest age, with recent forests often having a herb layer composed of grasses and wind-pollinated plant species, such as *Urtica dioica*.

The negative effect of herb layer cover on bee activity-abundance can result from a low bee activity-abundance in recent forests with a herb layer consisting of non-insect pollinated herbs. In older forests, with more insect-pollinated herbs in the herb layer, it may be caused by dilution effect. Large areas of insect-pollinated understorey plants may cause the pollinator community to spread over a larger area, decreasing the local activity-abundance. This has been observed in earlier studies (Jha & Vandermeer, 2009; Veddeler et al., 2006). Additionally, a high abundance of flowering plants near the pan traps can divert the attention of foraging pollinators from the pan traps, underestimating the actual activity-abundance (Cane et al., 2000; Roulston et al., 2007).

We found only a small negative effect of herb layer cover on the hoverfly community, in old forest fragments, but the effect was far less than for bees. The most abundant species in the forest edge were generalists, such as *Rhingia campestris*, which has larvae developing in cow dung and is typical for intensively grazed grasslands, or *E. balteatus* (Jauker et al., 2009). These species do not depend on forest habitat, and usually forage outside the forest. These generalist species are very flexible in their foraging resources (Jauker et al., 2009). While requiring pollen for egg development, unlike bees, hoverflies do not provide pollen to their larvae and, hence, have lower pollen requirements (Jauker et al., 2012). Therefore, hoverflies may be less dependent on the understorey, as non-floral resources such as honey dew can also be used instead of nectar (Van Rijn et al., 2013). Hoverfly activity-abundance was strongly correlated with landscape flower index, which may be a more suitable measure of foraging habitat for these generalist species. As agricultural habitat can provide large amounts of larval habitat for generalists, which can serve as egg-deposition sites, we expect that the amount of floral resources limits the population, while for bees nesting places may be limiting in agro-landscapes. In this case, the presence of good foraging habitat for bees, which is linked to the amount of herb layer, leads to a dilution of the population, while the hoverfly population increases with increasing floral resources.

The bee community in our study was dominated by ground-nesting solitary bees. Most specimens belonged to early flying *Andrena spp*. while cavity-nesting species were only found in very low numbers. Bee species richness was marginally positively correlated with the presence of bare soil (p = 0.061) and increasing sampling effort may have revealed a significant relation (Potts et al., 2005; Sardiñas and Kremen, 2014a). Cavity-nesters may have been overlooked as they may prefer the canopy for nesting places (Ulyshen et al., 2010), but even then, these may not be abundant in forest habitat (Sobek et al., 2009). In more urbanized areas, cavity-nesting species usually represent a larger share of the total bee community (Cane et al., 2006; Fortel et al., 2014). However, compared to other studies in rural landscapes, the share of cavity-nesting species was still very low (e.g. Forrest, 2015; Winfree et al., 2007). In agricultural habitat, such as in our study, nesting habitat may be limiting for these species. As typical for the region (Vandekerkhove et al., 2011), the forests were very poor in dead wood, which is additionally correlated with a low abundance of saproxylic beetles, which create potential nesting places by gnawing holes in dead wood (Sydenham et al., 2016). While the hoverfly community as a whole was not affected by forest cover, the subset of saproxylic species, which depend on forests for larval development, showed a positive relationship with forest cover.

4.2. Temporal changes in habitat quality

Responses to environmental factors depend on guild-specific ecological traits (Meyer et al., 2009; Williams et al., 2010), which can make interpretation of general trends difficult. Therefore, it is important to look at the community composition itself and the differing responses between species. Bees are phenologically diverse (Wojcik et al., 2008) and species that fly at different periods during the year may experience the habitat in different ways. While our data shows several forest characteristics influencing the pollinator community, some clear seasonal differences are visible. In spring, the bee community is much more species-rich in old forests, but only when a herb layer is present. The herb layer of these forests typically consists of insect-pollinated plant species such as *Anemone nemorosa* and *Ranunculus ficaria* (Masters and Emery, 2015; Stehlik and Holderegger, 2010), which can provide pollen and nectar for pollinators. These plant species typically flower in early spring, before most plants in other habitats flower. In summer, however, the herb layer in old forests is poor in floral resources, making forests less suitable as pollinator habitat (Wray and Elle, 2014). Therefore, we did not find an effect of herb layer in summer, while old forests were still slightly more species rich than recent forests, possibly because of the presence of nesting habitat. This seasonal difference explains the contrasting results of earlier studies. Studies carried out in spring (Taki et al., 2007; Watson et al., 2011) usually found a positive influence of forest cover on bee diversity and activity-abundance, while studies that were carried out later in the year found a negative effect (Winfree et al., 2007; Mandelik et al., 2012). This result is in line with Sydenham et al. (2014), who found that areas with a higher forest cover were dominated by spring active bees and with Wray and Elle (2014) who found that early-flying species were more often associated with forested ecosystems. While the forest itself may play a smaller role as pollinator habitat later in the season, forest edges can still provide nesting habitat and remain important habitat for bees (McKechnie et al., 2017).

Forest herbs generally flower before canopy closure. During this period, the forest and the forest edge receive relatively large amounts of solar radiation. However, later during spring, the canopy closes, strongly increasing the shading in forests and forest edges. Shade decreases pollinator activity, while sun exposure has a positive influence on the pollinator community (Herrera, 1995, 1997; McKinney & Goodell, 2010; Sydenham et al., 2014) as insects are poikilothermous and require solar irradiation for thermoregulation (Nyoka, 2010). In our data, a positive effect of sun exposure on bee and hoverfly activity-abundance was visible throughout the year, but in summer, the effect was much stronger as the differences between forest edges became much more pronounced.

As forests strongly differ in sun exposure and food resource availability during the year, species that fly in spring may benefit from the presence of forest fragments, while species that are active in summer may show a negative association with forests due to low light exposure and lack of floral resources.

4.3. Management implications

Forest fragments can serve as important habitat for wild pollinators in intensive agricultural habitat where suitable foraging and nesting habitat are lacking. Old forest fragments with a rich herb layer should be preserved, as these provide pollen and nectar for early spring bee species. Additionally, forest habitat is required for the conservation of several hoverfly species that depend on dead wood for reproduction.

Even though forests are poor foraging habitat later in the season, forest edges still serve an important role, especially as nesting habitat for ground-nesting bees. These warm, sun-exposed southern forest edges should be maintained to conserve the bee community. As our data shows a clear positive relationship with sun exposure, thinnings (Nyoka, 2010) and creation of open areas (Gikungu et al., 2011; Taki et al., 2013) might also have a positive effect on both bees and hoverflies, as far as the size of the forest patches allonws this. The low numbers of cavity-nesting bees in our study are probably linked with the low amount of dead wood in forest fragments in the region. Increasing the amount of dead wood is necessary to conserve a diverse community of cavity-nesting bees and saproxylic hoverflies.

5. Acknowledgements

We are grateful to the landowners for giving permission to carry out this research on their properties. Helena Theuwissen assisted with the sampling campaigns. The first author was supported by a grant provided by FWO-Vlaanderen (FWO14/ASP/195).

Appendix 3

Appendix 3.A.: Number of individuals caught and species lists

Appendix 3.A.1.: Hoverflies and bees during all five sampling periods. Numbers per month are pooled over the two years.

	Hoverflies	Bees
March	20	453
April	259	188
May	143	161
July	297	270
August	213	89

Appendix 3.A.2.: List of all bee species that were encountered in this study

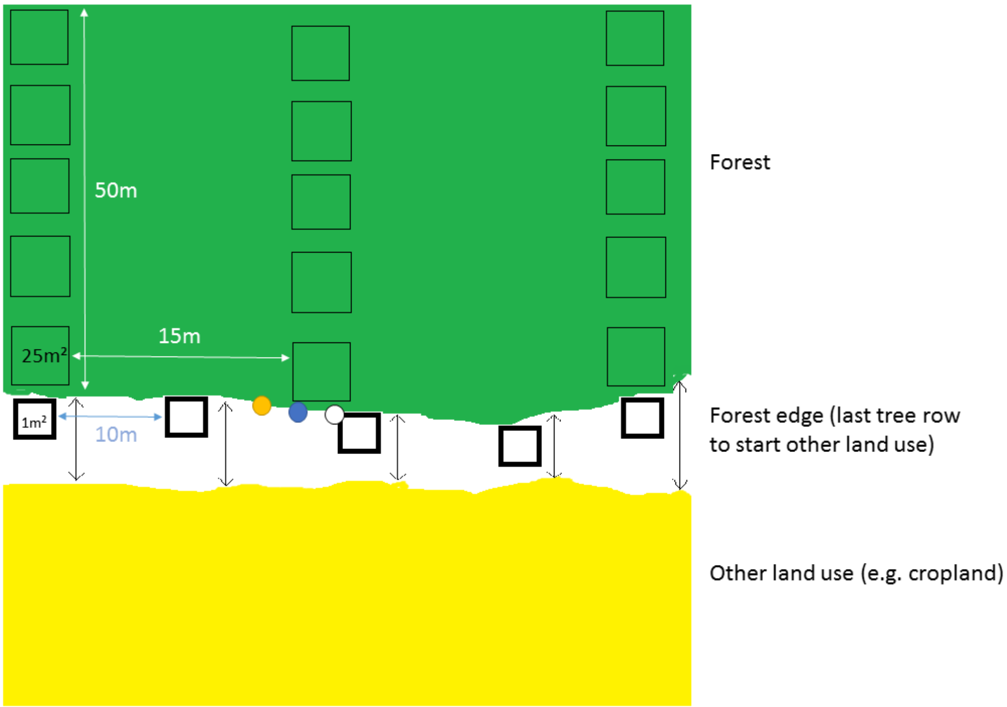
Species	**Amount**
Andrena bicolor Fabricius, 1775	228
Andrena clarkella (Kirby, 1802)	32
Andrena dorsata (Kirby, 1802)	8
Andrena flavipes Panzer, 1799	12
Andrena fucata Smith, 1847	3
Andrena fulva (Müller, 1766)	26
Andrena fulvago (Christ, 1791)	9
Andrena fulvata Stoeckhert, 1930	9
Andrena gravida Imhoff, 1831	1
Andrena haemorrhoa (Fabricius, 1781)	55
Andrena helvola (Linnaeus, 1758)	4
Andrena minutula (Kirby, 1802)	24
Andrena minutuloides Perkins, 1914	1
Andrena mitis Schmiedeknecht, 1884	1
Andrena nigroaenea (Kirby, 1802)	1
Andrena nitida (Müller, 1776)	1
Andrena ovatula (Kirby, 1802)	1
Andrena praecox (Scopoli, 1763)	12
Andrena strohmella Stoeckhert, 1928	1
Andrena subopaca Nylander, 1848	2
Andrena vaga Panzer, 1799	83
Andrena wilkella (Kirby, 1802)	1
Anthophora furcata (Panzer, 1798)	1
Anthophora plumipes (Pallas, 1772)	2
Apis mellifera Linnaeus, 1758	50
Bombus hortorum (Linnaeus, 1761)	4
Bombus hypnorum (Linnaeus, 1758)	25
Bombus lapidarius (Linnaeus, 1758)	9
Bombus pascuorum (Scopoli, 1763)	130
Bombus pratorum (Linnaeus, 1761)	103
Bombus sylvestris (Lepelier, 1832)	3
Bombus terrestris (Linnaeus, 1758) s.l.	59
Bombus vestalis (Geoffroy, 1785)	7
Ceratina cyanea (Kirby, 1802)	1
Chelostoma campanularum (Kirby, 1802)	1
Chelostoma rapunculi (Lepeletier, 1841)	1
Coelioxys inermis (Kirby, 1802)	1
Colletes cunicularius (Linnaeus, 1761)	21
Halictus rubicundus (Christ, 1791)	4
Halictus tumulorum (Linnaeus, 1785)	2
Heriades truncorum (Linnaeus, 1758)	1
Hylaeus communis Nylander, 1852	2
Hylaeus confusus Nylander, 1852	1
Lasioglossum calceatum (Scopoli, 1763)	21
Lasioglossum fulvicorne (Kirby, 1802)	2
Lasioglossum laticeps (Schenck, 1869)	6

Lasioglossum lativentre (Schenck, 1853)	3
Lasioglossum leucopus (Kirby, 1802)	2
Lasioglossum leucozonium (Schranck,	4
Lasioglossum malachurum (Kirby, 1802)	15
Lasioglossum minutissimum (Kirby, 1802)	1
Lasioglossum morio (Fabricius, 1793)	26
Lasioglossum nitidiusculum (Kirby, 1802)	1
Lasioglossum parvulum (Schenck, 1853)	9
Lasioglossum pauxillum (Schenck, 1853)	15
Lasioglossum punctatissimum (Schenck,	13
Lasioglossum sexnotatum (Kirby, 1802)	3
Lasioglossum sexstrigatum (Schenck,	6
Lasioglossum villosulum (Kirby, 1802)	3
Lasioglossum zonulum (Smith, 1848)	13
Megachile centuncularis (Linnaeus, 1758)	6
Nomada fabriciana (Linnaeus, 1767)	7
Nomada flava Panzer, 1798	7
Nomada flavoguttata (Kirby, 1802)	1
Nomada lathburiana (Kirby, 1802)	13
Nomada leucophthalma (Kirby, 1802)	23
Nomada ruficornis (Linnaeus, 1758)	5
Osmia bicornis (Linnaeus, 1758)	10
Osmia cornuta (Latreille, 1805)	2
Sphecodes ephippius (Linnaeus, 1767)	1

Appendix 3.A.3.: List of all encountered hoverfly species

Species	**Amount**
Baccha elongata (Fabricius, 1775)	3
Brachypalpoides lentus Meigen, 1822	4
Chalcosyrphus nemorum (Fabricius, 1805)	4
Cheilosia albitarsis (Meigen, 1822)	1
Cheilosia chrysocoma (Meigen, 1822)	1
Cheilosia pagana (Meigen, 1822)	12
Chrysogaster solstitialis (Fallén, 1817)	2
Dasysyrphus albostriatus (Fallén, 1817)	4
Dasysyrphus venustus (Meigen, 1822)	2
Didea fasciata Macquart, 1834	2
Episyrphus balteatus (De Geer, 1776)	177
Eristalis arbustorum (Linnaeus, 1758)	4
Eristalis horticola (De Geer, 1776)	4
Eristalis intricaria (Linnaeus, 1758)	1
Eristalis nemorum (Linnaeus, 1758)	26
Eristalis pertinax (Scopoli, 1763)	41
Eristalis tenax (Linnaeus, 1758)	11
Eupeodes corollae (Fabricius, 1794)	11
Eupeodes luniger (Meigen, 1822)	2
Ferdinandea cuprea (Scopoli, 1763)	24
Helophilus pendulus (Linnaeus, 1758)	35
Heringia brevidens (Egger, 1865)	1
Heringia vitripennis (Meigen, 1822)	15
Melangyna quadrimaculata (Verrall, 1873)	1
Melanostoma mellinum (Linnaeus, 1758)	92
Melanostoma scalare (Fabricius, 1794)	43
Meliscaeva auricollis (Meigen, 1822)	6
Myathropa florea (Linnaeus, 1758)	38
Neoascia podagrica (Fabricius, 1775)	23
Pipiza bimaculata Meigen, 1822	3
Platycheirus albimanus (Fabricius, 1781)	35
Platycheirus angustatus (Zetterstedt, 1843)	4
Platycheirus clypeatus (Meigen, 1822)	2
Platycheirus scutatus (Meigen, 1822)	3
Pyrophaena rosarum (Fabricius, 1787)	2
Rhingia campestris Meigen, 1822	182
Riponnensia splendens (Meigen, 1822)	1
Sphaerophoria scripta (Linnaeus, 1758)	5
Syritta pipiens (Linnaeus, 1758)	8
Syrphus ribesii (Linnaeus, 1758)	14
Volucella bombylans (Linnaeus, 1758)	17
Volucella pellucens (Linnaeus, 1758)	3
Xanthogramma pedissequum (Harris, 1776)	1
Xylota segnis (Linnaeus, 1758)	53
Xylota sylvarum (Linnaeus, 1758)	9

Appendix 3.B.: Environmental variables

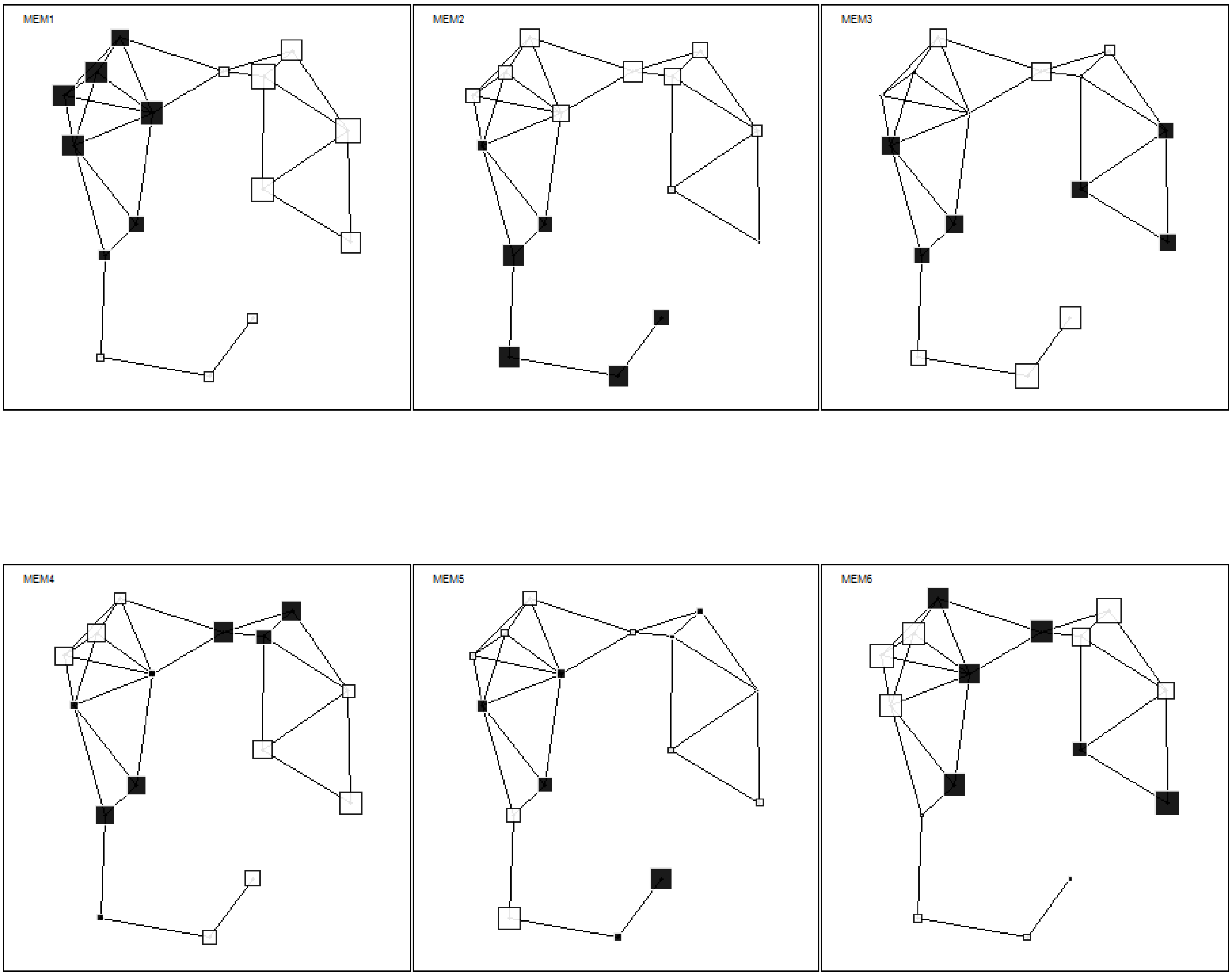


Appendix 3.B.1.: Setup showing the assessment of the environmental variables used in the model. Within the thick squares, measuring 1m² in area, the cover of bare soil (BARESOIL) and Rubus*-cover (RUBUS) were measured, while at the same place forest edge width (WIDTH) and slope (SLOPE) were measured along the full width of the forest edge (black double-pointed arrows). Herb layer cover (HERB) was measured in 25m²-squares along three 50m transects from forest edge to forest interior (thin-lined squares). Amount of dead wood (DW) was measured within the complete 45x50m²-area bordered by the outer two herb-layer transects. The position of the pan traps is indicated by the yellow, blue and white circles. Sun exposure (SUN) was measured here.*

Appendix 3.B.2.: Correlation table showing the pearson correlation between the environmental variables. Variables with a pearson correlation coefficient above 0.50 are indicated in bold.

	AGE	*BARESOIL*	*WIDTH*	*SLOPE*	*EDGE*	*FOREST*	*SUN*	*DW*	*HERB*	*FLOWER*
BARESOIL	0.117									
WIDTH	-0.395	0.494								
SLOPE	0.002	**0.560**	**0.565**							
EDGE	-0.194	-0.193	0.190	-0.102						
FOREST	0.362	-0.134	-0.098	-0.218	**0.741**					
SUN	-0.033	0.036	0.165	-0.271	0.078	0.163				
DW	0.226	**0.607**	0.193	0.227	0.032	0.123	-0.095			
HERB	-0.294	-0.484	-0.302	-0.169	-0.179	-0.426	0.195	**-0.501**		
FLOWER	0.058	-0.263	-0.257	0.061	-0.363	-0.192	-0.290	-0.149	0.101	
RUBUS	0.042	0.022	-0.182	0.032	-0.067	-0.011	**-0.632**	-0.187	-0.115	-0.013

Computed correlation used Pearson-method with listwise-deletion.



Appendix 3.B.3.: The six positively correlated Moran's eigenvector maps. White squares indicate positive values, while black squares indicate negative values. Size is proportional to the value of each sample point. Sites were considered as neighbours when the distance between them was less than 1750m.

Chapter 4: The effect of mass-flowering orchards and semi-natural habitat on pollen availability and bumblebee colony performance

Adapted from:
Proesmans, W.; G. Smagghe; I. Meeus; D. Bonte & K. Verheyen. The effect of mass-flowering orchards and semi-natural habitat on pollen availability and bumblebee colony performance. (Submitted to *Landscape Ecology*).

Abstract

Bumblebees are important pollinators, both for agricultural crops and wild plants. In agro-landscapes dominated by insect-pollinated crops both mass-flowering crops and semi-natural habitat can serve as foraging habitat for pollinators. We expected that mass-flowering crops can have a positive influence on colony performance during flowering by providing large amounts of pollen, and that after mass-flowering, the effect of semi-natural habitat would be stronger.

To assess the effect of semi-natural habitat on bumblebee colony performance, we placed artificial colonies of *Bombus terrestris* in 28 apple and pear orchards during and after mass-flowering. We measured colony growth and took pollen samples from foraging workers. The causal relationships between landscape, pollen quality, amount of pollen collected and colony performance were studied using general linear models and structural equation models (SEM).

In contrast to our expectations, we found a negative correlation between orchard cover and amount of pollen collected during mass-flowering, resulting in a lower colony performance. During flowering, colony performance and pollen diversity were positively correlated with cover of open semi-natural habitat, while later in summer, colony performance was positively correlated with forest cover. The amount of collected pollen differed between the two periods and no correlation was found between the performances of colonies placed at each location during and after the flowering.

Despite being a potentially good foraging habitat, landscapes dominated by flowering orchards function as potential ecological traps for bumblebees. Bumblebees collected pollen from various habitats, depending on the time of the year and colony growth was positively correlated with area of semi-natural habitat.

Landscapes dominated by mass-flowering orchards represent adverse habitats for bumblebees during flowering. Heterogeneous landscapes, containing a mix of various types of semi-natural habitat increase the habitat quality for bumblebees. We advise to maintain these diverse patches of semi-natural habitat, as mass-flowering crops alone are insufficient to support bumblebee colonies.

1. Introduction

Bumblebees are important pollinators in agricultural landscapes, both for agricultural crops and wild plant species (Stanley and Stout, 2014). However, since the second half of last century, bumblebee populations experienced strong declines. The decreasing number of bumblebees is caused by various drivers, of which habitat destruction and agricultural intensification are probably the most important (Williams and Osborne, 2009). Specific causes of this decline are a decrease in food resources (Gabriel and Tscharntke, 2007; Holzschuh et al., 2008), degradation of landscape elements that can provide nesting places (Lye et al., 2009) and changing practices, such as the decreased use of leguminous fodder crops, such as red clover (*Trifolium pratense* L.) (Goulson et al., 2005; Scheper et al., 2014).

Bumblebees have several requirements to sustain a viable population. Like solitary bees they depend on multiple different habitats for nesting and foraging (Westrich, 1996). While solitary species in temperate regions are usually active for only a short period during the year, bumblebee colonies persist for several months and require a continuous source of pollen and nectar during this period to survive and to reproduce (Pywell et al., 2005). Especially late during the flying season, absence of sufficient pollen sources seems to limit colony growth (Fitzpatrick et al., 2007; Rundlöf et al., 2014). Furthermore, bumblebee colonies require relatively large amounts of pollen, compared to solitary bee species (Rotheray et al., 2017), which makes them extra susceptible to low availability of foraging resources (Müller et al., 2006).

Agricultural landscapes, despite often being poor in wild flowering plants (Carvell et al., 2006), can play an important role as foraging habitat for bumblebees, due to the presence of mass flowering crops, such as canola, potatoes or fruit trees (e.g. Holzschuh et al., 2013; Westphal et al., 2003). Additionally, patches of semi-natural habitat (SNH), including species-rich grasslands, forests, hedgerows and road verges, provide foraging resources (Croxton et al., 2002; Öckinger and Smith, 2007; Steffan-Dewenter and Tscharntke, 1999). Most common bumblebee species are generalists, with colonies able to switch flower resources throughout the year. Due to their colonial lifestyle and large size, colonies of *B. terrestris* require large amounts of pollen and therefore often forage in large resource patches (Sowig, 1989). Woody plants make up a large share of the collected pollen both during and after mass-flowering. Even individual flowering trees and shrubs often have large amounts of flowers, therefore serving as large pollen sources. Especially in spring, during mass-flowering, woody plants tend to be very important for bumblebees, as other species are not yet flowering (Kämper et al., 2016).

Earlier studies have already shown a link between landscape context and bumblebee colony performance (e.g. Hines and Hendrix, 2005; Parmentier et al., 2013; Williams et al., 2012) or between pollen sources and colony performance (Génissel et al., 2002; Tasei and Aupinel, 2008), but only few studies looked at both in field experiments (Kämper et al., 2016). Additionally, most research was carried out only within a short time frame, usually a few weeks, therefore ignoring the changes in floral resources during the active period of bumblebees, and possibly missing the effects of phenology of flowering plants on bumblebee colony performance.

The goal of this study was to assess the influence of surrounding landscape context and pollen resources on *Bombus terrestris* (Linnaeus, 1758) colony performance in an agricultural landscape with mass-flowering crops that depend on insect pollination. The experiment was carried out in two consecutive periods: in spring, during mass flowering of apple trees and in early summer, in absence of mass flowering crops. In this way, the effect of the presence of mass flowering crops on both the composition of collected pollen and the colony performance was evaluated. We anticipated the surrounding landscape to have a strong effect on colony performance, with semi-natural habitat (forest, semi-natural grassland) having a positive influence on colony performance by providing more diverse pollen sources than agricultural land. We expected this effect to be strongest in summer, when the fruit trees in our study landscape do not provide foraging resources and the agricultural land is not expected to support a large community of flowering plants that provide pollen and nectar. Additionally, we expected pollen diversity to be highest at sites with more SNH.

2. Material & Methods

2.1. Study Area

The study was carried out in the southeast of Flanders, Belgium, in a 45 x 20 km area (Figure 4.1a). The study area has a temperate oceanic climate with mild winters. The region is the most important fruit-growing region of Belgium and is characterized by landscapes dominated by apple and pear orchards in the western part and cropland in the eastern part. Locally, larger forest fragments and patches of semi-natural grassland occur. The soils consist of loam in the southern half of the study region and of sandy loam in the northern half.

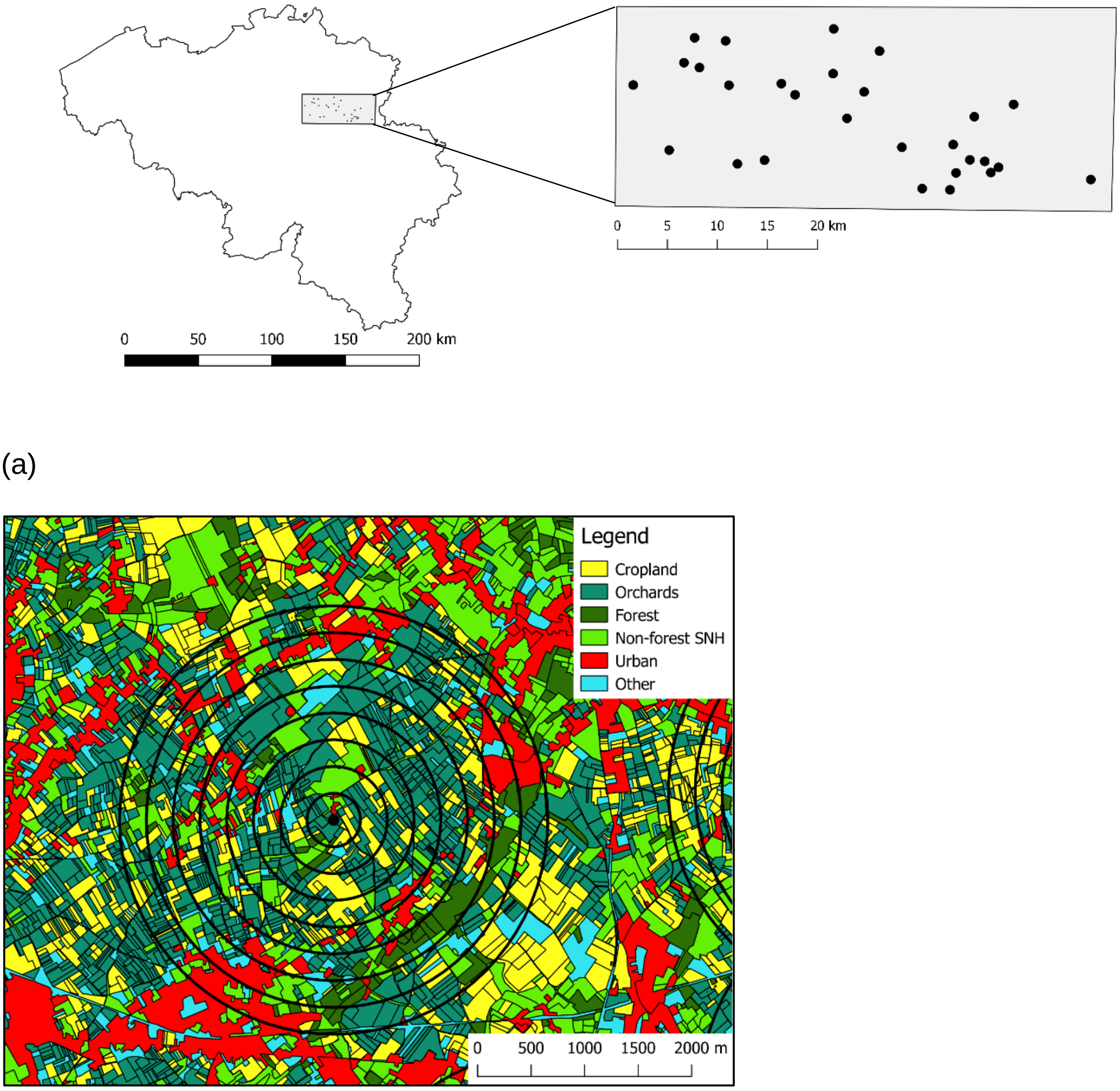
2.2. Bumblebee nests

The experiment was carried out during two six-week periods: the first time from the beginning of April to the end of May, co-inciding with the mass-flowering of the fruit trees in the orchard. The same setup was repeated from the beginning of June to the second half of July, to assess the effect of the landscape on colony performance without the mass flowering in the orchards. Colonies of *B. terrestris*, reared at Biobest (Westerlo, Belgium), were placed in 28 apple and pear orchards. Distance between colonies was at least 1250m to reduce overlap in foraging range. To maximize the difference in surrounding landscapes, the orchards were selected to fit into four categories: landscapes dominated by fruit orchards, cropland, semi-natural grassland and deciduous forest respectively (Appendix 4.A.).

To isolate the nests against cold and moisture, styrofoam bee-coats® (Biobest, Westerlo, Belgium) were used. During mass-flowering, the initial average nest mass was 473.9 (S.D. 7.1) g, containing

25.7 (S.D. 4.3) workers, while after mass-flowering, the nests weighed on average 473.8 (S.D. 10.2) g, containing 22.6 (S.D. 5.6) workers.

After one week, all nests were surveyed to assure that the colonies were actively foraging. During the rest of the experiment, the nests were checked weekly and weighed every two weeks to measure the biomass increment. Nests with a dead queen were removed and omitted from further analyses. In the first run of the experiment, one single nest was excluded due to the queen’s death, while during the second run two nests were omitted. After six weeks, queen pupae appeared and the nests were collected and weighed. The total number of workers and queen pupae was counted.



(a)

(b)

Figure 4.1: (a) map of Belgium with the study area enclosed by the grey rectangle. The 28 bumblebee nests are indicated by black dots. (b) Landscape around a single bumblebee nest. Circles show buffers with a radius of 250 to 2000 metres around the nests with 250m intervals. Within these buffers, the area of all land use classes was measured for further statistical analysis.

2.3. Landscape

The landscape was classified into 5 different land-use classes, using the Biological Valuation Map (BWK) (De Knijf et al., 2010) and the Flemish dataset of LPIS (ALV, 2016): cropland (including temporary grasslands), orchards (including intensively managed apple, pear and cherry orchards), deciduous forests, non-forest semi-natural habitat (including semi-natural grasslands, marshland, heathland, road verges) and urban (including gardens). The total cover of each land-use class was calculated within a radius ranging from 250m to 2000m around each nest, with a 250m increment (Figure 4.1b.), to include all possible foraging ranges mentioned for *B. terrestris* (Knight et al., 2005a; Osborne et al., 1999; Kerstin Walther-Hellwig and Frankl, 2000; Wolf and Moritz, 2008). Additionally, the total amount of semi-natural habitat was calculated in the same way, the latter being the sum of all forest and semi-natural grassland types. GIS-analyses were all carried out using QGIS 2.16 (QGIS Development Team, 2015).

2.4. Pollen

Three weeks after the nests were put in the orchards, pollen was sampled from foraging bumblebees. At each location, the nest entrance was closed and five workers returning to the nest were caught using an insect net. The pollen load of each bumblebee was scored on a 0-5 scale (0 = carrying no pollen; 1 = carrying small amounts of pollen, not forming a solid clump, 2 = pollen clumps small, covering less than half the tibial width, 3 = pollen clumps covering less than the whole tibial width, 4 = pollen clumps covering more than the full tibial width, 5 = pollen clumps covering more than double the tibial width).

Pollen was collected from both corbiculae of the workers using a clean insect pin and the pollen was stored in a dry eppendorf tube and frozen before further identification. All sampling took place between 10:00 and 16:00 under dry, sunny weather (Peat and Goulson, 2005). The pollen samples were processed following the standard protocols, stained with basic fuchsin and mounted in glycerine (Moore et al., 1994). To achieve homogenization, pollen clumps were thoroughly mixed in the glycerine. Pollen were identified to the highest possible taxonomical resolution under x1250 magnification with phase contrast (JENAMED, Carl Zeiss, Jena), using Beug (2004) for identification. In each pollen slide, five straight transects with random starting point were followed, and on each transect, 50 pollen grains were identified, up to a total of 250 pollen grains per sample. The amount of each pollen type was multiplied by the pollen load of the sample and all pollen samples per nest were summed to estimate the composition of the collected pollen per nest. The Simpson diversity index of the total collected pollen was calculated and used in further analyses as a measure for pollen diversity. During the second run of the experiment, only nectar flights were observed in two nests. These nests were omitted from analyses that include pollen composition.

2.5. Analysis

All analyses were carried out using R 3.4.3 (R Core Team, 2018). To achieve normality, nest biomass increment, number of queen pupae and number of workers were squareroot-transformed.

The nest performance during the two periods of the experiment was analysed separately. To assess the optimal spatial scale, a general linear model was created, with the total area of orchards, non-forest semi-natural habitat and forest as fixed variables and the biomass increment as response variable. This analysis was performed on all analysed scales, both during and after mass-flowering. The scale with the highest R^2 was selected as the spatial scale to use in the analyses (Holland et al., 2004). During mass-flowering, the landscape composition at a scale of 750 m had the strongest influence on colony biomass increase, while after mass-flowering, it was strongest at a 1000 m radius (Appendix B).

First, general linear models (glm) were performed to assess the effect of the different land use types on colony growth. The area of orchards, forests, non-forest SNH and urban habitat were included as land use classes in the models. A backwards model selection was performed, and variables with a p-value below 0.10 were retained. Following the same procedure, additional glm were performed to detect a correlation between amount of pollen collected or pollen diversity and land use.

As land use types were expected to influence the colony performance through the available pollen resources, we also fitted glms on the relationship between (i) land use type and cumulative worker pollen load, (ii) land use type and pollen diversity and (iii) cumulative pollen load and pollen diversity on colony growth. Models testing the effect of pollen diversity contained both the Simpson diversity of the collected pollen and the share of the three most commonly collected pollen types in each period.

To assess whether the landscape composition has a consistent effect throughout the year, the correlation between the biomass increments of the nests at the same location during the two consecutive periods was calculated. Only locations where the nests developed during both periods were taken into account (n=25).

Based on the correlations between landscape composition, pollen quantity, pollen composition and nest performance, a causal relationship was hypothesized. To test this, structural equation models (SEM) were made (Grace, 2006) using the lavaan-package in R (Rosseel, 2012). Separate models were made for the colonies during and after mass-flowering. All variables were standardized by subtracting by their mean and dividing through their standard error.

First, a model was created, based on our hypotheses on how these factors influence each other. Latent variables were created for landscape composition, pollen composition, pollen quantity and colony performance. A Bollen-Stine test with 1000 bootstraps was performed to test for normality (Kim and Milsap, 2014). Nonsignificant paths ($p > 0.10$) were dropped and the best SEM was selected based on its AICc. At each path, we indicated the standardized regression coefficients, which represent the amount of change on a parameter if the other one changes one standard deviation. The model fit was tested using a chi-squared test ($p > 0.05$) and the comparative fit index (CFI > 0.90) (Bentler, 1990).

3. Results

3.1. Colony growth

During the first period, the bumblebee nests grew on average with 197.7 (S.D. 209.2) g, with 15 out of 27 active nests producing queen pupae after six weeks. Colony growth was strongly correlated to the cumulative amount of pollen collected (Figure 4.2.; Table 4.1.). However, we found no significant effect of pollen composition or pollen diversity on colony growth. Presence of orchards had a marginally negative effect on colony growth.

Table 4.1.: Model statistics of the best models on the correlation between biomass increment and (i) pollen characteristics (cumulative pollen load and pollen diversity) or (ii) land use (best model at radius with highest R^2); and models on the correlation between pollen characteristics (cumulative pollen load and diversity) and land use. None of the land use classes had a significant effect on the cumulative pollen load or pollen diversity during the second run of the experiment.

Period	Response variable	Expl. var.	N	df	Slope	t-val.	p-val.	R^2
1	Biomass increment	Cum. pollen load	27	25	0.88 ± 0.18	4.81	<0.0001	0.48
1	Biomass increment	Orchards (750m)	27	25	-0.14 ± 0.07	-2.06	0.050	0.14
2	Biomass increment	Pollen diversity	24	22	6.34 ± 3.59	1.77	0.091	0.12
2	Biomass increment	Urban (1000m)	26	24	-0.12 ± 0.06	-2.22	0.036	0.17
1	Pollen diversity	Orchards (750m)	27	25	-0.0072 ± 0.0017	-4.30	0.0002	0.42
1	Amount Rosaceae	Orchards (750m)	27	25	0.89 ± 0.25	3.56	0.0015	0.34
2	Pollen diversity	Any land use	24	-	-	-	NS	NS
1	Cum. pollen load	Orchards (750m)	27	25	-0.14 ± 0.05	-2.94	0.007	0.26
2	Cum. pollen load	Any land use	24	-	-	-	NS	NS

During the second period, the nest biomass increment was 153.0 (S.D. 147.9) g, with 17 out of 26 active nests producing queen pupae after six weeks. Colony growth was marginally positively correlated with pollen diversity, but negatively correlated with urban land.

Colony growth during the first and the second period were not correlated to each other (r = 0.03, p = 0.88).

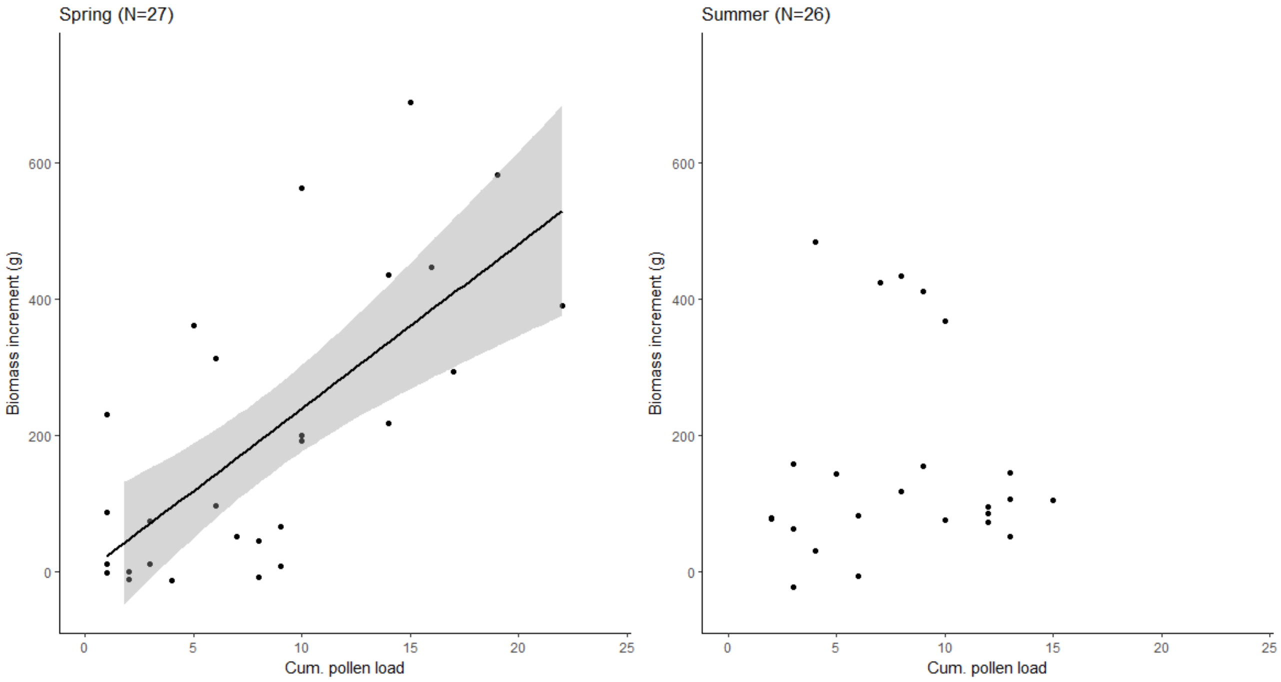
3.2. Pollen collection

During the first period of the experiment, nine morphospecies of pollen were collected from foraging workers. Most pollen was collected from Rosaceae (68.2%), followed by *Salix* spp. (15.7%) and *Acer* spp. (12.1%). These three plant sources accounted for 96% of all collected pollen during this period (Appendix 4.C.1.). As the nests were placed in apple and pear orchards and no other Rosaceae were abundantly flowering in the study area at the time of pollen collection, we consider it highly likely that the large majority of Rosaceae pollen that was collected belongs to these two species.

During the second period, most of the collected pollen belonged to the *Tilia*-type (53.4%), followed by *Papaver rhoeas* type (14.6%) and *Lysimachia* type (13.4%). 17 other morphospecies accounted for 18.5% of the total collected pollen (Appendix 4.C.2.). While during the first period 96.9% of all pollen was collected from woody plants, only 57.9% of all pollen collected during the second period originated from shrubs or trees. Additionally, 5.6% of all pollen collected during the second period belonged to plants that are primarily wind pollinated, such as *Castanea sativa*, *Urtica* spp. and grasses.

The amount of pollen collected during the first period was strongly negatively correlated to the area of orchards (Table 4.1.). Land cover also had a strong influence on pollen diversity and composition, with pollen diversity being negatively associated with orchard cover. Furthermore, the amount of Rosaceae pollen collected increased with the orchard cover.

During the second period, no significant relationship was found between the amount of collected pollen, pollen composition or pollen diversity and land use.

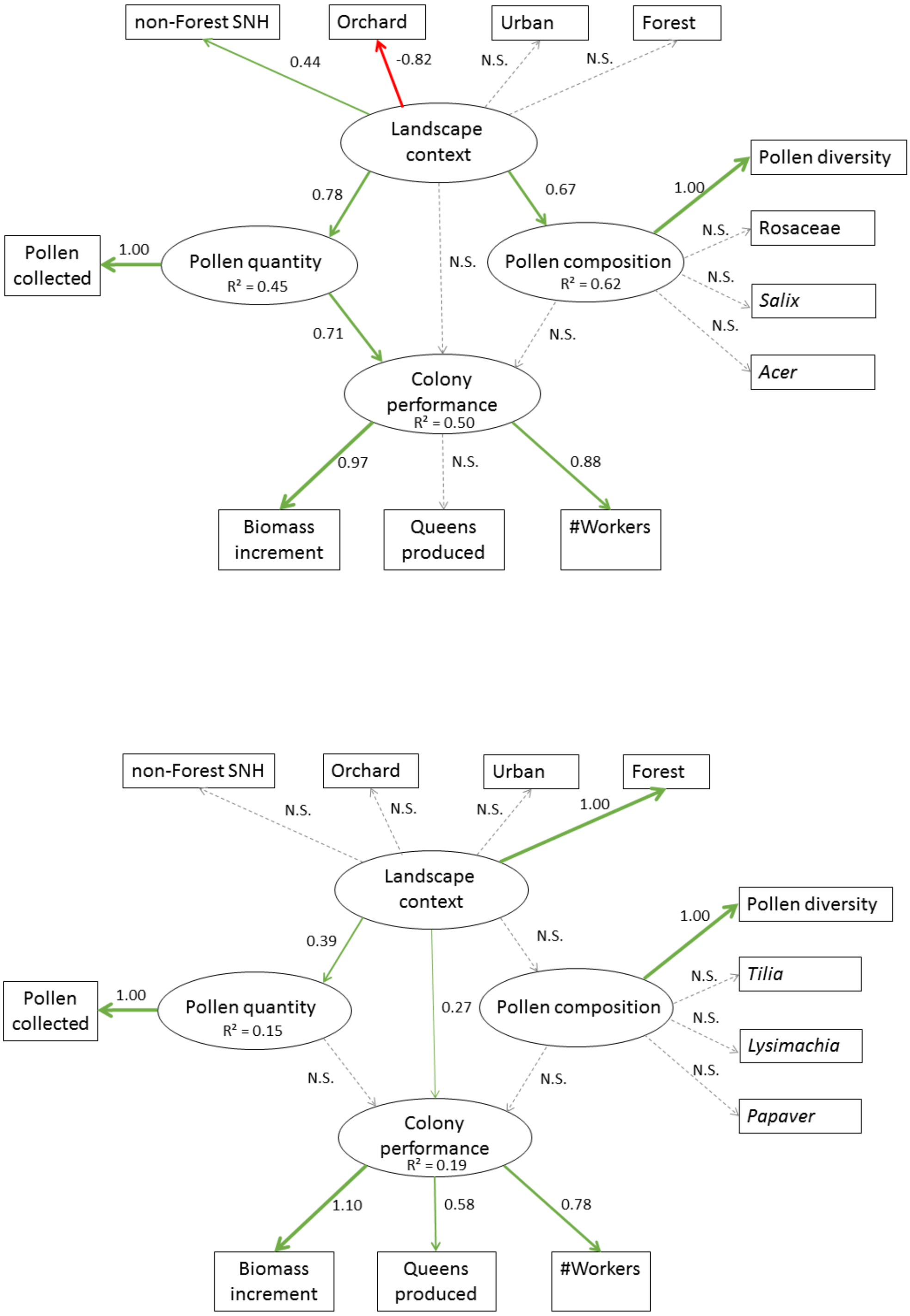


(a) (b)

Figure 4.2: Relationship between cumulative pollen load of sampled workers and colony growth (a) in spring and (b) in early summer.

3.3. Structural equation models

The structural equation models (Figure 4.3.) synthesise the results from the general linear models and confirm the strong connections between landscape context, pollen quantity, pollen composition and colony performance. During mass-flowering, the landscape context had a significant effect on both pollen quantity and pollen composition, with the total area of orchards decreasing pollen diversity and pollen load in foragers, while non-forest SNH had a positive effect on both. Only the amount of pollen collected had a direct influence on the colony performance, while landscape context had only an indirect effect. After mass-flowering, forest cover had a positive effect on both the amount of pollen collected and the colony growth. No correlations between land use and pollen quality or pollen quality and colony performance were found after mass-flowering.



(a)

(b)

Figure 4.3: SEM explaining the relationships between landscape context, pollen quantity, pollen composition and colony performance (a) in spring (n=27, χ² (7) = 12.36, p = 0.09, CFI = 0.93) and (b) in summer (n=24, χ² (7) = 2.74, p = 0.91, CFI = 1.00). Observed variables are given in rectangular boxes, while latent variables are displayed in oval boxes. Positive correlations are indicated by green arrows, while negative correlations are indicated by red arrows. Arrow thickness is proportional to the standardized coefficient of the path. Grey, dashed lines indicate non-significant paths. Non-significant paths were not included in the final model. Standardized coefficients are indicated on the arrows. The R² of dependent variables is displayed in the boxes.

4. Discussion

4.1. Effect of landscape context on pollen availability and colony growth

We hypothesized that during mass-flowering of the orchards, these would serve as important foraging habitat and that the effect of semi-natural habitat would be minimal due to the large abundance of pollen resources. In our study, apple and pear trees were indeed the most important pollen source during spring. However, contrary to our expectations, in landscapes dominated by orchards, bumblebees collected less pollen, leading to a lower colony performance (Mattila and Otis, 2006). One possible reason for the apparently low availability of pollen is competition with managed honeybees. Although orchards may provide large amounts of pollen and nectar during flowering season, high densities of honeybee hives are usually placed during flowering. Due to these unnaturally high densities (Geldmann and González-varo, 2018), bumblebees and other wild pollinators may suffer from competition with honeybees (Goulson and Sparrow, 2009; Shavit et al., 2009; Thomson, 2004, but see Steffan-Dewenter and Tscharntke, 2000) or pathogen spillover (Fürst et al., 2014). The negative effect of competition with honeybees is stronger in homogeneous landscapes (Herbertsson et al., 2016), making bumblebees in intensive agricultural landscapes dominated by orchards more susceptible than in more diverse agro-landscapes. Additionally, wild pollinator densities can increase in presence of mass-flowering crops (Holzschuh et al., 2013; Kovács-Hostyánszki et al., 2013), potentially further increasing the competition for pollen. Despite the ample presence of foraging resources, which, based on the identity of the collected pollen, attract the majority of foraging workers, flowering orchards could therefore be considered as ecological traps for bumblebees (Kallioniemi et al., 2017), as these attract foraging workers, while not providing sufficient pollen. Although we expected that mass-flowering apple trees would have a positive effect on bumblebees, colonies in landscapes with only a small area of orchards performed better.

4.2. Effect of semi-natural habitat on colony performance

We studied the role of landscape composition for bumblebee foraging. Both during and after mass-flowering, colony performance was positively correlated with presence of semi-natural habitat. In spring, during mass-flowering, more pollen were collected in areas with more non-forest semi-natural habitat. After mass-flowering, colony growth was slightly better at locations with a higher surrounding forest cover, where *Tilia* and *Castanea* could serve as important pollen sources. Bees are known to forage in different habitats (Mandelik et al., 2012). Although semi-natural habitat can serve as an important pollen and nectar source throughout the season (Földesi et al., 2015; Requier et al., 2015; Scheper et al., 2014), *B. terrestris*, having a very broad diet, is able to forage in agricultural (Odoux et al., 2012) and urban (Chapman et al., 2003) habitats. During mass-flowering, most pollen was collected from fruit-bearing trees in orchards, while after mass-flowering, the main pollen sources were plants typical for forest and urban urban (*Tilia*, *Lysimachia*) and agricultural (*Papaver*) habitat. These land use types may therefore also serve as suitable foraging habitat for *B. terrestris* during specific periods of the year (Goulson et al., 2002, but see Bukovinszky et al., 2017).

As the bumblebees were placed in artificial bumblebee nests, we did not investigate the role of the landscape as nesting habitat. While our study found a relatively weak positive effect of SNH on colony performance, it may have a strong effect on nesting place availability, leading to a higher colony density in landscapes with a higher cover of SNH

4.3. Seasonal aspect of foraging habitat

A gap in pollen availability during the flying season can limit bumblebee colony growth or survival (Vanbergen and the Insect Pollinators Initiative, 2013). We showed that colony growth during and after mass-flowering on a single location were not correlated. In our study, colonies at various locations performed differently during and after mass-flowering, and the amount of pollen collected differed strongly between the two periods. This implies that while a landscape could provide sufficient pollen resources to sustain a bumblebee colony at a given time, only two months later, the same location could be a hostile environment for bumblebees. While one type of land cover could provide the necessary foraging resources for bumblebees during part of the season, it could be poor in floral resources at other times of the year (Williams et al., 2012). For long-term survival of a bumblebee population, it is therefore necessary that sufficient foraging resources are consistently available within flying distance of bumblebee colonies during the flying season (Aleixo et al., 2016; Decourtye et al., 2010; Franzén and Nilsson, 2008), although the exact locations and land use types that provide pollen and nectar may change throughout the year.

While *B. terrestris* colonies are active for a large time of the year (Rasmont et al., 2008), most floral resources are only present during a short period. We did not find a single pollen morphospecies that was collected during both periods of the experiment. With changing flower resources, the role of the landscape as foraging habitat also changes. While most pollen during the first period was collected on mass-flowering fruit-trees, linden trees, which in the study region are mostly associated with (sub)urban habitat, were the major pollen source during the second period.

The major foraging habitat within a certain period also influences the foraging distance, hence altering the spatial scale on which the landscape influences the colonies. During mass-flowering, when most pollen was collected in the orchards themselves, the landscape effects were strongest within a 750 m radius, while after mass-flowering, when several more distant foraging habitats were used, landscape effects were strongest at a 1000 m scale (Danner et al., 2016).

5. Conclusion

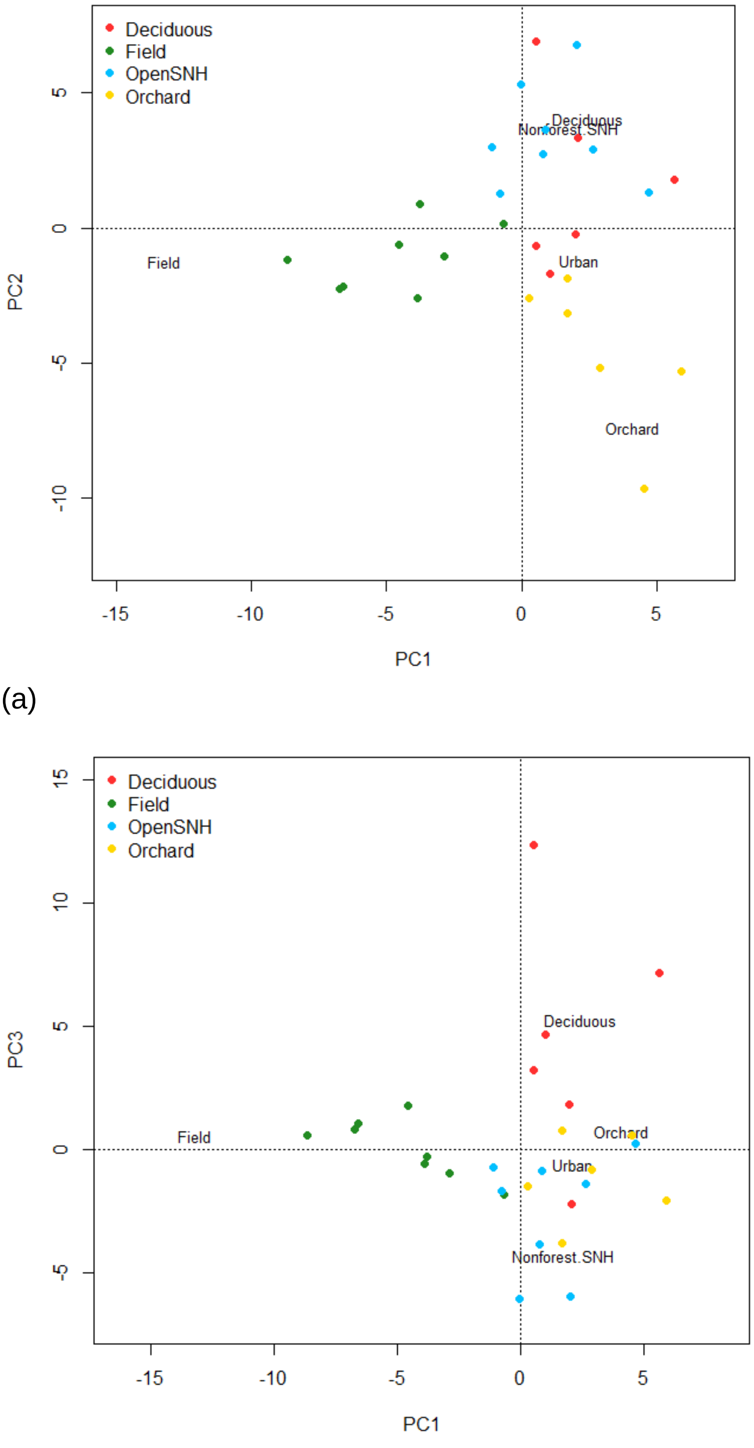
While orchards can serve as foraging habitat for bumblebees during mass-flowering, bumblebees fare better in landscapes that are more diverse. Our study showed that bumblebees forage in different habitat types depending on the time of the year. Therefore, to maintain a healthy bumblebee population, it is important to provide a diverse landscape several types of SNH, which can provide pollen during different times of the season. We found that landscapes dominated by large, homogenous areas of orchards are negatively correlated with bumblebee colony performance. While other studies show that pollinators can benefit from mass-flowering crops (Holzschuh et al., 2013; Riedinger et al., 2014), we showed that preservation of semi-natural habitat in agro-landscapes has beneficial effects on *B. terrestris* colony performance by providing more pollen. Pure dependence on a succession of mass-flowering crops is probably less effective to maintain bumblebee colonies in agricultural landscapes than providing sufficient semi-natural habitat.

6. Acknowledgements

We are very grateful to Tim Beliën (pcfruit) for his help in finding suitable locations for the experiment and to the farmers that allowed the experiment to be carried out in their orchards. We thank Felix Wäckers (Biobest) for providing artificial bumblebee nests. The first author was supported by a grant by FWO-Vlaanderen (FWO14/ASP/195).

Appendix 4

Appendix 4.A: Classification of landscapes used in the study

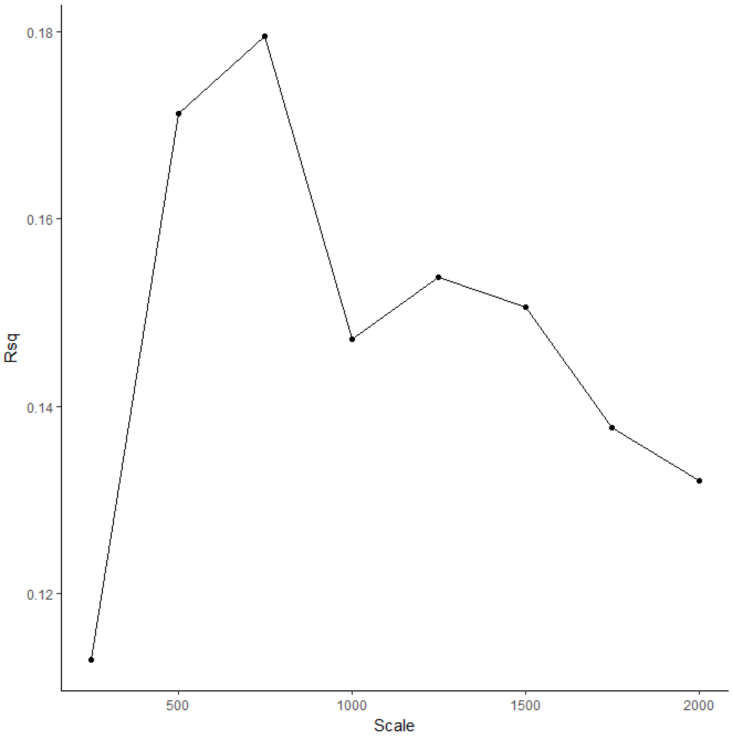


(a)

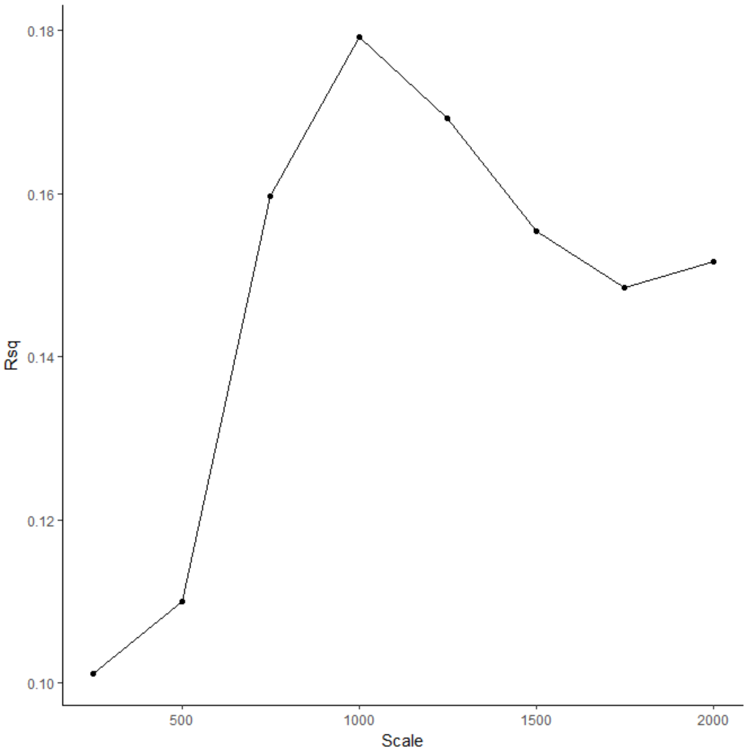
(b)

Appendix 4.A.1. Biplot (pca) of the locations of the bumblebee nests in relation to the five used categories of land cover classes. The analysis was carried out at a radius of 1000m. Sites were selected to have a maximal gradient in land use classes with landscapes dominated by deciduous forests, fields, open semi-natural habitat or orchards. The biplots show (a) axis 1 and 2 and (b) axes 1 and 3.

Appendix 4.B.: R²-plots at different spatial scales



(a)



(b)

Appendix 4.B.1. : R-squared values of spatial models related to the measured scale (a) in spring and (b) in summer

Appendix 4.B.2.: Pearson correlations between all habitat types at (a) a 750 m scale and (b) a 1000 m scale. Significantly correlated land use types ($p < 0.05$) are indicated in bold.

750m	Non-forest SNH	Forest	Orchard	Cropland	Urban
Non-forest SNH	1.00	0.13	**-0.42**	**-0.45**	0.031
Forest	0.13	1.00	-0.32	**-0.39**	-0.078
Orchard	**-0.42**	-0.32	1.00	-0.21	0.15
Cropland	**-0.45**	**-0.39**	-0.21	1.00	**-0.49**
Urban	0.031	-0.078	0.15	**-0.49**	1.00

(a)

Landuse.1000	Non-forest SNH	Forest	Orchard	Cropland	Urban
Non-forest SNH	1.00	-0.013	-0.33	-0.34	-0.17
Forest	-0.013	1.00	-0.22	**-0.36**	-0.16
Orchard	-0.33	-0.22	1.00	**-0.36**	0.21
Cropland	-0.34	**-0.36**	**-0.36**	1.00	**-0.41**
Urban	-0.17	-0.16	0.21	**-0.41**	1.00

(b)

Appendix 4.C.: Pollen composition of clumps collected by foragers

Appendix 4.C.1.: Pollen composition of clumps collected by foragers in spring in the whole study area (2016)

Morphospecies	**Proportion (%)**
Rosaceae	68.2
Salix	15.7
Acer	12.1
Lamium album	1.8
Ranunculus	1.0
Aesculus	0.9
Taraxacum	0.3
Plantago lanceolata	<0.1
Brassicaceae	<0.1

Appendix 4.C.2.: Pollen composition of clumps collected by foragers in summer in the whole study area (2016)

Morphospecies	**Proportion (%)**
Tilia	53.4
Papaver rhoeas type	14.6
Lysimachia	13.4
Scrophulariaceae sp.	4.4
Castanea	3.7
Polygonium aviculare type	2.3
Chelidonium majus	1.7
Indeterminate	1.5
Poaceae	1.5
Calluna vulgaris	0.9
Viburnum opulus	0.8
Vicia	0.6
Urticaceae	0.5
Solanum	0.3
Apiaceae	0.2
Taraxacum	0.1
Symphytum	<0.1
Cirsium	<0.1
Trifolium pratense	<0.1
Fabaceae sp.	<0.1

Chapter 5: Pollination services provided by small forest fragments

(Based on: Proesmans, W.; D. Bonte, G. Smagghe, I. Meeus & K. Verheyen. Pollination services provided by small forest fragments. Submitted to Biodiversity & Conservation).

Abstract

Agricultural intensification and habitat loss are important causes of declines in insect pollinators. In agricultural landscapes, small forest patches often form the most abundant type of semi-natural habitat. These forests have the potential to serve as habitat for insect pollinators and therefore indirectly contribute to pollination services.

We assessed the bee and hoverfly community in 16 forest fragments in an agricultural landscape in Belgium, using pan traps and transect walks. To evaluate their contribution to pollination, we used strawberry and blueberry plants as phytometers. Numbers of pollinator visits and fruit set and fruit biomass were measured to assess pollination. We hypothesized that the pollinator community benefited from local forest characteristics such as herb layer cover and forest age, and landscape characteristics, such as forest cover and the amount of edge habitat, and that this resulted in higher pollination services, leading to higher fruit set and fruit quality.

Bee diversity and activity-abundance was positively correlated with sun exposure and negatively correlated with herb layer cover and forest cover, which may be attributed to a dilution effect. We did not find a correlation between local or landscape characteristics and the hoverfly community. Phytometers at sites with a high bee activity-abundance were visited more often and visitation rate was positively correlated with fruit set in both strawberries and blueberries. As only a limited subset of the pollinator community contributed to pollination of the phytometers used in the study, a direct correlation between pollinator abundance in the forest fragments and fruit set was not detected.

1. Introduction

Intensively managed agricultural landscapes occupy large areas of Western Europe. During the past century, these landscapes have undergone strong modifications, including increasing pesticide and fertilizer use, destruction of small landscape elements such as hedgerows to increase parcel size and a decrease in crop variation (Geiger et al., 2010; Matson et al., 1997; Tscharntke et al., 2005). Most of these changes had a detrimental effect on biodiversity in general (e.g. Donald et al., 2001; Guerrero et al., 2012; Stoate et al., 2001) and on pollinator species richness and abundance in particular (Biesmeijer et al., 2006; Holzschuh et al., 2007; Le Féon et al., 2010). Declines in pollinator diversity and abundance can lead to pollen limitation, both in (semi-)natural ecosystems (Cunningham, 2000) and in crops (Deguines et al., 2014; Kremen et al., 2002). If these declines persist, this may lead to problems in the agricultural sector, causing economic losses and shortages of certain crops (Gallai et al., 2009).

The total value of insect pollination has been estimated in hundreds of billions of Euros per year (Gallai et al., 2009). It is estimated that 75% of all crops and 35% of global crop production is in some way dependent on animal pollination (Klein et al., 2007). While some crops, such as squash (Kennedy et al., 2013) and melons (Winfree et al., 2008, 2007b) are completely dependent on insect pollination for successful fruit set, other crops, such as apples (Stern et al., 2001), strawberries (Klatt et al., 2014) and sunflower (Greenleaf and Kremen, 2006) show a strong increase in productivity and fruit quality with increased pollination services (Aizen et al., 2009).

While agricultural land is often an adverse habitat for pollinators, these landscapes usually still contain some patches of semi-natural vegetation. Due to the loss of species-rich grasslands (Luoto et al., 2003; Wesche et al., 2012), small forest fragments often form the largest share of semi-natural habitat in these agro-ecosystems. These small forest fragments can provide important ecosystem services (Decocq et al., 2016). Several studies acknowledge the importance of forest habitat for the pollinator community, often showing a higher abundance and diversity of pollinators in landscapes with a higher forest index (Farwig et al., 2009; Watson et al., 2011). Additionally, specific local forest characteristics related to availability of foraging and nesting or larval habitats have an effect on diversity, abundance and composition of the pollinator community (Grundel et al., 2010; **Chapter 3**).

While the availability of semi-natural vegetation is known to have a direct effect on the presence and species richness of pollinators (Nayak et al., 2015), this should not per definition optimise pollination services as not all species from the pollinator community will contribute to this. However, because diverse communities will increase the likelihood of maintaining an essential subset of the crop-visiting species, a more diverse pollinator community should be able to increase pollination services. Their importance is eventually expected to increase when multiple crops are considered.

Our research question was whether local and landscape characteristics in these small forest fragments improve pollination services and therefore lead to a higher fruit set in the tested phytometers. We hypothesized that differences in the pollinator community, driven by local and landscape characteristics, affect the pollination services that the community delivers. In this research, we used two crops that depend on pollination for successful fruit set, but have a different flower morphology and therefore are expected to attract different species of pollinators. We hypothesized that (a) forest fragments with beneficial local characteristics for pollinators, being sufficient nesting and foraging habitat, leads to a more diverse and abundant pollinator community, (b) that insect-pollinated plants at sites with a richer pollinator community will be visited more frequently by insects and (c) that this will lead to a higher fruit set and fruit quality.

2. Material & Methods

2.1. Study landscape

The research was carried out in a 25 km² rural landscape around Glabbeek, in the centre-east of Belgium. The region is characterized by intensive agriculture, dominated by cropland (37.9%), low-stem apple and pear orchards (11.3%) and grasslands (27.5%). The main crop grown in the fields is corn, while wheat, beets and potatoes are also commonly cultivated. Grasslands in the region are typically very species-poor due to intensive agricultural management, including use of high levels of fertilizers, frequent mowing or high densities of cattle.

The selected landscape has a forest index of 7.4%, and contains scattered, small forest fragments. Sixteen contrasting forest fragments, ranging in size from 0.4 to 11.7 ha, were selected. The forest fragments differed in age from recently planted forests (<17 years old) to ancient forest (present on maps in 1775). All fragments were deciduous forests dominated by sessile oak (*Quercus robur* L.), red oak (*Quercus rubra* L.) or ash (*Fraxinus excelsior* L.). While older forests had a mixed species and tree-age distribution, recent forest patches were even-aged and dominated by a single tree species.

2.2. Forest and landscape characteristics

The experimental setup was installed in the southern edge of each forest fragment, on the interface between the forest patches and agricultural land, as south-oriented forest edges are considered as the best pollinator habitat due to their poikilothermous lifestyle. Characteristics influencing the value of the forest fragments as foraging habitat for pollinators were measured in May 2015 (Table 5.1.). Forest age was defined as the time that a forest patch has continuously existed as forest, with the oldest forests being present since at least 1775, while the most recent forest fragments were only present on map data since the year 2000. Herb layer cover was determined in three 50 m transects running from the southern forest edge to the forest interior. On each transect, the herb layer cover was measured in five equally spaced 5 x 5 m² plots. Sun exposure differed strongly between sites and was measured three times during the day (10:00, 13:00 and 16:00) at the point where pan traps were placed. Locations that were shaded two times or more were categorized as ‘shaded’, while other locations were classified as ‘exposed’. The plant community was assessed within a 200 m radius around the study sites by surveying the plant community in six 2 m wide and 200m long, radially oriented transects starting at the sampling location. All insect-pollinated plants were identified to genus level and their cover was measured and scored on a 0-5 Tansley scale (Alberdi et al., 2010). A weighted sum of the plant taxa present ($Flower\ index\ = \sum_{taxon=1}^{n} Tansley_{taxon}$, with Tansley the score on the Tansley scale for the given plant taxon), was used as a measure for floral resource abundance.

The total deciduous forest cover and the length of edge habitat were calculated within a 400 m radius around the study sites, which is a suitable scale to investigate wild pollinators (Steffan-Dewenter et al., 2002), while avoiding spatial autocorrelation in land-use composition between sites. Edge habitat included both forest edges and hedgerows. QGIS 2.16 (QGIS Development Team, 2015) was used for the spatial analyses.

Table 5.1: Analysed forest and landscape characteristics.

Variable	**Explanation**
Forest age	Area-weighted average age of all stands in the forest patch, based on map data from 1775, 1850, 1910 and 2000 (Valdés et al., 2015)
Herb layer cover	Herb layer cover in the forest patches, from the edge to 50 m into the forest interior
Sun exposure	Exposure of the forest edge, based on solar incidence at three points of the day (categorical: shaded/exposed)
Flower index	Abundance index of insect-pollinated plant taxa
Forest cover	Forest cover within a 400 m radius around the study sites
Edge habitat	Total length of forest edges and hedgerows within a 400 m perimeter around the study sites

2.3. Pollinator community

Blue, yellow and white pan traps (Ø 20 cm, Motip® Fluor Blue, Motip® Fluor Yellow, Motip® High Gloss White) were attached to the outer tree row in the southern forest edge at a height of 1.3 m. The traps were filled with water and a few drops of biodegradable detergent to break the surface tension. The pan traps were set out for 96 hours at each location, both in the middle of April and at the end of May. During the sampling, transect walks were performed along the southern forest edge in each location. Along a length of 50 m, all bees and hoverflies within 2 m from the observer were caught with an insect net for a period of 15 minutes. Both pan trapping and transect walks took place under favourable weather circumstances (no rain, cloud cover <50%; wind speed <5 m s^{-1}). Specimens captured with pan traps and specimens caught during transect walks that could not be identified on the wing up to species level were transferred to 70% ethanol, washed, dried, pinned and identified up to species level. For bees, only females belonging to non-kleptoparasitic species were used in further analyses, as only these actively collect pollen (Taki et al., 2007).

Both the pan trapping and the transect walks were repeated for two consecutive years (2015-2016) to account for inter-annual variation (Oertli et al., 2005), resulting in a total of four days of pan trapping and one hour of transect walks at each location.

2.4. Phytometers

Strawberries (*Fragaria x ananassa* Duch.) and blueberries (*Vaccinium corymbosum* L.) were used as phytometers. They were placed at the same locations as pan trapping and transect walks were carried out. Percentage fruit set in relation to total number of flowers and fruit biomass were used as proxies to measure pollination services. Varieties were selected based on their dependence on insect pollination to have a high yield. Strawberries of the cultivar 'Korona' were used as phytometers, as fruit set and fruit quality of this variety strongly depend on insect pollination (Klatt et al., 2014). 'Elsanta' was planted to assure cross-pollination, as the flowering time of both varieties is similar. For blueberries, two varieties were selected as phytometers: 'Bluecrop' and 'Goldtraube, which have similar flowering times and show a strong increase in fruit set and fruit quality following insect pollination (Bieniasz, 2007; Prodorutti and Frilli, 2008).

Phytometers were placed at the study sites in the spring of 2017. The phytometers were all planted in the southern forest edge of the selected forest patches at the end of March (Appendix 5.A.). All plants were of equal size and age, to minimize intrinsic differences in vitality and flowering intensity between plants. To rule out effects of soil characteristics, the blueberry plants were kept in pots, which were dug in the soil. The strawberries were planted directly into the soil to assure survival. At each location, five 'Korona' and two 'Elsanta'-plants were planted, yielding a total of 80 'Korona' and 32 'Elsanta' plants. For the blueberries, three shrubs of each variety were planted in an alternating pattern at each study site, totalling 48 shrubs of each variety for the whole study. As the study region experienced an exceptionally dry spring, all plants were watered on a weekly base.

During flowering of the strawberries, which started in mid-April and lasted until the end of May, and the blueberries, lasting from the beginning of May to the beginning of June, pollinators visiting the plants were counted at the plot level. All insect pollinators were counted and identified on the wing up to the highest possible taxonomic level. Both the strawberry plants and the blueberry shrubs were observed at each location during three periods spread over the flowering period, each lasting one hour. Each site was visited once in the morning (09:30-12:00), at noon (12:00-14:30) and in the afternoon (14:30-17:00). Pollinator observation took place under favourable weather circumstances (cloud cover <50%, wind speed <5 m s^{-1}, no rain).

During flowering, the number of flowers on each plant was counted during each visit. Both number of blooming flowers and total number of flowers were counted. In models including the flower number, the maximum number of flowers counted on each plant was used. After fruit ripening, the number of fruits from each plant was counted, and all fruits were weighed, considering fruit biomass as a proxy for fruit quality (Garratt et al., 2014).

2.5. Statistical analysis

Given the low number of pollinators observed on the strawberry plants, the relationship between the pollinator community in the forest edges and number of flower-visitors was only analysed for the blueberries. As bees represented the large majority of flower visitors on the blueberry plants, only the bee community was further analysed.

To assess the effect of inter-annual variation in the bee community, netted and pan-trapped bees were pooled per year and per site, and analyzed at the species-level. The species-matrix was squareroot-transformed. We performed a PCA to assess the effect size of year and site identity. To test the significance of these factors, we performed a permutational analysis of variance (PERMANOVA) on a Bray-Curtis matrix between sites and years, using 9999 permutations.

A general linear model was fit to test the relation between bee Shannon diversity and forest characteristics (cf. Table 5.1.), using backwards model selection, retaining variables with a p-value below 0.05. To assess the relation between bee activity-abundance and site characteristics, a generalized linear model was fit, using a Poisson-error distribution and a log-link function. Backwards model selection was used, keeping variables with a p-value below 0.05. As forest cover and edge length were strongly positively correlated with each other (df = 15; r = 0.74; p = 0.001), both variables were analysed in two separate models. The best model was selected based on the AICc of both models.

To assess whether pollinator activity-abundance at the study sizes was correlated to the number of flower visitors on the phytometers, generalized linear models were fit with the number of flower visitors as response variable and bee abundance and bee diversity as explanatory variables. As diversity and activity-abundance were strongly correlated (df = 15; r = 0.67, p = 0.004), both were used in two separate models, the best model being selected based on the model AICc. Because phytometers with more flowers attracted higher numbers of pollinators, flower number was used as a covariate in both models. As the Poisson models were overdispersed, a negative binomial distribution was used (Ver Hoef and Boveng, 2007).

The relation between the number of flower-visiting pollinators on the phytometers and the % fruit-set was tested using generalized linear mixed models, with the number of flower-visiting insects as a fixed effect and plant identity nested in site identity as random effects. A binomial error distribution and a logit-link were used. Fruit set in ‘Korona’ strawberries and ‘Bluecrop’ blueberries were analysed separately. ‘Goldtraube’ blueberries were not analysed because of the low fruit set.

The effect of pollination on fruit quality was analysed on ‘Korona’ strawberries and ‘Bluecrop’ blueberries by fitting a general mixed model with fruit biomass as response variable and number of insect visitors as fixed effect. Plant identity nested in site identity were used as random effects.

3. Results

3.1. Pollinator community in forest edges

Pan trapping yielded 125 bees, while 119 specimens were caught during sweep netting, resulting in 244 individuals belonging to 36 species. The most abundant genus was *Bombus*, which accounted for over half of the caught bee species (125 individuals, 51.2%). *Andrena* (56 individuals, 23.0%) and *Lasioglossum* (45 individuals, 18.4%) were the second and third most abundant genus. Honeybees (*Apis mellifera*) were scarce in our study (9 individuals, 3.7%). Most of the non-*Bombus* bees belonged to solitary or communal ground-nesting taxa (103 individuals, 42.2%), while numbers of above-ground nesting solitary bees were very low (7 individuals, 2.9%).

Pan trapping yielded 209 hoverflies, while 193 individuals were caught during transect walks, accounting for 33 different species. The most abundant species was *Rhingia campestris* (176 individuals, 43.8%), followed by *Episyrphus balteatus* (34 individuals, 8.5%) and *Platycheirus albimanus* (25 individuals, 6.2%). A comprehensive species list is given in Appendix 5.B.1.

The bee community was slightly influenced by inter-annual variation ($F = 1.84$, $df = 1$, $p = 0.028$, $R^2 = 0.045$), but the effect of site identity was much stronger ($F = 1.56$, $df = 15$, $p < 0.001$, $R^2 = 0.58$) (Appendix 5.C.). Bee activity-abundance in the forest edges was negatively correlated with forest cover and herb layer cover, but positively correlated with sun exposure, while bee diversity was only significantly correlated to sun exposure. Hoverfly activity-abundance and diversity were not significantly correlated to any environmental variable. All best models are displayed in Table 5.2. and a conceptual model on how forest characteristics may affect pollination services is given in Figure 5.1.

3.2. Flower visitors

Blueberries and strawberries were visited by a different subset of the pollinator community. We recorded 157 pollinator visits on the blueberry plants, the majority of which was carried out by three bumblebee species, being *Bombus pratorum* (Linnaeus, 1761), *B. pascuorum* (Scopoli, 1763) and *B. hypnorum* (Linnaeus, 1758) (132 individuals; 84.1%). Solitary bees represented 14 visits (8.9%), while hoverflies were observed 10 times (6.4%). One single wasp, belonging to the family Vespidae was observed.

We observed 41 flower visits on strawberry flowers. Hoverflies were the most abundant pollinators (17 individuals, 41.5%), followed by bumblebees (13 individuals, 31.7%) and solitary bees (9 individuals, 22.0%). Two butterflies were also observed visiting the flowers. A complete list of insect visitors on the phytometers is given in Appendix 5.B.2.

Given the low number of pollinators observed on the strawberry plants, no further analyses were carried out on the relation between the pollinator community in the forest edges and the number of flower visitors on the strawberry plants. While the number of pollinators attracted to the blueberry plants was mainly correlated to the number of flowers on the phytometers, a significant positive correlation with bee abundance in the forest edge was found.

Table 5.2: Best models for the analysed response variables. Table shows model coefficients ± standard error. Significance levels of the variables are indicated by ($^{\$}$) $p < 0.10$; (*) $p < 0.05$; (**) $p < 0.01$; (***) $p < 0.001$.

Response variable	**Explanatory variables**				**Model R²**
Bee diversity	Intercept 1.41 ± 0.14***	Sun exposure 0.47 ± 0.17*			0.34
Bee act.-abund.	Intercept 3.45 ± 0.23***	Sun exposure 0.57 ± 0.15***	Forest cover -0.094 ± 0.019***	Herb layer cover -0.0075 ± 0.0020***	0.91[a]
Flower visitors	Intercept -0.43 ± 0.48	Bee act-abund. 0.051 ± 0.020*	Flower abundance 0.011 ± 0.002***		0.76[a]
% Blueberry fruit set	Intercept -2.81 ± 0.41***	Flower visitors 0.11 ± 0.03***			0.41[b]
% Strawberry fruit set	Intercept -2.43 ± 0.55***	Flower visitors 0.21 ± 0.11$^{\$}$			0.20[b]

[a]McFadden pseudo-R^2; [b]R-squared calculated using Standardized Generalized Variation (SGV)

3.3. Percentage fruit set

Percentage fruit set in blueberries was significantly positively correlated with the number of pollinators that visited the plants (Figure 5.2a.). For strawberries (Figure 5.2b.), a marginally significant ($p = 0.054$) positive effect could be detected as well, despite the low number of pollinators observed on the plants. We did not find a significant effect of pollinator diversity on fruit set. No significant correlation between number of flower visitors and fruit biomass could be detected on blueberries or strawberries.

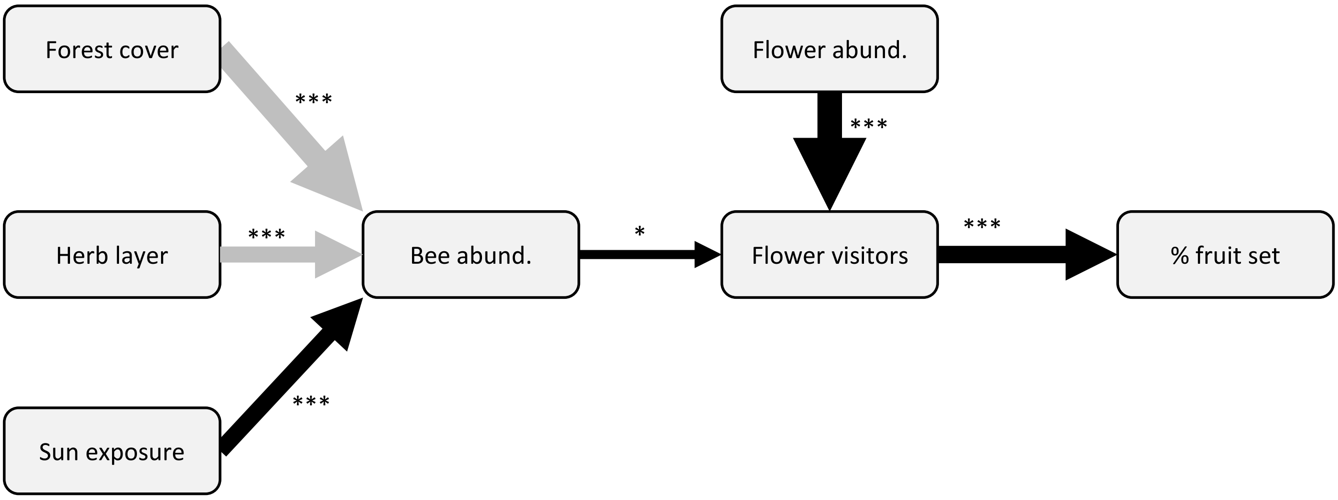


*Figure 5.1.: Conceptual model on how forest characteristics influence bee abundance in the studied forest edges, resulting in higher flower visitors and a higher fruit set in the blueberry plants. Arrow width is proportional to the standardized coefficients in the models. Black arrows indicate positive correlations, grey arrows indicate negative correlations. Significance of the arrows: *p < .05; **p < .01; ***p < .001. Non-significant correlations are not displayed in the model.*

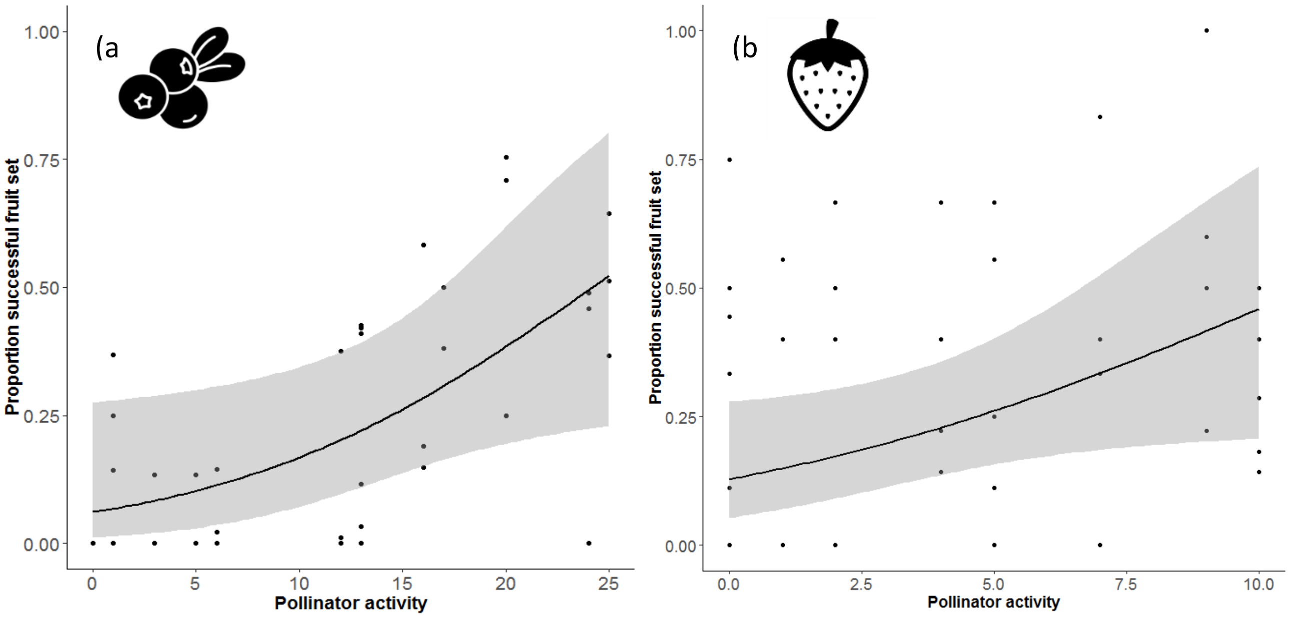


Figure 5.2: Relation between the number of pollinator visits and the relative fruit set, defined as the proportion of flowers that effectively set fruit, in (a) blueberries and (b) strawberries. Each point indicates a single plant. Pictograms by b farias, the Noun Project (thenounproject.com/bfarias/)

4. Discussion

We found that environmental variables at the local and the landscape scale affected pollinator diversity and activity-abundance. Additionally, this indirectly affected the number of flower visitors and the percentage of fruit set in the phytometers. However, no direct correlation between environmental characteristics and pollination services could be detected.

As the influence of site identity on the bee community composition was much stronger than the effect of inter-annual variation, we concluded that placing phytometers for one single year can give a representative image of flower visitors in the study area. Bee activity-abundance was negatively correlated with forest cover and herb layer cover. This inverse relationship may be caused by a dilution effect (Holzschuh et al., 2011; Kovács-hostyánszki et al., 2013). A rich herb layer inside the forest provides a large amount of pollen and nectar resources in spring. Therefore, the bee community is more strongly diluted at larger potential foraging patches, resulting in a lower pollinator visitation rate. This effect is well described on larger spatial scales, where mass-flowering crops cause pollinator dilution, leading to a lower degree of pollination in wild plant (Holzschuh et al., 2011; Kovács-hostyánszki et al., 2013), but also on a smaller scale, where more attractive plant species lead to a lower pollination in other species (Bartomeus et al., 2008), or to lower pollinator catch rates (Stephen and Rao, 2007). Bee nesting habitat may be scarce in agricultural landscapes due to soil tilling on fields (Shuler et al., 2005; Ullmann et al., 2016), soil compaction due to high cattle densities on meadows (Kimoto et al., 2012), and forest management practices where dead wood is removed from the forest (Vandekerkhove et al., 2011). Consequently, nesting habitat may be a stronger limiting factor in this type of landscape than foraging habitat **(Chapter 2)**, causing the observed dilution when foraging resources are present in large quantities. Additionally, bee activity-abundance and diversity was strongly correlated with sun exposure. Bees are thermophilic animals (Sydenham et al., 2014) and sun-exposed locations are known to positively affect the local bee community (Williams and Winfree, 2013).

We did not find any correlation between local and landscape characteristics and hoverfly diversity or activity-abundance. The hoverfly community is ecologically very diverse and larvae develop in various habitats, ranging from aphidophagous species that can successfully reproduce in agricultural habitats to saproxylic or phytophagous taxa that depend on often very specific (semi-)natural habitats (Speight et al., 2016). Hence, the hoverfly community is expected to be less sensitive to the negative effects of agricultural intensification than bees (Jauker et al., 2009). This high ecological diversity makes it hard to identify local or landscape factors that affect the hoverfly community as a whole.

Blueberries and strawberries generally attracted a different subset of the total pollinator community. The majority of pollinators on blueberry plants were bumblebees and small solitary bees that were able to enter the deep flowers completely. While *B. pascuorum* was the only long-tongued bumblebee species observed (Bäckman and Tiainen, 2002), the short-tongued *B. pratorum* and *B. hypnorum* were also common flower visitors. These species are known to display 'nectar robbing' behaviour, biting a hole in the side of the corolla to reach the nectar (Irwin et al., 2010). While the observed visitors did not show this behaviour, and seemed able to reach the nectar in the flowers, bite marks were observed on the corollae of some flowers. Strawberries were visited by a more diverse group of pollinators than blueberries. As open, easily accessible flowers, they were commonly visited by generalist bees, hoverflies and butterflies, giving a more complete image of the pollinator community.

Both strawberries and blueberries showed a strong correlation between number of flower visitors and fruit set, which, for blueberries, correlated with a higher bee activity-abundance. Other studies report higher abundances (Julier and Roulston, 2009), species richness (Garibaldi et al., 2013; Mallinger and Gratton, 2015) or diversity (Klein et al., 2003) as leading drivers of higher fruit set in wild plants or agricultural crops. In this study, we found that pollinator activity-abundance had a stronger influence than species-diversity on both number of flower visitors and fruit set. However, pollinator diversity was positively correlated with pollinator abundance, and sites with a higher diversity in niches may harbour higher numbers of pollinators (Woodcock et al., 2014), making it hard to discern the real drivers. An increased pollinator abundance logically leads to higher numbers of flower visitors (Holzschuh et al., 2012), but not all pollinators are equally attracted to the same plant taxa. Flowers like the ones in blueberry, because of their morphology, attract a specific subset of pollinators with a longer tongue, or species that, due to their small size, can enter the flowers. As increased species diversity leads to an increase in functional diversity (Naeem, 2002), a more diverse pollinator community is bound to achieve better pollination in different plant taxa than a less diverse community.

Despite the indirect correlations between environmental characteristics and percentage fruit set, we did not find a direct significant correlation. A possible explanation is that the phytometers we used were visited only by a subset of the total pollinator community. The blueberry plants were disproportionally more frequently visited by bumblebees than by other insect pollinators. As bumblebees have a higher activity range than hoverflies and smaller, solitary bees (Greenleaf et al., 2007), they are less affected by local environmental characteristics.

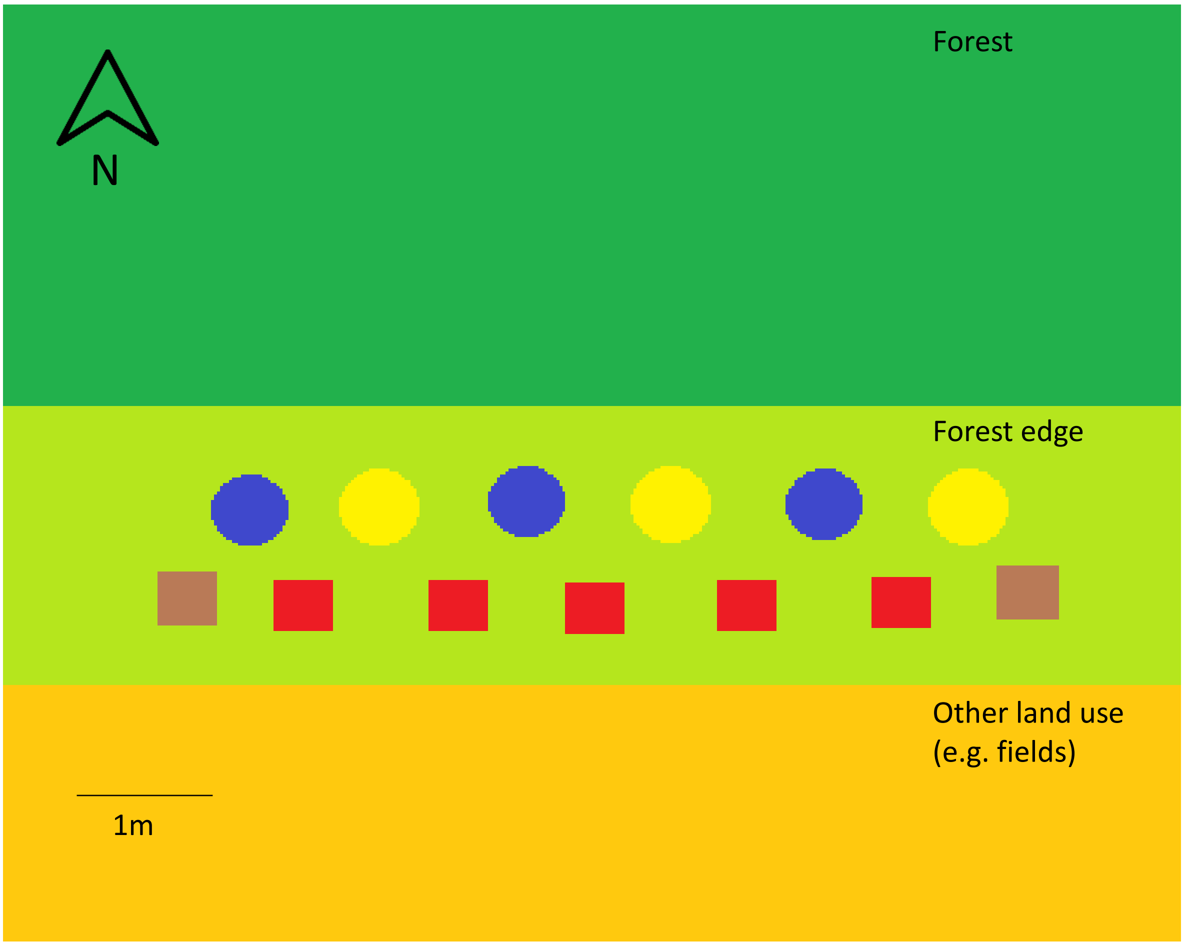
While forest fragments in intensively managed agricultural landscapes play an important role in conserving the pollinator community, a direct link with pollination services was not obvious in our study. However, indirectly, characteristics that caused a higher pollinator abundance in the forest edge, increased the local number of flower visitors, which resulted in a higher fruit set. It is therefore expected that a clear correlation exists between site and landscape characteristics that increase pollinator abundance and pollination as a service when pollination services are tested in a higher number of plant species. As these are all expected to attract different subsets of the pollinator community, a bigger, more representative part of the pollinator community will be sampled as flower visitors, giving a more complete image of pollination services delivered by the total pollinator community. In addition, further research is needed to assess whether increased pollinator value of these forest fragments will lead to a spillover in pollination services to the surrounding agricultural landscape.

5. Acknowledgements

We are grateful to the landowners for their permission to carry out the research on their properties. Thierry Michelsen (Plantencentrum Maréchal) kindly provided the strawberry and blueberry plants used in this study. The first author was supported by a grant provided by FWO-Vlaanderen (FWO14/ASP/195).

Appendix 5

Appendix 5.A.: Experimental Setup



Appendix 5.A.1.: Setup of the blueberries (circles) and strawberries (squares) in the forest edge. Bluecrop (blue) and Goldtraube (yellow) were planted in an alternating pattern, while Elsanta strawberries (brown) flanked the Korona plant (red).

Appendix 5.B.: Species lists

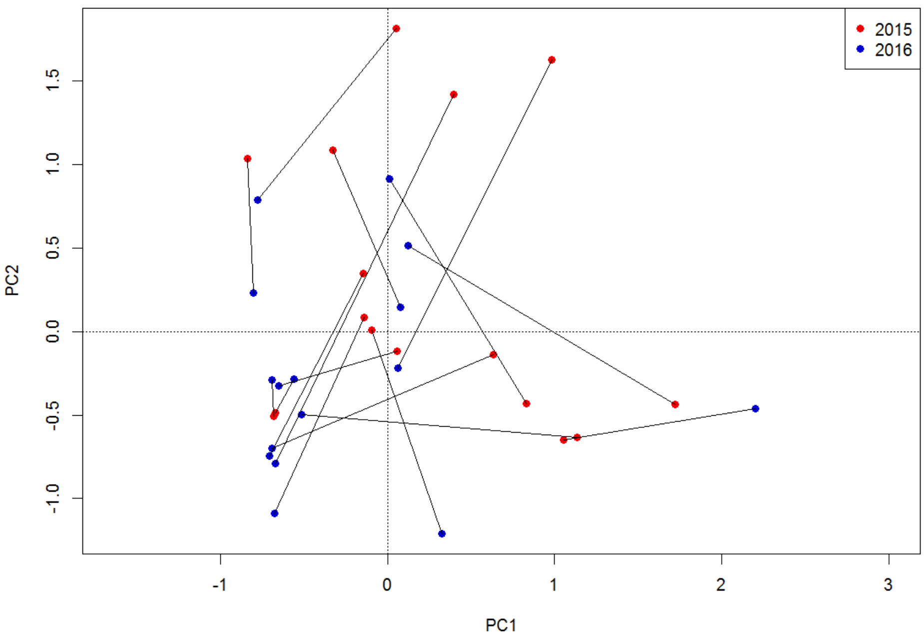
Appendix 5.B.1.: Species list of bee and hoverfly species caught by pan trapping and transect walks (Glabbeek, BE, 2015-2016)

Species	Abundance	Species	Abundance
Bees		**Hoverflies**	
Andrena bicolor	13	*Brachypalpoides lentus*	4
Andrena flavipes	1	*Chalcosyrphus nemorum*	1
Andrena fucata	1	*Cheilosia albitarsis*	1
Andrena fulva	4	*Cheilosia chrysocoma*	1
Andrena fulvago	9	*Cheilosia pagana*	2
Andrena fulvata	5	*Dasysyrphus albostriatus*	2
Andrena haemorrhoa	12	*Dasysyrphus venustus*	2
Andrena minutula	2	*Didea fasciata*	2
Andrena subopaca	2	*Episyrphus balteatus*	34
Andrena vaga	6	*Eristalis horticola*	1
Andrena wilkella	1	*Eristalis nemorum*	6
Anthophora plumipes	1	*Eristalis pertinax*	15
Apis mellifera	9	*Eristalis tenax*	3
Bombus hortorum	1	*Eupeodes corollae*	1
Bombus hypnorum	16	*Eupeodes luniger*	2
Bombus lapidarius	4	*Ferdinandea cuprea*	8
Bombus pascuorum	24	*Helophilus pendulus*	9
Bombus pratorum	54	*Heringia vitripennis*	2
Bombus terrestris s.l.	26	*Melanostoma mellinum*	13
Halictus rubicundus	1	*Melanostoma scalare*	16
Halictus tumulorum	1	*Myathropa florea*	19
Hylaeus sp.	1	*Neoascia podagrica*	2
Lasioglossum (Evylaeus) sp.	1	*Platycheirus albimanus*	25
Lasioglossum fulvicorne	1	*Platycheirus angustatus*	1
Lasioglossum lativentre	1	*Platycheirus scutatus*	3
Lasioglossum leucopus	1	*Rhingia campestris*	176
Lasioglossum malachurum	4	*Riponnensia splendens*	1
Lasioglossum morio	12	*Syritta pipiens*	2
Lasioglossum parvulum	3	*Syrphus ribesi*	5
Lasioglossum pauxillum	9	*Volucella bombylans*	12
Lasioglossum punctatissimum	5	*Volucella pellucens*	3
Lasioglossum sexnotatum	1	*Xylota segnis*	23
Lasioglossum zonulum	7	*Xylota sylvarum*	5
Megachile centuncularis	1		
Osmia bicornis	3		
Osmia cornuta	1		
	244		**402**

Appendix 5.B.2.: Number of flower visits per species for both strawberry and blueberry (Glabbeek, BE, 2017)

Phytometer	Species	No. of flower visits recorded
Strawberry	Diptera	
	Episyrphus balteatus	1
	Heringia sp.	1
	Platycheirus albimanus	14
	Rhingia campestris	1
		17
	Hymenoptera	
	Andrena (Micrandrena) sp.	1
	Bombus hypnorum	2
	Bombus pascuorum	6
	Bombus pratorum	5
	Lasioglossum sp.	4
	Osmia bicornis	3
	Sphecodes sp.	1
		22
	Lepidoptera	
	Anthocharis cardamines	1
	Pieris napi	1
		2
Blueberry	Diptera	
	Episyrphus balteatus	2
	Platycheirus albimanus	6
	Rhingia campestris	2
		10
	Hymenoptera	
	Anthophora plumipes	1
	Bombus hypnorum	18
	Bombus pascuorum	47
	Bombus pratorum	67
	Lasioglossum sp.	10
	Osmia bicornis	3
	Vespidae sp.	1
		147

Appendix 5.C.: Inter-annual variation of the bee community



Appendix 5.C.1.: PCA of the bee community per site and per year. Each point represents one specific site in 2015 (red) or 2016 (blue). The points representing one single site in two consecutive years are connected by a line.

Chapter 6: Synthesis

Although small forest fragments make up a large proportion of the total semi-natural habitat in intensively managed agricultural landscapes, until a few years ago, research on the ecosystem services they deliver was very limited. In recent years, a lot of research focused on several ecosystem services provided by these forest fragments, such as nutrient cycling (De Smedt et al., 2018), biodiversity conservation (Varela et al., 2018), carbon sequestration (Ziter et al., 2013) and social values (Dramstad et al., 2006). However, research on the role of these small forest fragments in conserving the pollinator community and pollination services, and even on the role of deciduous forest as pollinator habitat in temperate regions was extremely limited (e.g. Grundel et al., 2010).

Our research showed that forest fragments in agricultural landscapes harbour a rich pollinator community. Local availability of reproductive and nesting habitat clearly has a positive effect on the pollinator community, while at a larger scale, presence of semi-natural habitat boosts species diversity **(Chapters 2 & 3)** and, at the species level, colony performance in *B. terrestris* **(Chapter 4)**. While we did not find a direct link between habitat quality and pollination services, we found that a better habitat quality leads to a higher activity-abundance of pollinators in the forest edge, leading to higher numbers of flower-visitors, which increased pollination services **(Chapter 5)**.

In this synthesis chapter, we summarize our findings, and we attempt to generalize the role that small forest fragments and forests in general can play in conserving bees and hoverflies and in improving pollination services. We also provide some guidelines for managing forest fragments and agricultural landscapes in general and provide some perspectives for future research.

1. Small forest patches: pollinator oases in agricultural deserts?

Intensively managed agricultural land can generally be considered as an adverse environment for most pollinators: while some generalists tend to benefit from mass-flowering crops (Holzschuh et al., 2013; Westphal et al., 2003), pollinator abundances generally dwindle with increasing distance from semi-natural habitat (Bailey et al., 2014; Carvalheiro et al., 2010). Conventionally managed cropland is usually not an appropriate nesting habitat for bees due to absence of nesting habitat for above-ground nesting bees and tilling, which destroys nests of below-ground nesting species (Shuler et al., 2005). While some generalist species of hoverflies with aphidophagous larvae, such as *Episyrphus balteatus*, are able to reproduce in cropland (Jauker et al., 2009; Speight et al., 2016), species with slightly more specific requirements concerning reproductive habitat, such as saproxylic hoverflies, are generally absent from these fields.

Furthermore, in those landscapes, even very small forest fragments have the potential to deliver beneficial ecosystem services, such as biological pest control, erosion control or water regulation (Decocq et al., 2016). Although the positive effect of larger forested areas at the landscape scale is known (Farwig et al., 2009; Watson et al., 2011), the role of these small forest fragments as pollinator habitat has never before been thoroughly investigated. Small forest patches can shield the pollinator community from the frequent disturbances in agricultural habitat, while providing foraging and reproductive habitat.

Our study showed that a diverse and abundant pollinator community is present in the edges of these small forest patches. Additionally, we showed that the presence of foraging and reproductive habitat have a positive effect on the pollinator community **(Chapters 2 & 3)**. Especially the bee community benefited from the presence of potential nesting and foraging habitat. A rich herb layer in old forest fragments, presence of bare soil in south-oriented, sun-exposed forest edges and forest cover had a positive effect on bee species richness. Bee activity-abundance in forest edges was positively correlated with presence of nesting habitat, such as the presence of bare soil. However, bee activity-abundance in forest edges was negatively correlated with increasing presence of foraging habitat in the direct vicinity: herb layer cover had a negative effect on bee activity-abundance. This negative correlation may have been caused by a dilution effect: the presence of large patches of suitable foraging habitat dilutes the bee community, decreasing their density in the direct vicinity of the pan traps (Jha and Vandermeer, 2009; Veddeler et al., 2006). Additionally, pan traps may become less attractive to pollinators in the vicinity of abundant food resources (Baum and Wallen, 2011; Morandin and Kremen, 2013).

The hoverfly community, on the other side, did not show a strong correlation with most forest and landscape characteristics **(Chapters 2 & 3)**. Sun-exposed forest edges had a strongly significant positive effect on hoverfly species richness and activity-abundance. Additionally, the hoverfly community was more species-rich in old forests, which may be linked to the higher presence of larval habitat for saproxylic species, being old trees with rot holes and dead wood. These saproxylic species were more abundant at sites with a higher forest cover, as forest cover is likely to be correlated with a higher amount of suitable larval habitat (Ouin et al., 2006). In contrast to bees, hoverfly activity-abundance was not correlated with herb layer cover but with floral index. While bees may largely use the herb layer as foraging habitat, the hoverfly community, which was dominated by generalist species, and consists almost completely of polylectic species, is able to utilize a wider variety of nectar and pollen sources (Branquart and Hemptinne, 2000b; Meyer et al., 2009). This enables most species to forage on a wide variety of plant species inside and outside the forest patches.

In general, it can be stated that the hoverfly community as a whole is less sensitive to forest and landscape characteristics than the bee community **(Chapters 2 & 3)**. The bee community in our study was dominated by ground-nesting, solitary species, and was therefore relatively homogenous, while the hoverfly community consisted of species with a diverse larval ecology, ranging from aphidophagous to saproxylic, phytophagous or mud-inhabiting detritivorous species. These species, because of their strong ecological differences, may react in different ways to environmental characteristics, making it hard to infer general drivers of the hoverfly community. The ecologically more homogenous bee community, on the other hand, reacts in a more consistent way to environmental drivers. A second reason is that bees, as central place foragers, may be more sensitive than hoverflies (Westrich, 1996). This means that suitable foraging and nesting habitat need to be close to each other. As the activity range of most bees is limited to a few hundreds of meters (Gathmann and Tscharntke, 2002; Zurbuchen et al., 2010b) and even small increments in foraging distance may limit reproductive success (Zurbuchen et al., 2010a), they may be less mobile than hoverflies, making them more sensitive to local site characteristics. Hoverflies, on the other hand, do not build nests, and may therefore be better able to uncouple foraging and egg-laying habitat. Additionally, many species are able to reproduce in cropland or intensively managed pasture, such as *Rhingia campestris*, which has larvae developing in dung, and is typically associated with pasture (Lucas et al., 2017).

While some hoverflies are able to reproduce in agricultural land, bees are usually unable to build nests in cropland due to the frequent disturbances, and depend, at least for nesting, on more stable habitats. Additionally, bees typically have higher pollen requirements than hoverflies, as they do not only require the protein in pollen for egg development, but also as food source for their larvae. Agricultural landscapes dominated by species-poor grasslands and non-insect-pollinated crops may therefore limit bees more strongly than hoverflies, which are able to benefit even from very small patches of grassland or scarce flower resources (Jauker et al., 2009), making bees more dependent on small patches of semi-natural habitat.

Several studies show that pollinators can forage on mass-flowering crops inside the agricultural matrix (Diekötter et al., 2014; Holzschuh et al., 2013; Riedinger et al., 2014; Westphal et al., 2003). However, our experiment with *Bombus terrestris* **(Chapter 4)** showed a strongly negative correlation between mass-flowering fruit trees and colony performance. While not focusing solely on forest fragments, we also found a positive relationship between colony performance and open semi-natural habitat. Additionally, (forest) trees formed an important part of the pollen diet of the bumblebee colonies, both during and after mass-flowering. This indicates that forests do not only deliver suitable nesting places for bees, but that they also act as important food sources, even in agricultural landscapes where mass-flowering crops are abundantly present near the nests.

Based on these findings, we can conclude that small forest fragments, embedded in an intensively managed agricultural matrix, have the potential to serve as refugia inside a dynamic and generally adverse landscape. Small forest patches can play a role as a foraging and reproduction habitat for both bees and hoverflies. Some hoverfly species may be less dependent on semi-natural habitat than bees, while saproxylic forest specialists depend on these forest fragments because of the presence of micro-habitats for egg deposition. Bees, on the other hand, have a higher dependence on semi-natural habitat, and are therefore very sensitive to local and landscape characteristics influencing the value of these forest fragments as habitat.

2. Environmental effects and spatial scale

In our study, we looked at both local and landscape factors influencing the pollinator community. Both play a role in shaping the pollinator community. However, for landscape factors, care should be taken to investigate responses at the right scale. While small-bodied solitary bees have a very short activity range, up to a few hundreds of metres (Zurbuchen et al., 2010b), bumblebees may fly well over 1500 m for a single foraging trip (Osborne et al., 2008; Walther-Hellwig and Frankl, 2000). In our study, we measured landscape variables at different scales, selecting the most appropriate scale based on model fit (Holland et al., 2004). When looking at the whole bee or hoverfly community **(Chapter 2, 3, 5)**, a scale of a few hundreds of metres was appropriate. When studying bumblebees, however **(Chapter 4)**, land use within a 750-1000 m radius was found to fit bumblebee colony performance best, which was in line with other data on pollinator foraging distances.

We also found a seasonal difference in scale at which bumblebees perceive the landscape, showing a maximal correlation with land use in a 750m radius in spring, while in summer their response was best explained by land use within a 1000m radius. This result was explained by the differential availability of food resources: spring bumblebees mainly foraged on fruit orchards near their nests, while in summer it was necessary to cover larger distances during foraging trips. Therefore, in summer the spatial fscale at which land use affected the bumblebee colonies was slightly larger.

Not only species differ in the way they perceive the landscape. Male and female bees have a different behavioural pattern and activity-abundance of both sexes may depend on land use within a different spatial scale. Although male bees visit flowers as a food source, they do not actively collect pollen and usually stay near nesting aggregations (Peeters et al., 2012), probably making male activity-abundance less dependent on large-scale landscape characteristics. Females, on the other hand, need relatively large amounts of pollen and nectar, which can be hundreds of metres away from their nests (Westrich, 1996), leading to responses at a higher spatial scale. For this reason, activity-abundance of male bees can be considered as a proxy for nesting-habitat availability, while activity-abundance of females is linked to a more complex interplay of foraging and nesting habitat. While this behavioural difference between males and females is very strong in bees, it is expected to be of lesser importance in hoverflies, which do not build nests. Although female hoverflies require pollen as a protein source to lay eggs (Haslett, 1989; Hickman et al., 2010), they are no central place foragers. Hence, males and females are expected to respond to landscape variables at similar scales. Therefore, it may be interesting for future research to look at differences in response to environmental characteristics by male and female pollinators.

3. Context matters: season- and guild-specific responses

Many studies deduce results from pollinator datasets that were sampled during a short period in the year. While it might be tempting to draw general conclusions about the effect of environmental factors on the pollinator community, seasonality can often be a confounding factor, strongly influencing the results. First of all, forest fragments, as well as the surrounding landscapes can change thoroughly throughout the year. In spring, especially the herb layer of older forest fragments, if present, may serve as a food source for pollinators, while some canopy species, such as *Castanea sativa*, *Prunus avium* and *Acer* spp. are also visited by pollinators during their flowering. In our study **(Chapter 3, Chapter 4)**, we found that for this reason the effects of herb layer cover on the bee community differed between spring and summer, especially in older forest fragments. Furthermore, we found a strong positive effect of sun exposure on bee and hoverfly species richness in summer, while in spring we did not find a significant effect. Canopy closure makes forests much darker in summer than in spring (Kudo et al., 2008), which is not only linked with a decrease in herb layer flora (Schemske et al., 1978), but may also have a direct negative effect on pollinators, especially bees, which are poikilothermous, and usually thermophilic (Sydenham et al., 2014). While forests may be an excellent habitat for bees and hoverflies in spring, they may therefore be less suitable in summer. Additionally, in agricultural landscapes, mass-flowering crops provide relatively short-lived pulses of abundant pollen and nectar (Diekötter et al., 2014). While other studies indicated that these crops may prove beneficial for some generalist species (Jauker et al., 2012), this effect only lasts for the duration of the mass-flowering and mainly benefits generalist species with a short flying season that overlaps completely with the mass-flowering. For these species, fields or orchards can change on a very short term from areas devoid of food resources to extremely large pollen and nectar sources. We found that, in fruit orchards, bumblebees foraged on the fruit trees, using their pollen as the major pollen source during mass-flowering. However, after flowering in the orchards, pollen was mainly collected in other habitats and bee colony performance became correlated with the presence of other land use types.

A second, closely linked, reason is that many bee and hoverfly species are only active during a short period of the year. For example, most common *Andrena* species in North-Western Europe have a single generation per year, which generally flies for a few weeks or months in spring. Other taxa, such as some *Lasioglossum* species, have a more complex life cycle, where females build a nest in early spring to produce sexually inactive workers. In summer, a sexual generation appears and nests start producing males, after which fertilized females overwinter (Peeters et al., 2012). For these species, pollen and nectar requirements may therefore change throughout the season, as with bumblebees, which may also need more abundant food sources during late season, when the colonies grow (Rundlöf et al., 2014). Concerning hoverflies, many forest specialists, such as *Brachypalpoides lentus*, *Temnostoma* spp. and *Brachyopa* spp. fly only in spring (Reemer et al., 2009). This results in pollinator communities that taxonomically, and often ecologically strongly differ between spring and summer, and may therefore respond differently to environmental drivers.

In addition to the temporal factor, it is also necessary to consider the ecological differences between taxonomical groups of pollinators. In our study, we focused on bees and hoverflies, as both are important pollinators, with a well-described ecology. We generally analysed responses in both groups separately **(Chapters 2 & 3)**, as they are ecologically strongly different. Many studies focus solely on bees (e.g. Holzschuh et al., 2007; Le Féon et al., 2010; Potts et al., 2005), hoverflies (e.g. Meyer et al., 2009; Schweiger et al., 2007), or other pollinators (e.g. Krauss et al., 2003; Shlyakhtenok and Agunovich, 2001; Taki et al., 2008). While these studies are important and provide valuable insights, it is important to note that these specific ecological requirements play an important role in shaping the pollinator community. Therefore, it is valuable to look at multiple pollinator guilds and compare their specific responses to environmental characteristics.

4. The complete chain: from habitat quality to ecosystem services

Bees and hoverflies play an important role in pollinating both wild plants and agricultural crops, making them both ecologically and economically extremely important. Several studies link a high pollinator abundance or species richness to increased pollination services. Most of these studies only look at the direct link between pollinator presence and pollination services. However, the link between local and landscape characteristics and the pollinator community is also an important factor, which indirectly may affect pollination services.

As we showed that local and regional environmental characteristics have a strong effect on pollinator species richness, abundance and community composition, this raises the question whether this results in differences in pollination services. As not all pollinators are equally effective (Rader et al., 2009), and different plants may be pollinated by a different subset of the total pollinator community, the answer to this question is not straightforward. In our study, we showed that a higher number of flower visitors resulted in a higher fruit set for two plant species that were taxonomically and morphologically strongly different. However, a direct link between environmental characteristics and pollination was not found. On the other hand, a higher pollinator activity-abundance in forest edges was correlated to a higher number of flower visitors, indirectly resulting in a higher fruit set. When using plants with a simple, open morphology as phytometers, a larger subset of the pollinator community visits the flowers. Combined with a larger sample size, it is expected that a clear link between local and landscape characteristics and pollination services will be detected, at least at a local scale (although increased pollinator abundance does not always leat to increases in pollination services, Breland et al., 2018).

5. Management of small forest fragments and agro-landscapes

Based on the results of our study, we can propose several measures to improve the habitat value of small forest patches in agricultural landscapes for pollinators.

(a) Especially older forest fragments with a rich understorey were found to have a positive effect on the bee community **(Chapter 3)**. These forest fragments are impossible to replace on the short or middle-long term after conversion to other land use types (Honnay et al., 2002), and, although local legislation may provide some protection (e.g. Bosdecreet in Flanders), in many regions, these forest fragments are often not legally protected (Götmark and Thorell, 2003). It is therefore very important to safeguard the persistence of these forest fragments. Older forest fragments may also have a positive effect on the hoverfly diversity **(Chapter 2)**, given the higher amount of reproductive habitat for forest specialists (Reemer, 2005).

(b) Small forest fragments in intensively managed agricultural landscapes can serve as refuges for pollinators, as well as for other organisms (Keppel et al., 2012). In addition to typical forest species that completely depend on this habitat type, other, more generalist species, that are unable to survive in intensively managed cropland, can also use forests as refuges (Keppel et al., 2012). We found a clear positive correlation between forest area and abundance of saproxylic hoverflies **(Chapter 3)**. In addition to conservation of existing forest remnants, we therefore expect that increasing the forested area in these landscapes, will have a positive effect on pollinator diversity. Larger areas of forest may sustain larger populations of insects that use it as habitat (Connor et al., 2000) and contain more species, including those that depend on larger areas to maintain a viable population (Galli et al., 1976; Tscharntke, 1992).

(c) Local site characteristics in forests and forest edges affect the pollinator community **(Chapter 2, 3)**. Maintaining sufficient nesting habitat for ground-nesting bees by providing sufficient areas of sun-exposed bare soils, will lead to a higher activity-abundance of ground-nesting species (Sardiñas and Kremen, 2014b). Careful management of forest edges is necessary to provide these microhabitats.

(d) In all our experiments investigating the pollinator community **(Chapters 2, 3 and 5)**, the number of cavity-nesting bees was extremely low. In our study areas, the amount of dead wood in forest fragments, which is a potential nesting habitat for many cavity-nesting species, was extremely low. Forest management that spares dead and dying trees and avoids removing dead wood from the forest, is expected to increase the amount of nesting opportunities for these species, while also providing more larval habitat for saproxylic hoverflies (Reemer, 2005). Earlier research (Sydenham et al., 2016) also showed a facilitative effect of cavity-nesting beetles, which are associated with these old forests and bore holes in wood, thus creating potential nesting habitat for cavity-nesting bees.

(e) In addition to specific management advice at the level of the forest fragments, we want to stress the importance of managing agricultural landscapes as a whole. In **Chapter 3** we found a positive correlation between landscape floral abundance and hoverfly activity-abundance, as hoverflies are even able to benefit from very small floral patches (Jönsson et al., 2015; Kohler et al., 2008). Although we did not find a significant correlation in our study, a similar effect can be expected for bees (Potts et al., 2003; Quistberg et al., 2016). Additionally, we found that bumblebee colonies showed a better colony performance in landscapes with higher shares of forest and open semi-natural habitat **(Chapter 4)**, depending on the season. Outside these fragments of semi-natural habitat, agricultural landscapes are often very poor in food resources. To increase the amount of pollen and nectar sources, conserving and installing of small landscape elements such as hedgerows and tree rows may play an important role (Hannon and Sisk, 2009; Kallioniemi et al., 2017; Van Den Berge et al., 2018). Additionally, sustainable management of semi-natural grasslands and field edges, potentially by using agro-environmental schemes (Pywell et al., 2006), increase the flower richness in the landscapes.

6. Future research

Given the importance of forests in conservation of biodiversity and their widespread occurrence, both globally and in North-Western Europe, together with the large amounts of attention that pollinators have received over the past few years, it is striking that research on wild pollinators is so rare in these ecosystems. Most published studies focus mainly on the relation between the pollinator community and the presence of forest at the landscape level in intensively managed agricultural (e.g. Morandin and Winston, 2006; Nayak et al., 2015) or semi-natural (e.g. Diaz-Forero et al., 2013; Taki et al., 2007; Winfree et al., 2007) landscapes. However, research involving forest characteristics, focusing on the direct role that forests play for pollinators, is very rare (but see Grundel et al., 2010).

First of all, it would be interesting to further investigate the role the forests themselves play. As forests form complex, three-dimensional ecosystems, this may give rise to a vertical stratification with strongly different pollinator communities in the understorey and in the canopy. This phenomenon has been recorded for several insect taxa, such as moths (Pallieter De Smedt et al., 2018), wasps (Sobek et al., 2009), dipterans (Maguire et al., 2014) and beetles (Maguire et al., 2014). However, for bees and hoverflies, data on this subject is limited to a few studies on the bee community in American (Ulyshen et al., 2010) and German deciduous forests (Sobek et al., 2009). The canopy contains different food resources than the understorey and contains potential nesting places for cavity-nesting bees and larval habitats for saproxylic hoverflies that use rotting holes (Reemer, 2005). Differential resource use by different pollinator species may give rise to vertical stratification in the community, caused by these ecological differences. Further research in this topic may yield a more complete view on the pollinator community in forests, and valuable information about resource use by forest pollinators.

To gain further insights in the role forest fragments play as pollinator habitat, it may also be interesting to look at what foraging resources are used by pollinators. Catching pollinators inside forest fragments and in agricultural landscapes near forest patches and analysing the species of pollen and nectar they carry or feed on may yield more information on what plant species they visit. Especially in spring, we expect that both the herb layer and the canopy contain plant species that can serve as important pollen and nectar sources, and play a role in maintaining the pollinator community. Other pollen sources outside forests, collected in cropland, grassland or other land use types, can form an important share of some species' diet (Requier et al., 2015). In this way, it would be possible to identify the relative importance of each type of land use for various pollinator species. This is in line with our experiment with *B. terrestris* **(Chapter 4)**, but could be carried out on multiple species, leading to additional information on how availability of pollen and nectar sources structures the pollinator community.

Another interesting study would be the comparison of other types of semi-natural habitats with forests in similar landscapes. A big part of our research focused on small forest fragments and south-oriented forest edges, while other elements, such as hedgerows, tree rows, talus and semi-natural grasslands, when present, can also serve as refugia for pollinators, when present in agricultural landscapes. These elements all differ in availability of reproductive and foraging habitat, leading to the expectation that they all harbour a strongly differing pollinator community. Therefore, it is expected that their value for pollinators, and therefore for pollination, can strongly differ between the habitat types.

While we investigated the effect of local and landscape characteristics on the pollinator community, with a focus on small forest fragments, the main drivers of pollinator declines are probably agricultural intensification (including use of agro-chemicals) and diseases (even more by deliberate transport of managed pollinators around the globe). While forests and other semi-natural habitat may form refugia for pollinators in intensively managed agricultural landscapes, these topics are of utmost importance to conserve the pollinator community. To maintain a sustainable pollinator community, it may therefore be necessary to look at improving the agricultural land itself, and provide guidelines and legislations at a higher level.

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Curriculum vitae

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Scientific Publications

Peer reviewed scientific articles included in Web of Science

Houben, A. M.; **W. Proesmans**; W. Bert & T. J. Artois (2014). Revision of *Acrochordonoposthia* Reisinger, 1924 (Rhabditophora, Typhloplanidae, Protoplanellinae) with the description of one new species. *Zootaxa* 3790(1):36-50. DOI: 10.11646/zootaxa.3790.1.2

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Scientific activities

Participation in symposia with oral presentation

Proesmans, W. Miljoenpotengemeenschappen in kleine bosfragmenten langs een latitudinale gradiënt. *Startersdag in het natuur- en bosonderzoek.* 28 March 2014; Brussels, Belgium

Proesmans, W. Importance of small forest fragments in agricultural landscapes for two pollinator guilds. *Student Conference on Conservation Science*. 29 August – 2 September 2017, Tihany, Hungary

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Proesmans, W. A survey of the Belgian Tardigrada fauna. *14th International Symposium on Tardigrada.* 30 July – 3 August 2018; Copenhagen, Denmark

Tutor of Master Dissertations

Helena Theuwissen (2016). The influence of small forest fragments and the surrounding agricultural land use on pollinator communities. Ghent University