Potential of SemiNatural Habitats to support PEST CONTROL and POLLINATION

– including a case study on pumpkin

by

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Declaration

I, the author of this work, certify that this work contains no material, which has been accepted or submitted for the award of any other degree at any university or other tertiary institution. The work has been independently prepared. All aids and sources have been clearly specified. The contribution of other authors have been documented and reference lists are given.

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In chapter 2 **Sonja C. Pfister**, carried out field and laboratory work in Germany, GIS in Germany and partially also GIS for the Italian and Swiss case study region, carried out the statistical analysis and led the writing. Louis Sutter carried out field and laboratory work in Switzerland and contributed to writing. Matthias Albrecht contributed to statistical analysis and to writing. Simone Marini carried out field and laboratory work in Italy and GIS for the Italian case study and contributed to writing. Jens Schirmel contributed to statistical analysis and writing. Martin H. Entling coordinated the study and contributed to writing. All authors participated in the design of the study and gave final approval for publication.

In chapter 3 Martin H. Entling, Matthias Albrecht, Louis Sutter, Jens Schirmel and **Sonja C. Pfister** conceived the ideas and designed methodology; Philipp-Martin Bauer, **Sonja C. Pfister** and Louis Sutter collected the data; Jens Schirmel, Philipp-Martin Bau, Louis Sutter, and **Sonja C. Pfister** analysed the data; Jens Schirmel led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

In chapter 4 **Sonja C. Pfister** carried out field and laboratory work, statistical analysis and led the writing; Jens Schirmel contributed to writing; Martin H. Entling coordinated the study and contributed to writing. All authors participated in the design of the study and gave final approval for publication.

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Summary

Natural pest control and pollination are important ecosystem services for agriculture. They can be supported by organic farming and by seminatural habitats at the local and landscape scale.

The potential of seminatural habitats to support predatory flies (chapters 2 and 3) and bees (chapter 7) at the local and landscape scale was investigated in seminatural habitats. Predatory flies were more abundant in woody habitats and positively related to landscape complexity. The diversity and the abundance of honey and wild bees were positively related to the supply of flowers offered in the seminatural habitats.

The influence of organic farming, adjacent seminatural habitats and landscape complexity on pest control (chapter 4) and pollination (chapter 6) was investigated in 18 pumpkin fields. Organic farming lacked strong effects both on the pest control and on the pollination of pumpkin.

Pest control is best supported at the local scale by the flower abundance in the adjacent habitat. The flower supply positively affected the density of natural enemies and tended to reduce aphid densities in pumpkin fields.

Pumpkin provides a striking example for a dominant role of wild pollinators for pollination success, because bumble bees are the key pollinators of pumpkin in Germany, despite a higher visitation frequency of honey bees. Pollination is best supported by landscape complexity. Bumble bee visits and as a result pollen delivery in pumpkin were negatively related to the dominance of agricultural land in the surrounding landscape.

The influence of aphid density (chapter 8) and pollination (chapter 5) on pumpkin yield was evaluated. Pumpkin yields were not affected by aphid densities observed in the pumpkin fields and not limited by pollination at the current levels of bee visitation.

In conclusion, especially seminatural habitats, that provide diverse, continuous floral resources, are important for natural enemies and pollinators. A sufficient proportion of different seminatural habitat types in agricultural landscapes should be maintained and restored. Thereby natural enemies such as predatory flies, wild pollinators such as bumble bees, and the pest control and pollination provided by them can be supported.

Zusammenfassung

Natürliche Schädlingskontrolle und Bestäubung sind wichtige Ökosystemdienstleistungen für die Landwirtschaft. Diese können durch ökologische Landwirtschaft und naturnahe Lebensräume in der näheren oder weiteren Umgebung gefördert werden.

Das Potential naturnaher Lebensräume räuberische Fliegen (Kapitel 2 und 3) und Bienen (Kapitel 7) auf lokaler und Landschaftsebene zu fördern wurde in naturnahen Lebensräumen untersucht. Räuberische Fliegen bevorzugten verholzte Habitate und reagierten positiv auf die Landschaftskomplexizität. Die Vielfalt von Bienen und die Häufigkeit von Honig- und Wildbienen in den naturnahen Lebensräumen wurde vor allem positiv von den vorhandenen Blütenressourcen beeinflusst.

Der Einfluss von ökologischer Landwirtschaft, angrenzenden naturnahen Lebensräumen und Landschaftskomplexizität auf natürliche Schädlingskontrolle (Kapitel 4) und Bestäubung (Kapitel 6) wurde in 18 Kürbisfeldern untersucht. Ökologische Landwirtschaft hatte keine starken Effekte auf die natürliche Schädlingskontrolle oder die Bestäubung von Kürbis. Die natürliche Schädlingskontrolle kann vor allem lokal durch das Blütenangebot in den angrenzenden Lebensräumen gefördert werden, weil dieses die Dichten der natürlichen Läusefeinde positiv beeinflusste und tendenziell die Läusedichte in den Kürbisfeldern reduzierte.

Kürbis ist ein beeindruckendes Beispiel für eine Schlüsselrolle von Wildbienen für den Bestäubungserfolg, weil Kürbis in Deutschland vor allem von Hummeln bestäubt wird trotz der höheren Besuchsdichten von Honigbienen. Die Bestäubung kann am besten durch Landschaftskomplexizität gefördert werden. Die Anzahl von Blütenbesuchen von Hummeln und infolgedessen auch die übertragene Pollenmenge wurden negativ von der landwirtschaftlich genutzten Fläche in der umgebenden Landschaft beeinflusst.

Der Einfluss von Läusedichten (Kapitel 8) und Bestäubung (Kapitel 5) auf den Kürbisertrag wurde ermittelt. Der Kürbisertrag wurde nicht beeinflusst von den beobachteten Läusedichten und war nicht bestäubungslimitiert bei der derzeitigen Menge an Bienenbesuchen.

Insbesondere naturnahe Lebensräume, die stetige und vielfältige Blütenressourcen bereitstellen, sind wichtig für Schädlingskontrolleure und Bestäuber. In Agrarlandschaften sollte ein ausreichender Anteil an verschiedenen Typen von naturnahen Lebensräumen erhalten und wiederhergestellt werden. Dadurch können natürliche Schädlingskontrolleure wie räuberische Fliegen, Bestäuber wie Hummeln, und die von ihnen geleistete Schädlingskontrolle und Bestäubung in Agrarlandschaften gefördert werden.

Abbreviations & Definitions

Agri-environment scheme (AES) = Incentives of the European Union for farmers to preserve biodiversity through organic farming or managed and unmanaged seminatural habitats

CAP = common agricultural policy of the European Union

CH = Switzerland, refers to Swiss case study in the QuESSA project

DE = Germany, refers to the German case study in the QuESSA project

Ecosystem Service (ES) = human benefit from ecosystems, e.g. pollination and pest control

Environmental friendly farming: replaces anthropogenic inputs, such as pesticides, inorganic fertilizers and energy, by a management that supports ecosystem service providing organisms. It includes in-production managament such as organic farming and out-of-production management such as the management of seminatural habitats.

EU = European Union

HA = herbaceous areal seminatural habitat e.g. grassland, meadow

HL = herbaceous linear seminatural habitat e.g. grassy- herbaceous field margins

IT = Italy, refers to Italian case study in the QuESSA project

LS = Landscape sector in 1 km radius around the focal seminatural habitat or field

Seminatural habitat (SNH) = any habitat containing a community of non-crop plant species

Natural pest control or conservation biological control = control pests by preserving and enhancing natural enemies already present in the area WA = woody areal seminatural habitat e.g. forests, shrubland

WL = woody linear seminatural habitat e.g. hedgerows, tree lines

QuESSA = European Research Project, in which this doctoral thesis is embedded, that aims to identify key seminatural habitats and quantify the contribution of seminatural habitats to key ecosystem services including pest control and pollination for sustainable agriculture

Chapter 1 Introduction

1.1 Ecosystem services

Ecosystem services are benefits humans obtain from ecosystems including inter alia provision of food and water, climate regulation, support by nutrient cycling and cultural services (MEA 2005). Since the industrial revolution humans have changed ecosystems tremendously, mainly to increase short-term gains of single providing ecosystem services, such as the provision of food, water, timber and fuel (Foley et al. 2005; MEA 2005). But this reduces human well-being in the long term, because it comes at the cost of a large irreversible biodiversity loss and the global degradation of 60% of ecosystem services, which are needed to provide human well-being in the long term (Foley et al. 2005; MEA 2005).

Agriculture is a major force driving the Earth beyond the planetary boundaries contributing to biodiversity loss, climate change, as well as nitrogen and phosphorus pollution (Rockstrom et al. 2009; Foley et al. 2011; Steffen et al. 2015). During the last decades, agriculture has expanded by the conversion of grasslands and forests into cropland and has been intensified by the increased input of fertilizers, pesticides, irrigation and the use of heavy machinery (Tscharntke et al. 2005; Hazell & Wood 2008; Foley et al. 2011). Today, agriculture is the largest land use covering 38% of the land worldwide (FAOSTAT 2017) and even 47% in Germany (STATISTA 2017). Current agricultural landscapes are characterized by a high proportion of agriculture, large crop fields and few, fragmented, small remnants of seminatural habitats (Marshall & Moonen 2002; Tscharntke et al. 2005).

The yield increases achieved by the expansion and intensification of agriculture cause many environmental costs e.g. contamination and soil degradation (Tscharntke et al. 2012a). In addition, agricultural intensification reduces yields, because it disrupts natural pest control and pollination (Pimentel & Peshin 2014; Potts et al. 2016). Those ecosystem services are very important for agriculture, but the service providers, natural enemies and pollinators, are negatively affected by agricultural intensification and need suitable habitats to persist in agro-ecosystems (Holland et al. 2016; Potts et al. 2016; Rusch et al. 2016).

1.1.1 Pest control

Pest control is an important ecosystem service for agriculture (Sandhu et al. 2015). In conventional intensive farming pesticides are the primary pest control tools. Since the 1960s the pesticide use increased and nowadays 3 million tonnes of pesticides are used globally per year (440,000 tonnes in Europe in 2014; Pimentel & Peshin 2014; FAOSTAT 2017). For farmers pesticides are the easiest way to control pests, because there is a knowledge and transfer gap on how natural enemies can be managed best and cost-efficiently to provide reliable pest control (Dedryver et al. 2010). However, there are several disadvantages of pesticides. First, despite the use of pesticides still 40% of the potential food production is lost or destroyed by pests and yield losses increased with increased pesticide use (Pimentel & Peshin 2014). Thus, pesticides are only partially effective, because pests are resistant or evolve resistance against pesticides and because pesticides reduce natural biological control (Geiger et al. 2010; Pimentel & Peshin 2014). Second, pesticides negatively affect the biodiversity and abundance of non-target organisms e.g. natural enemies, wild plants, birds, fish and pollinators (Geiger et al. 2010; Pimentel & Peshin 2014; Goulson et al. 2015). Third, per year 3 million people are poisoned by pesticides during the application and through the food chain (Pimentel & Peshin 2014). Therefore, the public became wary of pesticides and alternative approaches such as integrated pest management and organic farming have been developed (Pimentel & Peshin 2014). These pest management approaches rely (more) on natural pest control (or "conservation biological control"), whereby natural enemies already present in the farm area are preserved and enhanced to control the pests (Jonsson et al. 2008; Zehnder et al. 2007).

Natural pest control is a valuable ecosystem service for agriculture: even the current intensive conventional management profits from it (~12 US $ ha-1, Losey & Vaughan 2006), but far more integrated pest management (33 US $ ha-1, Landis et al. 2008) and the most organic farming (68 - 200 US $ ha-1, Sandhu et al. 2015); the latter two are restricted in the amount of pesticides used.

Natural pest control increases along with the species evenness among natural enemies (Crowder et al. 2010) and can increase with richness of predators (Letourneau et al. 2009; Cardinale et al. 2012; Griffin et al. 2013). Biodiversity effects depend on the mechanism: facilitation and niche partitioning have positive effects, whereas interference and intraguild predation have negative effects on pest suppression (Losey & Denno 1998; Vance-Chalcraft et al. 2007). Pest control can be strengthened by the complementarity of natural enemies in spatial (ground-dwelling vs. flying predators, ground vs. foliar) and temporal activity (day vs. night active) and specialization (Losey & Denno 1998; Diehl et al. 2013; Petersen & Woltz 2015). Generalist and specialist predators can both be effective pest control agents and complement each other (Diehl et al. 2013). Generalist predators, such as spiders and carabids, can be especially important early in the season to reduce pest densities, because they are already present when the pests invade the crops (Symondson et al. 2002; Toft 2005; Evans 2008). Specialist predators are often more important later in the season, because their abundance increases along with pest density due to prey localization and subsequent higher reproduction (Symondson et al. 2002; Diehl et al. 2013).

The abundance, diversity and evenness of natural enemies and pest control is influenced by local and landscape management (Crowder et al. 2010; Rusch et al. 2010; Chaplin-Kramer et al. 2011; Letourneau et al. 2011; Kremen & Miles 2012; Rusch et al. 2016). Pests can usually deal better with agricultural intensification than natural enemies (Tscharntke et al. 2007; Rusch et al. 2010). For example, aphids (Hemiptera: Aphididae) are well adapted to modern agriculture and have therefore become economically important pests (Blackman & Eastop 2000; van Emden & Harrington 2007; Dedryver et al. 2010). Especially in the Northern temperate region (North America, Europe, Central and East Asia) most crops suffer from aphid feeding damage and even more from transmitted plant viruses (Blackman & Eastop 2000; Dedryver et al. 2010). In their alate forms they are very mobile and can disperse via wind over several kilometers into the fields and emigrate in the event of disturbances, such as harvest or pesticide application (Reynolds & Reynolds 2009; Dedryver et al. 2010; Veres et al. 2013). In favourable habitats providing enough food they rapidly reproduce owing to parthenogenesis combined with a short generation time (Blackman & Eastop 2000; Dedryver et al. 2010). Further, resistance against insecticides has evolved in aphids. Therefore they can build up large populations, also in agricultural landscapes (Dedryver et al. 2010).

In contrast, most natural enemies are less mobile and productive than aphids and negatively affected by pesticides (Tscharntke et al. 2007; Geiger et al. 2010; Rusch et al. 2010). Therefore integrated pest management needs environmental friendly farming and has to act at the local and landscape scale (Dedryver et al. 2010).

1.1.2 Pollination

Pollination plays a significant role for plant reproduction, and therefore for agricultural production and the maintenance of terrestrial biodiversity (Ollerton et al. 2011). Animal pollination is worth around 235 - 577 billion US $ annually (Lautenbach et al. 2012; Potts et al. 2016). Over 300,000 (87.5%) flowering plant species are pollinated by animals (Ollerton et al. 2011). Via the food chain these plants maintain a large part of the terrestrial biodiversity. Thus, pollination deficits can have far-reaching effects (Potts et al. 2016). 75% of our worldwide leading food crops benefit from animal pollination (Klein et al. 2007). Especially for these pollinator-dependent crops, such as pumpkin, pollination is a valuable ecosystem service (Potts et al. 2016). Pollinator-dependent crops are mainly fruits, nuts and vegetables, which contain essential micronutrients. Therefore, pollination deficits can increase malnutrition (Chaplin-Kramer et al. 2014). Although the proportion of pollinator-dependent crops on the global food volume is small (5-8%), the production of these crops increased far above-average and as a result the dependency of global food production on pollination is now twofold higher than fifty years ago (Potts et al. 2016).

With over 20,000 species worldwide and 561 species in Germany bees (Hymenoptera: Apoidea) are the most important pollinators (Westrich et al. 2011; Winfree et al. 2011; Eardley et al. 2016). In contrast to most other pollinator taxa, bees show specialized pollen-collecting structures and behaviours and both, larvae and adult bees, are florivorous (Winfree et al. 2011). In temperate regions, mainly honey bees, *Apis mellifera* L., are used for managed crop pollination outdoors (IBPES 2016; Potts et al. 2016). Reliance on honey bees is potentially risky, however, because it relies on a single species. Furthermore, honey bees are likely to be more susceptible than indigenous wild bees to stressors such as diseases, because the human breeding reduced their genetic diversity (Winfree 2008). Consequently, a diverse community of wild pollinators can be important to ensure crop security (Winfree et al. 2007).

Garibaldi et al. (2013) showed that wild bees are more effective pollinators than honey bees and can increase the fruit set of a wide variety of important cash crops such as almond, spring rape, strawberry, watermelon, cucumber and squash. Wild bees are important pollinators, even in the presence of honey bees, because they ensure and enhance pollination through spatial and temporal complementarity, behavioural interactions and higher efficiency (Greenleaf & Kremen 2006; Hoehn et al. 2008; Garibaldi et al. 2011). Further, the pollination services of wild bees are consistent across fields with a similar landscape context, over days and years (Rader et al. 2012).

Managed and wild bees are declining globally owing to habitat loss, monotonous diets, pesticides, mismanagement of bees, climate change, diseases and their interactions, whereby many of these factors are related to agricultural intensification (Potts et al. 2010; Goulson et al. 2015; Potts et al. 2016). As a result, worldwide many pollinator-dependent crops suffer from pollination instability and deficit (Garibaldi et al. 2013; Garibaldi et al.

2016). By enhancing the visits of bees, especially of wild bees, fruit set and yield of these crops can be increased (Garibaldi et al. 2013; Garibaldi et al. 2016). Therefore, we need environmental friendly farming and an effective local and landscape management to safeguard pollinators and pollination (Potts et al. 2016).

1.2 Environmental friendly farming

Environmental friendly farming (or ecological intensification) is an alternative approach to conventional intensification. It replaces anthropogenic inputs, such as pesticides, inorganic fertilizers and energy, by ecosystem service management (Bommarco et al. 2013). Environmental friendly farming manages service providing organisms by promoting biodiversity and seminatural habitats (Bommarco et al. 2013; Tscharntke et al. 2012a). Thereby it can be very productive while minimizing negative environmental impacts (Pywell et al. 2015). Pywell et al (2015) showed in a five-year study that a conversion of 8% of the farm area into tailored seminatural habitats favouring pollinators and natural enemies is compatible with crop yields.

Ecosystem service management is needed, because pollinators and natural enemies need suitable habitats to persist in agro-ecosystems (Holland et al. 2016; Potts et al. 2016; Rusch et al. 2016). Therefore, communities in agro-ecosystems are often impoverished and dominated by a few common species with a high dispersal capacity (Tscharntke et al. 2005; Crowder et al. 2010; Kleijn et al. 2015). To enhance biodiversity and the persistence and presence of beneficials in agro-ecosystems, important resources such as food and habitats for the different life cycle stages must be provided (Landis et al. 2000; Rusch et al. 2010). For this purpose, a management at multiple scales is needed, because different groups of organisms respond to different scales depending on their mobility (Schweiger et al. 2007; Gonthier et al. 2014).

Since 1985 the European Union (EU) has promoted environmental friendly farming by limiting the use of high-risk pesticides and by so called “agri-environment schemes” (Geiger et al. 2010; Batary et al. 2015). Agri-environment schemes are incentives for farmers to preserve biodiversity through in-production, such as organic farming or diversified crop rotations, and out-of-production schemes, such as managed and unmanaged seminatural habitats (Batary et al. 2015). They are a part of the Common Agricultural Policy (CAP) of the European Union (Batary et al. 2015). In 2012 the European Commission spent 3.23 billion € for agri-environment schemes, 100 times more money than for the management of nature conservation sites (Batary et al. 2015). Germany spent 375 million €, representing 11% of the total EU expenditure, to have agri-environment schemes in 30% of the agricultural area (Batary et al. 2015). Approximately 20% of this area is organic farming (Batary et al. 2015; STATISTA 2017). The initial purpose of the European agri-environment schemes was to maintain and support biodiversity, but recently ecosystem services gain in importance (Batary et al. 2015). Since 2015 the new CAP includes subsidies for maintaining permanent grassland, crop diversification and “ecological focus areas” in the so called “Greening”, which should be at least 5% of the arable area of each holding (European Commision 2013). Ecological focus areas can be field margins, hedges, fallows, but also cover crops (European Commision 2013, 2016).

1.2.1 Organic farming

1.2.1.1 Organic farming in general

Environmental friendly farming includes in-production management via 1) a reduced pesticide use, 2) organic farming, or 3) the use of diversified crop rotations (Bommarco et al. 2013). Organic farming produces food by preserving and using natural resources and processes (European Commision 2007). 1% of the agricultural area worldwide is farmed organically (FAOSTAT 2017), while in the European Union the ratio amounts to 5.6% (FAOSTAT 2017) and in Germany it is already 6.5% (STATISTA 2017).

In the European Union organic farming is defined by the EU-Eco regulation 834/2007 (European Commision 2007). Organic arable farming is characterized by the prohibition of herbicides, synthetic fertilizers, synthetic fungicides and synthetic insecticides. Instead, weeds are removed mechanically and soil fertility is mainly obtained by nitrogen fixing legumes or other green manure crops (Hole et al. 2005; European Commision 2007; Norton et al. 2009). Yields in organic fields are 20 to 25% lower than in conventional ones (Ponti et al. 2012; Seufert et al. 2012). Yield gaps differ between crop types and regions and are lower in best management comparisons (only -13%, Seufert et al. 2012). Further, yields in organic farms could even be lower owing to areas under green manure (Ponti et al. 2012). On the other hand, green manures could fixate higher amounts of nitrogen between normal cropping periods than currently applied by synthetic nitrogen (modelled by Badgley et al. 2007). However, organic farming could increase food security (Badgley et al. 2007) and the net income of farmers (Sandhu et al. 2015), because it uses renewable resources and ecosystem services and reduces harmful trade-offs (Badgley et al. 2007; Sandhu et al. 2015).

Several studies and meta-analyses have shown that organic farming increases the evenness of natural enemy communities (Crowder et al. 2010), the abundance of birds, insects and plants by 50% (Bengtsson et al. 2005) and overall species richness by 30% (Tuck et al. 2014; also Bengtsson et al. 2005; Hole et al. 2005; Montañez & Amarillo-Suárez 2014). Especially plants profit from the prohibition of herbicides in organic farming. Organic farming increases plant species richness, especially of broad-leaved and insect pollinated plants (Roschewitz et al. 2005; Power et al. 2012), by 73% in the vegetation of fields (Tuck et al. 2014) and adjacent semi-natural habitats (e.g. Aude et al. 2004; Holzschuh et al. 2008) as well as by 36% in the seed banks (Roschewitz et al. 2005). Further, plant cover is much higher in organic farms (Bengtsson et al. 2005).

Pollinators and natural enemies are directly and indirectly favoured by organic farming (Krauss et al. 2011). Both natural enemies (Krauss et al. 2011; Lu et al. 2013) and pollinators (Holzschuh et al. 2007; Rundlöf et al. 2008; Hardman et al. 2016) are indirectly favoured via the higher cover and diversity of plants and floral resources owing to the renunciation of herbicides and legume cropping for soil fertility. Natural enemies further profit from the higher availability of alternative prey in organic farming. Aboveground prey availability is enhanced by the higher plant diversity and cover (Caballero-López et al. 2012a) and belowground prey by the use of farm manure for soil fertility (Birkhofer et al. 2008). Both are directly favoured through the prohibition of conventional insecticides, especially of neonicotinoids, which have adverse effects on natural enemies (Geiger et al. 2010; Krauss et al. 2011) and pollinators (Goulson & Kleijn 2013).

1.2.1.2 Effects of organic farming on pest control

Organic farming increases the abundance (Bengtsson et al. 2005), species richness (by 12%, Tuck et al. 2014) and evenness of natural enemies (Crowder et al. 2010). In addition, the pest control of aphid sentinels was higher in organic fields in homogeneous landscapes (Winqvist et al. 2011). Several studies found positive effects of organic farming on aphid pest control, but there is no meta-analysis. Aphid pest control by natural enemies such as lady beetles, lacewings, spiders and syrphid flies was higher in organic than in conventional fields of cotton (Lu et al. 2015), beans and peas (Sandhu et al. 2015), winter wheat (Krauss et al. 2011; Gosme et al. 2012; Sandhu et al. 2015), spring barley (Östman et al. 2003; Sandhu et al. 2015; Birkhofer et al. 2016) and apple (Dib et al. 2016). Further, organic farming can reduce the variability of pest control via parasitoids (Macfadyen et al. 2011). Organic farming likely not only increases pest control by higher predator-prey ratios, but also because even communities can exert strong pest control (Crowder et al. 2010). Yield increases owing to natural pest control are higher in organic farming, but yields are generally higher in conventional fields (Östman *et al.* 2003; Birkhofer *et al.* 2016). Natural biological control in organic farms can have a value of 68 – 200 US $ ha-1 and the extrapolated net value exceeds current costs of pesticides, even if only 10% of the global agricultural area is farmed organically (Sandhu et al. 2015).

1.2.1.3 Effects of organic farming on pollination

Organic farming supports around 50% more pollinator species than conventional farming (Tuck et al. 2014). In addition, organic farming enhances pollinator abundance in simple landscapes (Batary et al. 2011). Although organic fields contain a more diverse bee community than conventional fields, they are nevertheless functionally similar: both contain social, polylectic ground-nesting species with long flight seasons (Forrest et al. 2015). Further, organic farming at the field-level likely only attracts pollinators from the landscape, but does not offer nesting and floral resources year-round to really support them (Hardman et al. 2016). Thus natural habitats are needed, especially for oligolectic, solitary and above-ground nesting bee species (Forrest et al. 2015).

There is no meta-analysis studying the effect of organic farming on pollination itself, but five out of eight studies found positive effects on pollination (Morandin & Winston 2005; Power & Stout 2011; Andersson et al. 2012; Andersson et al. 2014; Hardman et al. 2016). Organic farming had neither an effect on the pollination of almond (Klein et al. 2012) and watermelon (Kremen et al. 2002) in North-America nor on the pollination of sentinel plants in semi-natural habitats adjacent to organic or conventional farming in Europe (*Lotus corniculatus*, Chateil & Porcher 2015). On the other hand, pollination success was higher in organic farms of field bean (Andersson et al. 2014), strawberry (Andersson et al. 2012), wild shrubs in field margins of grassland farms (*Crataegus monogyna*, Power & Stout 2011) and sentinel plants within fields (*Eschscholzia californica*, Hardman et al. 2016) in Europe, as well as of canola in North-America (Morandin & Winston 2005).

1.2.1.4 Landscape scale effects of organic farming

Organic farming can also have landscape scale effects in addition to the local effects on the fields and adjacent habitats. The proportion of organic farming in the landscape can increase species richness of plants (Rundlöf et al. 2010: 1 km), the abundance and species richness of pollinators (Holzschuh et al. 2008: 500 m), but did not directly affect natural enemies such as lady beetles, carabid beetles or parasitoids (Puech et al. 2015: 500 m).

1.2.2 Seminatural habitats

Environmental friendly farming also includes the out-of-production management of seminatural habitats (Batary et al. 2015). In general, out-of-production schemes enhance biodiversity more effectively than in-production schemes (Batary et al. 2015). Seminatural habitats (SNH) are defined as any habitat containing a community of non-crop plant species (García-Feced et al. 2015). SNH can be divided into two groups depending on their size: 1) large SNH such as grasslands and forests, and 2) small SNH such as hedgerows, herbaceous field and road margins (García-Feced et al. 2015). Building on these groups, SNH in this thesis are divided into four broad categories based on vegetation type (herbaceous vs. woody) and shape (linear vs. areal) (Holland et al. 2016):

1) woody areal (WA): forests, woodlots, shrublands
2) woody linear (WL): hedgerows, tree lines,
3) herbaceous areal (HA): grasslands
4) herbaceous linear habitats (HL), grass strips, field margins.

In agro-ecosystems, SNH play an important role for the abundance and diversity of beneficial organisms by providing 1) larval habitat, 2) refuge during disturbances such as pesticide spraying, ploughing and harvest, 3) shelter, 4) overwintering sites and 5) alternative food resources such as flowers and alternative prey (Landis et al. 2000; Bianchi et al. 2006; Rusch et al. 2010; Holland et al. 2016). However, the majority of agricultural landscapes in Europe contain less than 25% of SNH, many contain even less than 10% (García-Feced et al. 2015). The value for beneficials strongly depends on the type of locally present SNH, as well as their proportion and spatial distribution at the landscape scale (Shackelford et al. 2013; Holland et al. 2016; Rusch et al. 2016). Improving our understanding of the relative importance of different SNH types across spatial scales is crucial to enhance the effectiveness of pest control management and pollination, but large-scale data across a large number of SNH and landscapes across multiple countries is scarce (Jonsson et al. 2008; Holland et al. 2016).

Table 1.1 Groups of natural enemies with information on traits - food selectivity (depending on life stage), dispersal and mobility, vertical layer of activity (ground vs. foliar active), temporal activity (night vs. day) – and information on positive effects of SNH at the local scale and at the landscape scale reported in the literature. References corresponding to the [numbers] are given below the table.

Group	**Food selectivity**	**Dispersal and Mobility**	**Layer**	**Activity**	**SNH local**	**SNH landscape**
Spiders (Araneae)	All life stages: Generalist predators [1]	Immature: ballooning up to several km [2] Adults: sedentary - mobile	Ground + Foliar	Depends on the species, many at night [3,4]	Woody and herbaceous [5,6]	Yes, SNH [5]
Soldier beetles (Cantharidae)	Generalist predators, larvae consume more aphids than adults [7]	Common fliers [8]	Foliar	NA	Herbaceous [7]	Yes, SNH [8]
Ground beetles (Carabidae)	Some generalist predators [9]	Adults: few fly, good dispersers [8]	Ground	Day [3]	Mainly herbaceous [6]	Yes, SNH [10,11]
Gall midges (Cecidomyiidae)	Some aphidophagous predator such as *Aphidoletes* [12]	Larvae: few cm [13] Adults: flying	Foliar	NA	NA	Yes, SNH [12]
Lacewings (Chrysopidae)	Larvae: primarily aphidophagous predators [14] Adult: floral resources [14]	Adults: active flight, very mobile [16]	Foliar	Adults: Night [3]	Herbaceous [17,18]	No landscape effect [19]
Lady beetles (Coccinellidae)	Larvae: primarily aphidophagous predator [14] Adult: aphidophagous predator + floral resources	Larvae: NA Adult: active flight, very mobile [20]	Foliar	Day [3]	Woody and herbaceous [6]	Yes, SNH [19,21,22] Arable land [23]
Parasitoids	Larvae: host-specific aphid parasitoids [12] Adult: floral resources	Adults: several 100 m – 2 km [24]	Foliar	NA	Woody and herbaceous [5,6]	Yes, SNH [5,25]

Group	**Food selectivity**	**Dispersal and Mobility**	**Layer**	**Activity**	**SNH local**	**SNH landscape**
Predatory bugs (Anthocoridae, Reduviidae, Nabidae)	All stages: generalist and specialist predators [26] Adults: some use floral resources [27]	Active flight [7]	Ground + Foliar	Day [3]	Herbaceous [6]	Yes, herbaceous perennial habitat [28]
Syrphid flies (Syrphidae)	Larvae: different, aphidophagous syrphid flies [14] Adults: floral resources [29,30]	Active flight, up to 4 km [28,31,32], most species 0.5 – 1 km [31,33]	Foliar	Larvae: Night [34] Adults: Day	WL, WA edge, herbaceous [6]	Yes, SNH [28,32,33] Arable land [31,35,36]
Other predatory flies (Dolicho-podidae, Empididae)	Larvae: mainly predators on soft-bodied pests Adults: mainly predators + some use floral resources [29,37,38]	Adults: flying, mobile [39]	Foliar	Mainly day [39,40]	HA [28,42,43], HL [8,26,44], WL [45,46], WA [42,47]	Yes, SNH [46,48]
Rove beetles (Staphylinidae)	Generalist predators [9]	Good dispersers, active flight and dispersal by wind [49]	Ground	Day [3]	WL, herbaceous [6]	Yes [50]

[1] Toft 2005, [2] Reynolds *et al.* 2007, [3] Petersen & Woltz 2015, [4] Castello & Daane 2005, [5] Shackelford *et al.* 2013, [6] Holland *et al.* 2016, [7] Landis & Werf 1997, [8] Oaten 2011, [9] Dennis & La Fry 1992, [10] Weibull *et al.* 2003, [11] Burgio *et al.* 2015, [12] Rand & Tscharntke 2007, [13] Maisonhaute & Lucas 2011, [14] Freier *et al.* 2007, [15] Villenave *et al.* 2005, [16] Chapman *et al.* 2006), [17] Sarthou *et al.* 2014, [18] Tschumi *et al.* 2016b, [19] Taki *et al.* 2013, [20] Hodek *et al.* 1993, [21] Elliott *et al.* 2002, [22] Gardiner *et al.* 2009, [23] Caballero-López *et al.* 2012b, [24] Bianchi *et al.* 2006, [25] Thies *et al.* 2003, [26] Rieux *et al.* 1999, [27] Lu *et al.* 2013, [28] Werling *et al.* 2011, [29] Skevington & Dang 2002, [30] Branquart & Hemptinne 2000, [31] Haenke *et al.* 2009, [32] Power *et al.* 2016, [33] Kleijn & van Langevelde 2006, [34] Ximenez-Embun *et al.* 2014, [35] Meyer *et al.* 2009, [36] Inclán *et al.* 2016, [37] Smith 2012, [38] Ulrich 2004, [39] Delettre *et al.* 1997, [40] Gill *et al.* 2012, [41] Peng *et al.* 1992, [42] Bahrmann 1993, [43] Cauwer *et al.* 2006, [44] Frouz & Paoletti 2000, [45] Boness 1953, [46] Burel *et al.* 1998, [47] Pollet & Grootaert 1991, [48] Bortolotto *et al.* 2016, [49] Bohac 1999, [50] Dauber *et al.* 2005.

Table 1.2 Effects of different disturbances - agricultural intensification, including effects of pesticides and tillage, and isolation from SNH - on the abundance of bees in disturbed compared to undisturbed sites depending on bee species traits ([1] Williams et al. 2010) and effects of isolation from hedgerows (WL) and grassland (HA), or isolation from woodland edges (WA) on bee traits in bee communities *in fields* ([2] Carrie et al. 2017). Responses of bees with these traits in SNH compared to human-dominated habitats ([3] = Forrest et al. 2015: proportion of bees with these traits in abundance and richness compared to fields; [4] = Palma et al. 2015: presence compared to urban areas and cropland).

Trait	Effect of disturbance	Stronger sensitivity	undisturbed vs. disturbed	SNH > human habitat
Sociality	Agricultural intensification [1]	Solitary	Solitary less in intensive management	Abundance [3] and Presence [4] of solitary bees
	- Pesticides [1]	Social	Social less in sprayed Solitary more in sprayed	
	- Tillage [1]	Solitary	Solitary less in tilled	
	Isolation from SNH [1]	Solitary	All reduce with isolation	
	Isolation from WL/HA [2]	Solitary	*In field*	
	Isolation from WA [2]	Social	*In field*	
Food specialisation	Agricultural intensification [1]	Specialist	Both less in intensive management	Abundance [3] and Presence [4] of oligolectic bees
	- Tillage [1]	Specialist	Generalists more in tilled Specialists less in tilled	
	Isolation from WA [2]	Generalist	*In field*	
Tongue length				Presence of long-tongued bees [4]
Flight season	Isolation from WA [2]	Late foraging	*In field*	Presence of univolitine bees [4]
Nest location	Agricultural intensification [1]	Above-ground	Above-ground less in intensive management	Abundance and richness of above-ground bees [3]
	- Tillage [1]	Below-ground	Below-ground less in tilled	
	Isolation from SNH [1]	Above-ground	Both reduce with isolation	
	Isolation from WL/HA [2]	Below-ground	*In field*	
	Isolation from WA [2]	Below-ground	*In field*	
Nest construction				Richness of renting [3] and presence of nest excavating [4]
Body size	Isolation from WL/HA [2]	Small	*In field*	Not significant [3]
	Isolation from WA [2]	Small	*In field*	

1.2.3 Seminatural habitats at the local scale

1.2.3.1 Effects of local habitats on pest control

Field margins positively affect both, the richness and abundance of natural enemies in crops (especially of spiders), while the effects on richness are the strongest (Shackelford et al. 2013). SNH usually harbour more beneficials and neutral arthropods than pests owing to the stable conditions (Rusch et al. 2010). All SNH types (HA, HL, WA, WL) provide alternative prey and refuge during farming practices (Holland et al. 2016), but woody vegetation offers more shelter from harsh climate conditions (Rusch et al. 2010; Sarthou et al. 2014). Providing shelter is especially important for overwintering, because most natural enemies do not overwinter in fields (Pfiffner & Luka 2000). For example, only 20% of the species and 8 times less individuals of ground-dwelling arthropods overwintered in winter wheat fields compared to SNH with permanent vegetation (Pfiffner & Luka 2000). For some natural enemies preferred overwintering SNH types are known: spiders and carabids overwinter in hedgerows (Sotherton 1985; Pfiffner & Luka 2000; Pywell et al. 2005); carabids, lacewings, parasitoids and predatory bugs prefer grass strips and wet grassland over dry grassland and forest interior; whereas spiders and lady beetles also overwinter in forests (Sarthou et al. 2014).

Vegetation diversification generally enhances the abundance of natural enemies in crops by providing a higher diversity of resources, and thereby reduces the abundance of pests and crop damage (Letourneau et al. 2011). However, in their meta-analysis Letourneau et al. (2011) were able to show that only diversification with repellant or trap crops has positive effects on yield, whereas diversification with other crops has negative effects on yield. However, the meta-analysis did not include any studies on the effects of flower diversity on crop damage or yield (Letourneau et al. 2011). Positive effects of floral resources on natural enemies are recorded for herbaceous habitats, but woody habitats likely also provide floral resources (Haaland et al. 2011; Holland et al. 2016). Recent studies show that flower strips adjacent to wheat fields can reduce cereal leaf beetle damage and increase crop yield by 10% (Tschumi et al. 2015; Tschumi et al. 2016a). Such flower strips can enhance the in-field abundance and species richness of aphidophagous syrphid flies, lacewings, lady beetles and parasitoids (Ramsden et al. 2015; Tschumi et al. 2016b). Not all natural enemies use floral resources (e.g. spiders), but they can be positively affected by vegetation structure (Dix et al. 1995; Haaland et al. 2011). Table 1.1 gives an overview over different groups of natural enemies of aphids, the enemy traits and the reported positive local and landscape effects of SNH upon them. Summing up, herbaceous habitats and hedgerows can support natural enemies within the focal SNH and in crops thereby improving pest control. However, there is far less evidence that forests do so as well (Holland et al. 2016).

1.2.3.2 Effects of local habitats on pollinators

SNH are important for the persistence of bees in agricultural landscapes and positively affect their abundance and richness (Nicholls & Altieri 2013; Shackelford et al. 2013; Carvell et al. 2017). At the local scale, farm management or field-bordering SNH increase wild bee abundance in fields by ca. 75% (Kennedy et al. 2013). SNH are especially important for oligolectic, long-tongued, univoltine (= with a short flight season), solitary, above-ground nesting and nest-excavating species, which are more likely present and more abundant in SNH than in human-dominated habitats (urban areas or intensive cropland) (see Table 1.2; Williams et al. 2010; Forrest et al. 2015; Palma et al. 2015). However, the in-field presence of small-bodied and below-ground nesting bee species such as halictid bees is associated with a high proportion and proximity of hedgerows, grasslands and woodland edges (Carrie et al. 2017).

Bumble bees are large, social, polylectic and relatively long-tongued bees with a long flight season and many species nest below-ground (Goulson et al 2005, Carrie et al. 2017). Species with a long flight season are conditioned polylectic, which permits them to use many different floral resources, including crops. But they also need a continuity of floral resources throughout their entire flight season (Goulson et al. 2008; Mandelik et al. 2012). Overall, multivoltine and polylectic bees can deal much better with human-dominated habitats than univoltine and oligolectic species (Forrest et al. 2015; Palma et al. 2015). Long-tongued bees need SNH, probably, because the deep perennial flowers, with which they are associated, are mainly provided by SNH (Goulson et al. 2008; Palma et al. 2015). Farms offer bare soil for below-ground nesters, but far less above-ground nesting sites than SNH (Forrest et al. 2015). Therefore, below-ground nesting bees are less affected by agricultural intensification in total compared to above-ground nesters, although they are more affected by tillage (Williams et al. 2010; Forrest et al. 2015). Sociality is correlated with a long flight season, polylecy and excavating below-ground nests (Williams et al. 2010; Forrest et al. 2015; Carrie et al. 2017). Thus, social bees might be less affected by agricultural intensification than solitary bees owing to these traits, although they are more sensible to pesticides and isolation (Williams et al. 2010; Carrie et al. 2017). Further, eusocial bees such as honey and bumble need less time and energy than solitary bees to forage, to guard their territory and to find mates and oviposition sites owing to their division of labour and communication (Goulson 2003). Thus, owing to their higher efficiency, social bees are more flexible than solitary bees and can effort to have large foraging ranges (Goulson 2003). However, even if some common mobile and generalist species are able to persist in human-dominated habitats, large enough and connected SNH are needed to secure diverse bee communities (Marini et al. 2014; Palma et al. 2015).

In general, bees prefer open habitats over temperate forest (Winfree et al. 2011), but they are mainly affected by the provision of nesting sites and food (Goulson et al. 2015). Bees are primarily related to floral resources (Potts et al. 2009; Roulston & Goodell 2011; Holland et al. 2015). Both flower richness and floral cover enhance bee species richness and the number of bee visits (Ebeling et al. 2008). In addition, flower richness can contribute to a continuity of floral resources (Ebeling et al. 2008). A continuity of abundant and diverse floral resources is very important for wild bees, especially for polyphagous species with long flight seasons, and can therefore reduce the temporal variability of bee visits (Ebeling et al. 2008; Goulson et al. 2015). As a result, sown flower strips offering many pollen and nectar resources often contain more bee individuals and species than other strips (Haaland et al. 2011). Bees are mobile organisms, whereby their foraging range is mainly related to their body size (Greenleaf et al. 2007). Thus, pollinators mainly react at the landscape scale and pollination is related to the proximity to natural habitats and proportion of natural habitats in the surrounding landscape (Garibaldi et al. 2011; Kremen & Miles 2012, section1.2.4).

1.2.4 Seminatural habitats at the landscape scale

1.2.4.1 Effects of landscape complexity on pest control

Complex landscapes with a high proportion of seminatural habitats enhance the abundance and diversity of natural enemies, whereby the effects on richness are stronger (Bianchi et al. 2006; Chaplin-Kramer et al. 2011; Shackelford et al. 2013). In complex landscapes pest control on aphids is about 46% higher than in simple landscapes (Rusch et al. 2016) and consequently pest abundances are lower in most studies (Bianchi et al. 2006; Veres et al. 2013). Natural enemies and pest control are supported by woody and herbaceous habitats as well as agri-environment schemes at the landscape scale (Bianchi et al. 2006; Geiger et al. 2010). The scale depends on the mobility of the organism (Tscharntke et al. 2005), generalists usually operate at larger scales (1500 m) than specialists (700 m; Chaplin-

Kramer et al. 2011). Landscape complexity positively affects both generalists (spiders, soldier beetles, ground beetles, predatory bugs, rove beetles) and more specialized aphidophagous predators (gall midges, lady beetles, parasitoids, syrphid flies and other predatory flies) (see Table 1.1 and references therein). Sometimes, lady beetles and syrphid flies also react positively to arable land, because it provides abundant food resources during certain times of the year (Haenke et al. 2009; Meyer et al. 2009; Caballero-López et al. 2012b; Inclán et al. 2016). Thus, landscape effects can vary a lot among different species of the same functional group (Maisonhaute & Lucas 2011). Overall, a scale of 1 km seems to be predictive for the combined top-down control of all arthropod enemies on aphids (Rusch et al. 2016).

1.2.4.2 Effects of landscape complexity on pollination

In many studies and crops worldwide the abundance and species richness of crop visiting wild bees decrease with the distance from natural areas, because SNH usually provide better and more stable nesting sites and diverse floral resources than crops (Ricketts et al. 2008; Garibaldi et al. 2011; Winfree et al. 2011). Bee abundance and richness are negatively affected by habitat loss, especially via the conversion to agriculture and in extremely anthropogenic landscapes (Winfree et al. 2011). The isolation from natural habitats has stronger effects on the visitation rate (50% reduction in 600 m distance) than on the species richness of bees (50% reduction in 1.5 km distance; Ricketts et al. 2008). Bees return to their nests or brood cells and are therefore central place foragers (Cresswell et al. 2000). Their foraging distance limits the scale, at which they respond to the landscape (Cresswell et al. 2000). In general, smaller bee species have smaller foraging ranges than large bees and therefore react to smaller landscape scales (Greenleaf et al. 2007; Benjamin et al. 2014). Small bees react at scales of 250 – 300 m, whereas large bees react at scales of 750 – 1500 m (Steffan-Dewenter et al. 2002; Benjamin et al. 2014). All the other traits, which also influence the ability of bees to persist in agricultural landscapes are listed in Table 1.2.

Honey bees are not affected by natural habitat loss, because they are managed by beekeepers, who provide hives as nesting sites and additional food, if needed, and move bees between foraging habitats (Goulson 2003; Winfree et al. 2009). Although honey bees forage up to 12 km (Greenleaf et al. 2007), small agri-environment schemes influence the honey bee foraging activity only in 80 – 200 m distance (Henry et al. 2012). Bumble bees have foraging ranges up to 4 km (Greenleaf et al. 2007), but European bumble bees usually forage between 750 – 1500 m (Osborne et al. 2008a: *Bombus terrestris* L., Carvell et al. 2012: *B. lapidarius* L. and *B. pascuorum* Scopoli). In addition, the foraging range depends on the landscape configuration and provision of floral resources at the landscape scale (Hines & Hendrix 2005; Winfree et al. 2011). For example, bumble bees do not like to cross roads (Bhattacharya et al. 2003), and forage nearby, when enough floral resources are provided (Carvell et al. 2012; Carvell et al. 2017), but travel great distances to reach attractive species-rich habitats if nearby forage is missing (Jha & Kremen 2013). The survival of bumble bee populations increases with the proportion of high-value foraging habitat, which also offers floral resources in spring, in the surrounding (Carvell *et al.* 2017). Therefore, the proportion of forage offering seminatural habitats such as forests (e.g. Kremen et al. 2002; Sepp et al. 2004; Julier & Roulston 2009; Xie & An 2014) and grasslands (e.g. Jauker et al. 2009; Petersen & Nault 2014; Xie & An 2014) enhance the diversity and mainly the abundance of bees. Further, urban areas can have positive effects on the abundance of bumble bees and halictid bees (e.g. Carré et al. 2009; Theodorou et al. 2016), because especially gardens can offer nesting sites (Osborne et al. 2008b; Lye et al. 2012) and floral resources (Goulson et al. 2008).

While agricultural land cover negatively affects the abundance of crop-visiting bees (Bommarco et al. 2012; Benjamin et al. 2014), mass-flowering crops such as oilseed rape have various effects on pollinators. On the one hand mass-flowering crops dilute pollinators during the mass-flowering (Holzschuh et al. 2011; Kovács-Hostyánszki et al. 2013; Holzschuh et al. 2016). They attract pollinators, but most mass-flowering crops (oilseed rape, sunflower, orange) do not proportionally increase the population size of bumble bees (nest density), solitary bees and syrphid flies (Herrmann et al. 2007; Holzschuh et al. 2016). Only late flowering red clover really enhances bumble bee reproduction (Rundlöf et al. 2014). On the other hand, pollinators concentrate in nearby flower offering (seminatural) habitats after the mass-flowering (Westphal et al. 2003; Herrmann et al. 2007; Kovács-Hostyánszki et al. 2013).

Overall, landscape complexity positively affects wild bees (Concepción et al. 2012; Shackelford et al. 2013). An 10% increase of high-quality bee habitats in the surrounding landscape increases wild bee abundance by 37% (Kennedy et al. 2013). Further, the proximity to natural areas does not only increase wild bee visitation in many studies and crops worldwide, but also results in higher fruit set and crop yield (Ricketts et al. 2008; Garibaldi et al. 2011; Garibaldi et al. 2016).

1.2.5 Interactive effects between organic farming, adjacent seminatural habitats and landscape complexity

Organic farming, adjacent semi-natural habitats and landscape effects should be addressed together, because they likely interact (Díaz & Concepción 2016). It is hypothesized that local management such as organic farming or adjacent SNH has stronger effects in simple and intermediate (1-20% non-crop habitat) landscapes compared to cleared or complex landscapes (Tscharntke et al. 2012b). In cleared landscapes too few source populations remain to respond to local management, and in complex landscapes seminatural habitats support a high biodiversity of beneficials everywhere, so that effects of local management are not detectable (Tscharntke et al. 2012b). Therefore, it is recommended to increase the landscape complexity in simple landscapes, apply extensive local management in intermediate landscapes and to maintain complex landscapes (Díaz & Concepción 2016). As hypothesized by Tscharntke et al. (2012b) positive effects of agri-environment schemes on plant diversity are strongest in intermediate landscapes (Roschewitz et al. 2005; Concepción et al. 2012). In addition, there can also be an interactive effect between the local managements. For example, organic farming positively affects the quality of adjacent SNH (Aude et al. 2004; Holzschuh et al. 2010).

1.2.5.1 Interactive effects on pest control

Regarding pest control, only few studies on pest control combine the effects of landscape complexity and organic farming or adjacent SNH and no study combines all three. As hypothesized by Tscharntke et al. (2012b) organic management has stronger effects on species richness of predators in simple landscapes (Tuck et al. 2014). In the few existing studies on pest control often no interactive effects were found with adjacent flower strips (Woltz et al. 2012) or organic farming (Birkhofer et al. 2016), and a large-scale European study only found landscape effects on pest control potential in organic fields, but not in conventional fields (Winqvist et al. 2011). However, in one study aphid pest control in the late season was similar in fields with field margins in simple landscapes to pest control levels reached in complex landscapes with or without field margin (Chaplin-Kramer & Kremen 2012).

1.2.5.2 Interactive effects on pollination

Regarding pollinators, a meta-analysis of 71 European studies confirmed that agri-environment schemes (field-bordering SNH or organic management) are most effective in simple landscapes (1-20% of SNH), but still increase pollinator richness and abundance in complex landscapes (> 20% of SNH; Scheper et al. 2013). However, another meta-analysis that disentagled the relative influence of landscape composition and farm management on wild bee abundance and richness using data from 39 global studies found an additive positive effect of landscape complexity (Kennedy et al. 2013). At the local scale, farm management such as organic farming or multi-cropped fields or field-bordering SNH increases wild bee abundance by ca. 75% (Kennedy et al. 2013). A 10% increase of high-quality bee habitats in the surrounding landscape increases wild bee abundance by 37% (Kennedy et al. 2013). Further, some studies only found positive effects of organic management on crop pollination in complex landscapes (Kremen et al. 2002; Klein et al. 2012).

1.3 QuESSA

This doctoral thesis is embedded into the European project QuESSA (Quantification of Ecological Services for Sustainable Agriculture). The project aims to identify key seminatural habitats and to quantify the contribution of seminatural habitats to key ecosystem services including pest control and pollination. QuESSA is a large-scale study on the effects of seminatural habitats at the local and landscape scale on pollination and pest control in seven crops grown across eight European countries (Fig. 1). The project is funded by the European Union’s Seventh Framework Programme for research, technological development and demonstration under grant agreement No 311879.

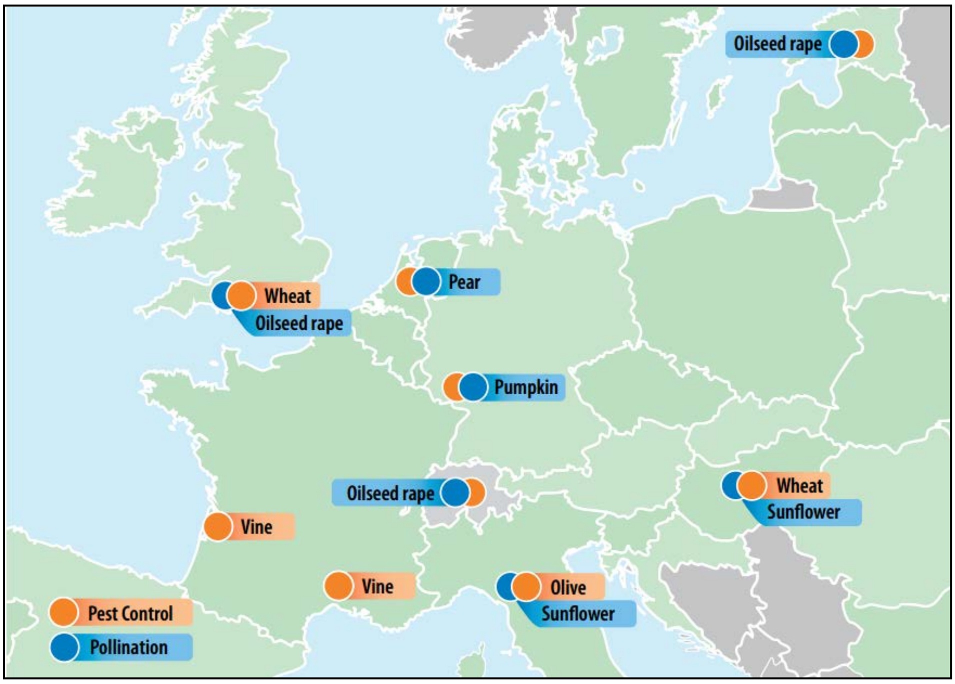

Figure 1.1 Case studies in the QuESSA project: 7 on pollination and 9 on pest control in eight European countries.

1.4 Pumpkin

In this doctoral thesis pumpkin *Cucurbita maxima* (Duchesne ex Poir) cv. Hokkaido was chosen as the study plant. Pumpkin belongs to the pollination-dependent leading food crops worldwide (Klein et al. 2007) and to the top ten vegetables grown outdoor in Germany (STATISTA 2017). In 2015 3485 ha of pumpkin and 1137 ha of squash were grown in Germany (STATISTA 2017). Pumpkin cultivation in Rhineland-Palatinate (RLP), one of the major vegetable growing areas in Germany (STATISTA 2017), started 15 years ago. Currently around 500 ha of pumpkin are cultivated in RLP (Statistisches Landesamt RLP 2014). The main cultivars are Hokkaido pumpkins with a weight of 1 to 1.5 kg. In Germany, average pumpkin yields of 20 tonnes per ha are obtained (STATISTA 2017). Pumpkin contains important micronutrients, for example vitamin A (168 µg/ 100g), iron (0.6 mg/ 100 g) and folate (23 µg/ 100g; EU-Regulation 2008/100/EG; Chaplin-Kramer et al. 2014; USDA Nutrient Data Laboratory 2016). Pumpkin can be grown with relative low labour-intensity compared to other vegetables and pumpkin fruits can be stored up to five months.

1.4.1 Pest control in pumpkin

Most studies investigated pest control in cereals (64% Bianchi et al. 2006; 53% Rusch et al. 2016), but studies in vegetables are still quite rare. So far, no study simultaneously investigated the effects of field management, adjacent habitats and effects at the landscape scale.

Pumpkin is highly suitable to apply conservation pest control of aphids. First, for a vegetable culture pumpkin has a long residence time on the field (12 – 21 weeks), thus there is sufficient time to build up natural enemy populations. Second, there is a potential to reduce insecticide applications that are used by some, but not all farmers to control aphids and viruses transmitted by them. Third, the marketable pumpkin fruit is not infected with aphids or beneficials, thus the use of natural enemies for aphid suppression in pumpkin does not result in problems with consumer acceptance (Dedryver et al. 2010).

1.4.2 Pollination of pumpkin

Pumpkin is a well suited vegetable to study pollination, because it is obligate cross-pollinated by insects (Hurd et al. 1971). First, insect pollination is essential in pumpkin because all cultivated *Cucurbita* species have unisexual flowers, so pollen transfer between male and female flowers is necessary for fruit set (Hurd et al. 1971). Second, the large numbers of ovules (400-700; Nepi & Pacini 1993; Canto-Aguilar & Parra-Tabla 2000) suggest a need for a high pollinating intensity. Third, although cucurbits have a long flowering period (on average 72- 80 days), the single flowers of pumpkin have only a short lifetime (6 hours – 1 day; Dmitruk 2008). Thus, rapid and effective pollinator visits are vital to crop yield. To attract pollinators, the *Cucurbita* flowers offer relatively rich rewards of pollen and nectar (Nepi & Pacini 1993; Dmitruk 2008). In Europe, the specialized pumpkin bees (*Peponapis* Say, *Xenoglossa* Cockerell) do not exist (Canto-Aguilar & Parra-Tabla 2000; Winsor et al. 2000), thus pumpkin flowers could in theory be pollinated by honey bees, bumble bees and halictid bees (Nepi & Pacini 1993; Roldán-Serrano & Guerra-Sanz 2005; Dmitruk 2008). However, the knowledge about the performance of these pollinators has been largely restricted to honey bees and there are no studies with Hokkaido pumpkin (Nepi & Pacini 1993; Roldán-Serrano & Guerra-Sanz 2005).

1.5 Objectives and outline of the thesis

The overall goal of this thesis was to evaluate the potential of seminatural habitats in our region to support pest control and pollination and how they can thereby contribute to sustainable agriculture. The main objectives were

(i) To quantify the potential of seminatural habitats to support natural enemies and pollinators, and thereby to discover explicitly which are the main local and landscape features of seminatural habitats influencing the abundance of natural enemies and pollinators.

(ii) To quantify the influence of seminatural habitats on pest control in pumpkin.

(iii) To quantify the influence of seminatural habitats on pollination of pumpkin.

1.5.1 Chapter 2

The thesis starts with an investigation which local and landscape features affect the abundance of predatory flies (Dolichopodidae, Empididae and Syrphidae) in 183 field-bordering seminatural habitats in 50 agricultural landscapes in Germany, Italy and Switzerland (objective i). The following specific questions were addressed:

1. Do woody habitats harbour more predatory flies than herbaceous habitats?
2. Does the proximity of watercourses enhance predatory fly densities?
3. Does the proportion of SNH at the landscape scale enhance predatory fly densities and shape effects of the local SNH type?

4. How do the responses to local and landscape features differ between predatory fly families?

1.5.2 Chapter 3

It follows a deeper insight which local and landscape features affect the composition, abundance and diversity of Syrphidae in 138 field-bordering seminatural habitats in 35 agricultural landscapes in Germany and Switzerland (objective i). The following research questions were adressed:

1. How do local SNH characteristics (i.e. type, shape and food resource availability) drive the community assemblage, abundance and species richness of Syrphidae?
2. How does SNH amount at the landscape scale affect the community composition, species richness and abundance of Syrphidae and how does it interact with local SNH effects?
3. How do drivers of abundance and species richness of aphidophagous Syrphidae differ from those of non-aphidophagous Syrphidae and what is the relative importance of drivers across these functional syrphid groups?

1.5.3 Chapter 4

Farmers are interested in the delivery of the services such as pollination and pest control and the effect on yields (objective ii and iii). Those were studied in 18 pumpkin fields in Germany.

In chapter 4 the effects of management, local and landscape features of seminatural habitats on aphids and their natural enemies were investigated (objective ii). The following hypotheses were tested:

1. Aphids on pumpkin are reduced at high densities of natural enemies (top-down control).
2. Organic farming favours aphid enemies more than aphids, thereby reducing aphid densities.
3. Seminatural habitats adjacent to pumpkin fields enhance natural aphid control.
4. Aphid control increases with the abundance of flowers in adjacent habitats.
5. Aphid control decreases with the proportion of agriculture in the surrounding landscape.

1.5.4 Chapter 5

In chapter 5 the sensitivity of commercial pumpkin yield to a potential decline among different groups of pollinating bees was evaluated.

The specific objectives in Chapter 5 were:

1. To determine the pollination requirements of Hokkaido pumpkins.
2. To determine the most effective pollinators of Hokkaido pumpkins.
3. To determine if there is a pollination deficit in the current pollination system.
4. To investigate the sensitivity of crop yield to bee declines, which includes the investigation of the impacts of both changes in the frequency of visits from pollinator taxa and changes in the species composition of the pollinator fauna.

1.5.5 Chapter 6

In chapter 6 the effects of field management, adjacent seminatural habitats, landscape complexity and insecticide intensity in the landscape on pollinators and pollination of pumpkin were quantified (objective iii). The following specific hypotheses were tested:

1. Pollen delivery is positively related to the number of pollinator visits (honey and bumble bees).
2. The number of pollinator visits is higher in organic fields and in fields with adjacent seminatural habitats (local management).
3. The proportion of agricultural land and insecticide intensity in the landscape reduce the number of pollinator visits and thereby pollen delivery (landscape effects).

1.5.6 Chapter 7

Chapter 7 and 8 contain additional information. In Chapter 7 the effects of seminatural habitats at the local and landscape scale on the abundance and richness of bees were investigated in 69 field-bordering seminatural habitats in 18 agricultural landscapes in Germany (objective i). It was hypothesized that:

1. The abundance and richness of bees differ between different local habitat types.
2. Bees are related to the provision of floral resources in the local habitats.
3. Landscape complexity supports bees.

1.5.7 Chapter 8

In Chapter 8 the effects on yield were investigated. First, the effects of different levels of aphid densities on pumpkin yield were quantified. It was assumed that high aphid densities reduce yield.

Second, the effects of field management, local adjacent habitats and landscape complexity on pumpkin yields were investigated in the 18 pumpkin fields, where pest control (chapter 4) and pollination (chapter 6) were studied. It was assumed that yields are lower in organic than in conventional fields.

1.5.8 Chapter 9

In Chapter 9 the results of chapter 2 – 8 are summarized and discussed. It concludes with suggestions for future research and recommendations for environmental friendly farming.

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Chapter 2 Positive effects of local and landscape features on predatory flies in European agricultural landscapes

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Highlights

- Hedgerows are particularly important local habitats for all studied predatory flies
- Moreover, nearby water and seminatural habitats in the landscape can be favorable
- Responses of predatory flies varied across European countries and families

Abstract

Provisioning of suitable habitats for predatory insects in agricultural landscapes can improve natural pest control and hence the sustainability of agriculture. Apart from Syrphidae, the spatial ecology of predatory flies remains little studied. We investigated the Lanresponse of Dolichopodidae, Empididae and Syrphidae to local features of seminatural habitats and to the composition of the surrounding landscape. We sampled adult predatory flies with pan traps in 183 field-bordering seminatural habitats along gradients of landscape composition in Italy, Germany and Switzerland. Local habitat type, the composition of the surrounding landscape and proximity to watercourses affected the abundance of predatory flies. Across countries, Empididae and Syrphidae were more abundant in woody (i.e. forests and in particular hedgerows) than in herbaceous habitats, whereas Dolichopodidae had lowest abundance in forests. The abundance of Dolichopodidae in Italy and Empididae in Germany were furthermore enhanced by the proximity of watercourses. Abundance of Dolichopodidae increased with the proportion of seminatural habitats in 1 km radius. Empididae were more abundant in landscapes with higher proportion of forests. We identified hedgerows as favorable habitats for predatory flies in agricultural landscapes. Moreover, our study reveals the importance of proximity to watercourses, which has rarely been considered when studying natural enemies of pests in agroecosystems. The varying responses indicate that preserving or restoring habitat-diverse, heterogeneous landscapes guarantees high numbers of predatory flies across families.

Keywords

Hoverflies, Dance flies, Long-legged flies, Landscape complexity, Conservation biological control, Field margin

2.1. Introduction

Ecosystem services provided by beneficial organisms such as pollination and pest control can be supported by habitat and landscape management (Garibaldi et al., 2011; Rusch et al., 2016; Shackelford et al., 2013). In agro-ecosystems, seminatural habitats (SNH) play an important role for these beneficial organisms by providing larval habitat, refuge during disturbances, overwintering sites and alternative food resources (Holland et al., 2016). Their value for beneficials such as natural enemies of crop pests may, however, strongly depend on the type of locally present SNH, as well as their proportion and spatial distribution at the landscape scale (Holland et al., 2016; Rusch et al., 2016; Shackelford et al., 2013). Improving our understanding of the relative importance of different SNH types across spatial scales is crucial to enhance the effectiveness of pest control management (Jonsson et al., 2008; Tscharntke et al., 2012), but large-scale data across a large number of SNH and landscapes across multiple countries is scarce (Holland et al., 2016).

Most existing studies investigating the potential of SNH to promote predatory insects have focused on a relatively small number of potentially important taxa. In this context predatory flies (Diptera) have rarely been studied except of syrphid flies (Syrphidae), which are important for aphid control and additionally for pollination (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Skevington and Dang, 2002). Diptera are a diverse and common insect group, which occur in a wide range of terrestrial and freshwater habitats all over the world. They are an important part of the food chain and contribute to several ecosystem services including pest control (Skevington and Dang, 2002). Worldwide, species of at least 42 dipteran families are known to be predacious in their main feeding stage as larvae, especially on beetles, bugs and other flies. Some predatory flies, such as long-legged flies (Dolichopodidae), robber flies (Asilidae) and the majority of dance flies (Empididae) are predators also as adults (Skevington and Dang, 2002). They are abundant in crops (Frouz and Paoletti, 2000; Zöphel et al., 2001) and prey on soft-bodied pests of arable and horticultural crops such as aphids (Aphididae), gall midges (Cecidomyiidae) and psyllids (Psyllidae) (Bortolotto et al., 2016; Rieux et al., 1999; Stark and Wetzel, 1987). Moreover they are important predators of black flies (Simuliidae) and lake flies (Chironomidae) (Ivković et al., 2007, 2012; Ulrich, 2004; Werner and Pont, 2003). However, little is known about how and over what spatial scales SNH drive densities of predatory flies in agricultural landscapes.

For several biological reasons, predatory flies may respond differently to diverse SNH types and to their abundance in the wider landscape. First, larvae of Empididae and of many Dolichopodidae live in the soil, in rotting vegetation, under bark or in freshwater habitats (Bickel and Dyte, 2013; Smith, 2012; Ulrich, 2004). They are usually associated with moist conditions and therefore are often more abundant in shaded habitats, such as hedgerows and forests (Cauwer et al., 2006; Gelbič and Olejníček, 2011; Pollet and Grootaert, 1996). Secondly, some Empididae (especially Empidinae), Dolichopodidae and almost all Syrphidae use flower resources as adults and may consequently prefer flower-rich habitats (Smith, 2012; Ulrich, 2004). Finally, many predatory flies require multiple habitats to complete their life cycle and therefore are quite mobile. For example, Empididae use different habitats (herbaceous habitats, water bodies, hedgerows) for larval development, feeding, swarming and mating (Delettre et al., 1992, 1997; Frouz and Paoletti, 2000). Thus, abundance and species richness of Empididae may be highest in heterogenous and complex landscapes with high amounts of different types of SNH (Burel et al., 2004; Delettre et al., 1997). Indeed, it could be hypothesized that most predatory flies may respond to SNH at a larger (landscape) scale compared to other beneficials due to their relatively high mobility and because they are not central place foragers such as bees, for example (Jauker et al., 2009; Rader et al., 2016; Sommaggio, 1999).

In the present study, we studied Dolichopodidae, Empididae and Syrphidae across different types of SNH along gradients of landscape composition in 50 agricultural landscapes from three European countries. We addressed the following research questions:

1. Do woody habitats harbor more predatory flies than herbaceous habitats?
2. Does the proximity of watercourses enhance predatory fly densities?

3. Does proportion of SNH at the landscape scale enhance predatory fly densities and shape effects of the local SNH type?
4. How do the responses to local and landscape features differ between predatory fly families?

2.2. Methods

2.2.1 Study areas and site selection

The study was conducted in 183 seminatural habitats (local scale) in 50 agricultural landscapes (landscape scale) in three European Countries: Germany, Switzerland and Italy (Fig. 2.1).

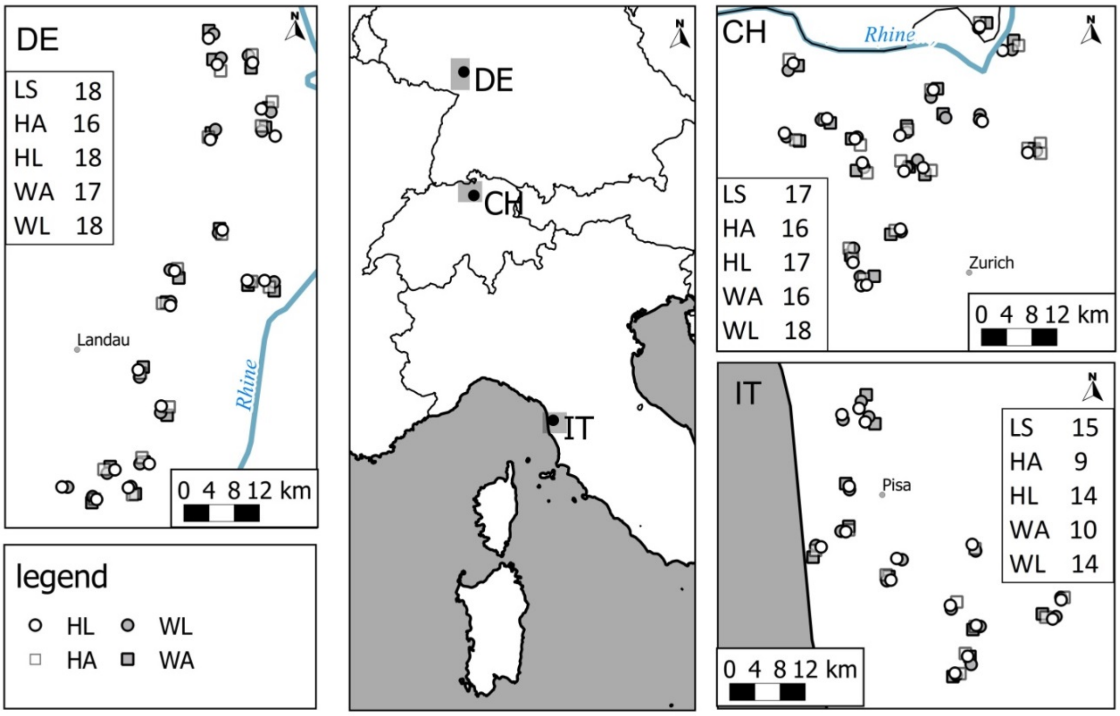

Figure 2.1 The three study sites in Germany (DE), Switzerland (CH) and Italy (IT) (overview in the map in the centre): The location of the sampled SNH (38 HA = grasslands/ fallows, 48 HL = grass margins, 43 WA = forests/ shrubland, 49 WL = hedgerows) is shown for each country in an inset.

In Germany, SNH were located in the Upper Rhine Valley between Kandel and Ludwigshafen (N: 49°4’ to 49°27’, E: 8°28’ to 8°6’). The region is characterized by intensive agriculture with only few grassland and forest fragments. Elevation ranges from 90 to 160 m a.s.l.. The climate is warm temperate with warm summers and fully humid (Kottek et al., 2006). The annual mean temperatures are around 10.5 °C and annual precipitation is 667 mm on average.

In Italy, SNH were located in the Pisa Plain, around the city of Pisa (N: 43°50’ to 43° 31’, E: 10°17’ to 10°40’). The Pisa plain is an alluvial plain characterized by intensive agriculture established mainly on reclamation area. Hedgerows are often present around main channels and small ditches, and further some woodlots and grasslands occur. Elevation ranges from -4 to 75 m a.s.l.. The climate is warm temperate with dry hot summers (Kottek et al., 2006). The annual mean temperature is 14.8 °C and the annual mean precipitation is 866 mm.

SNH in Switzerland were located in the northern part of the central Swiss plateau (cantons Zurich and Aargau, N: 47°36’ to 47°21’, E: 8°17’ to 8°38’) characterized by a mosaic of arable crops, grasslands and forest fragments. Elevation ranges from 344 to 688 m a.s.l. The climate is warm temperate with warm summers, fully humid and with a mean temperature of 9.4 °C and average annual precipitation of 1053 mm (Kottek et al., 2006). More information about the landscape characteristics of the study regions in the three countries is given in Table S2.1.

The investigated SNH were at least 1.5 m wide and 50 m long and had a minimum size of 150 m^2. They were always bordering a crop field. According to the predominantly occurring SNH in the agricultural landscapes of all three countries, we used four broad categories of SNH based on vegetation type (herbaceous vs. woody) and shape (linear vs. areal): woody areal (WA), woody linear (WL), herbaceous areal (HA) and herbaceous linear (HL) habitats. Areal SNH were at least 30 m wide (mean: 234 m), while linear SNH had a maximum width of 27 m (mean: 9 m). Woody SNH had at least 30% shrub/tree canopy cover (mean: 80%), while herbaceous SNH had up to 25% cover of trees or shrubs (mean: 0.7%) (Tab. S2.1). HA mainly consisted of grasslands and of some fallows (mainly in Italy), HL were grass strips and some improved field margins (mainly in Switzerland), WA consisted of forests, small woodlots and some shrublands, and WL were hedgerows and tree lines. In each country a set of all four different SNH types were located in 15 to 18 landscape sectors per country with 1 km radius (N_{total} = 183 SNH in 50 landscape sectors). The sampled SNH in a landscape sector were at least 200 m apart from each other.

We chose to consider proportion of SNH in 1 km radius, because this is often - despite species-specific differences in mobility - an important scale for Syrphidae (Haenke, 2012; Haenke et al., 2009; Kleijn and van Langevelde, 2006; Meyer et al., 2009) and natural enemies in general (Rusch et al., 2016). To determine the proportion of WA, WL, HA and total SNH in 1 km radius around the focal SNH, we classified aerial imagery data and digitized it in GIS. Proportion of HL in 1 km radius was not included, because grass strips are not easily detectable in land cover data and may be more ephemeral changing from one crop season to the next one than permanent grasslands, forests and hedgerows. The proximity to the next watercourse was calculated as the minimum distance [in meters] between the central point of the focal SNH to the nearest feature of a polyline layer of watercourses.

2.2.2 Sampling methods

Adult predatory flies were caught with standardized pan traps according to Westphal et al. (2008). Yellow pan traps are regularly used to sample adult Syrphidae (Burgio and Sommaggio, 2007; Inclán et al., 2016; Power et al., 2016), Empididae (Burel et al., 1998; Delettre et al., 1992, 1997) and Dolichopodidae (Frouz and Paoletti, 2000; Gelbič and Olejníček, 2011), but white and blue pan traps are also useful to sample a wider species pool of Empididae and Dolichopodidae (Pollet and Grootaert, 1994). To sample the local pool of species it is preferable to use a combination of different methods (e.g. pan traps, Malaise traps and emergence traps; Grootaert et al., 2001), because every method has strengths and limitations. However, pan traps are a standardized, reproducible method avoiding sampling bias owing to collector experience, that can collect natural enemies and pollinators at the same time during several days and can be applied across different habitats (Westphal et al., 2008). Therefore, pan trap triplets (yellow, white and blue) were a good sampling method for our pan-European project to test the response of predatory Diptera families to local habitat and landscape composition. We used two sets of three pan traps each with three colours (yellow, white and blue). The traps were made of 500 ml plastic bowls (http://www.pro-pac.de/) sprayed with UV-reflecting paint (Sparvar Leuchtfarbe, Spray-Colour GmbH, Merzenich, Germany). The traps were filled with 300-400 ml of water and a drop of detergent. One set was placed at the field edge (0.5 m into the SNH at the edge with the field and at least 10 m from any other edge). The second set was placed in the interior of the SNH (in areal SNH 12.5 m from the field edge and in linear SNH 1 - 10 m from the field edge). Traps were placed at the soil surface up to 150 cm above ground depending on average vegetation height of the herbaceous/ shrub layer. Traps were left active for four days at each sampling time. Sampling was conducted four times during the season: at the start of the vegetation period (T1), six weeks before the end of the vegetation period (T4; Rötzer and Chmielewski, 2001) as well as in May/ June (T2) and July (T3) (Tab. S2.1). Thus, sampling covered the important periods in terms of vegetation, activity of the sampled fly taxa and the periods relevant for natural pest control services to crops in the study landscapes. The collected specimens were stored in 70% ethanol. All material was sorted to the family level. It was distinguished between Syrphidae, Dolichopodidae and Empididae (including Hybotidae).

2.2.3 Statistical analyses

The data was analysed using linear mixed-effect models with landscape sectors as random effect (package “lme4”, Bates et al., 2015). We performed an automated model selection (dredge function) based on Akaike´s information criterion for small sample sizes (AICc) (package “MuMIn”, Barton, 2015). The linear mixed-effect models were fitted using maximum likelihood to compare models with different fixed effects and maximum two-way interaction (Bates et al., 2015). Response variables were the number of individuals of Syrphidae, Empididae and Dolichopodidae. Numbers were summed up across pan traps of an SNH and averaged over the sampling times to adjust for the different sampling effort in the three countries (only three sampling periods in Italy, Tab. S2.1). Response variables were log-transformed (log10(x+1)) to achieve normal distribution and homoscedasticity of residuals. When one or several traps were missing in a SNH (e.g. due to vandalism or damage by wind), the sum of the six traps was extrapolated from the average of the existing traps from that sampling round. Explanatory variables in all models were local SNH type (factor with four levels: WA, WL, HA, HL), the proximity to the next watercourse [m] (continuous) and the proportions of total SNH, forests (WA), hedgerows (WL) and grasslands (HA) in 1 km radius (continuous) as well as the interactions between the local SNH type and the other explanatory variables. Pearson correlation was checked for all possible pairs of continuous explanatory variables (package “Hmisc”, Harrell et al., 2016). SNH in 1 km radius was strongly correlated to forests (WA) in 1 km radius ($r = 0.94$, Tab. S2.2). The explanatory variables included in the best models were not significantly correlated with each other ($r < 0.2$). Model selection was done across countries and also per country, because owing to overfitting it was not possible to include interactions between all landscape variables and country in the models. In the overarching analyses of the data across countries, country was included as a fixed effect (factor with three levels: Germany, Switzerland, Italy) and landscape sectors as a random effect. Models were checked visually for normality and homoscedasticity of residuals and outliers. Models containing variables with p-values > 0.1 were not chosen, unless these variables were also part of an interaction term. The significance of effects of factors was tested with Wald chi²- tests (package “car”, Fox and Weisberg, 2010) and post-hoc Tukey tests (package “multcomp”, Hothorn et al., 2008). Marginal R^2 values were calculated to indicate the amount of variation explained by fixed explanatory variables (package “piecewiseSEM”; Lefcheck, 2016).

To identify the best-explaining scale we compared models with the proportion of SNH (accounting for SNH type: HA, WA, WL) in 1 km radius with models accounting for the proportion of SNH at smaller scales (Appendix 2). At scales < 1 km, the SNH in the surrounding landscape were weighed according to their proximity to the focal SNH. In the manuscript we only show results of models containing the unweighted proportion of SNH in 1 km radius for two reasons. First, because these models were always the best models (lower AICc; Tab. S2.4, Appendix 2). Second, the proportion of SNH types at the landscape scale, forests (WA) in particular, became increasingly correlated with the local presence of this habitat type when moving towards smaller spatial scales (Tab. S2.5, Appendix 2). Even at the 1 km scale proportion of forests was higher, when the local SNH was a forest than when the local SNH was another SNH type. To better distinguish between local and landscape-scale effects of a habitat type, especially of forests, this has to be considered in the study design (e.g. Farwig et al., 2009). However, the proportion of (certain) SNH in 1 km radius nevertheless added information to the local SNH type (Tab. 2.1).

2.3. Results

Overall we caught 16276 Dolichopodidae, 4565 Empididae and 9686 Syrphidae (Tab. S2.3). Abundances of all three predatory fly families differed between countries (Dolichopodidae: $\chi^2_{2,183} = 22.3$, $p < 0.001$; Empididae: $\chi^2_{2,183} = 74.1$, $p < 0.001$; Syrphidae: $\chi^2_{2,183} = 48.0$, $p < 0.001$). In Switzerland and Italy Dolichopodidae were the most abundant predatory flies, whereas in Germany Syrphidae were the most abundant.

2.3.1 Local habitat type

Overall predatory flies were more abundant in woody than in herbaceous SNH. Dolichopodidae were three to five times less abundant in forests (WA) than in the other SNH types (Fig. 2.2A). Empididae were three times more abundant in woody than in herbaceous habitats. This effect varied between countries and analysed per country it was only significant in Germany (Fig. 2.2B). Syrphidae were three times more abundant in woody than in herbaceous habitats (Fig. 2.2C). This effect also varied between countries and, as in Empididae, was driven by the German pattern. In contrast, in Switzerland

Syrphidae were more abundant in grass margins (HL) than in grasslands (HA) and there were no differences between local SNH types in Italy.

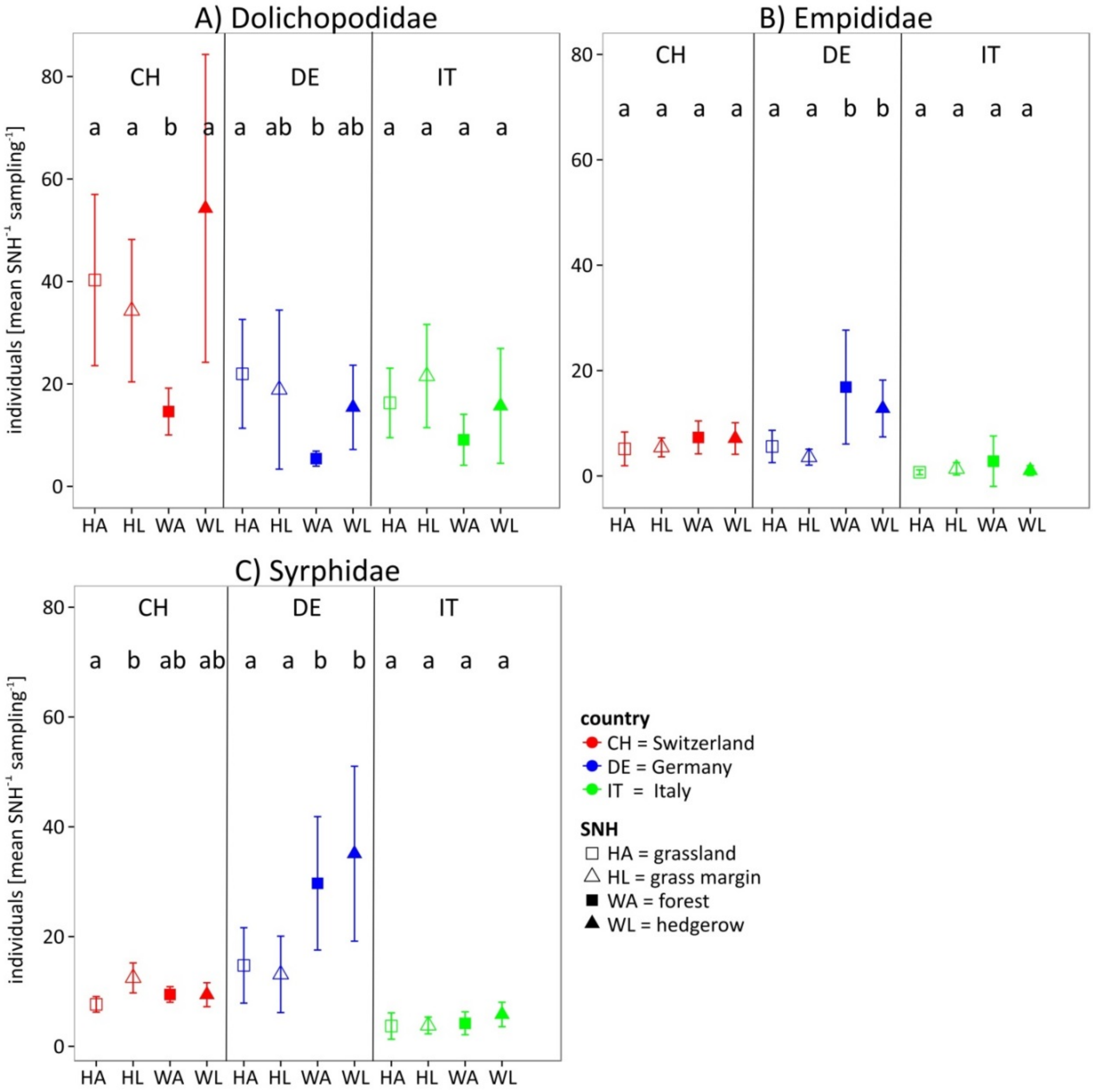

Figure 2.2 Differences in abundance of predatory fly families between habitat types and countries (mean ± standard error). Presented is the average abundance per SNH and sampling. Significant differences per country are indicated with different letters.

A) Dolichopodidae were less abundant in forests (WA) (CH: $\chi^2_{3,67} = 27.9$, $p < 0.001$; DE: $\chi^2_{3,69} = 10.1$, $p = 0.018$; IT: $\chi^2_{3,47} = 4.4$, $p = 0.22$; overall: $\chi^2_{3,183} = 27.9$, $p < 0.001$),

whereas B) Empididae (CH: $\chi^2_{3,67} = 2.6$, $p = 0.45$; DE: $\chi^2_{3,69} = 30.5$, $p < 0.001$, IT: : $\chi^2_{3,47} = 0.26$, $p = 0.97$; overall: $\chi^2_{3,183} = 16.6$, $p < 0.001$) and C) Syrphidae (CH: $\chi^2_{3,697} = 12.3$, $p = 0.0065$; DE: $\chi^2_{3,69} = 28.4$, $p < 0.001$; IT: $\chi^2_{3,47} = 4.9$, $p = 0.18$; overall: $\chi^2_{3,183} = 16.6$, $p < 0.001$) were most abundant in woody habitats (WA and WL).

2.3.2 Watercourses

The abundance of Dolichopodidae in Italy (Fig. 2.3A) and the abundance of Empididae in Germany (Fig. 2.3B) were positively related to the proximity to the next watercourse. In contrast, we found no effect of the proximity to the next watercourse on the abundance of Syrphidae ($t_{168} = -1.4$, $p = 0.15$).

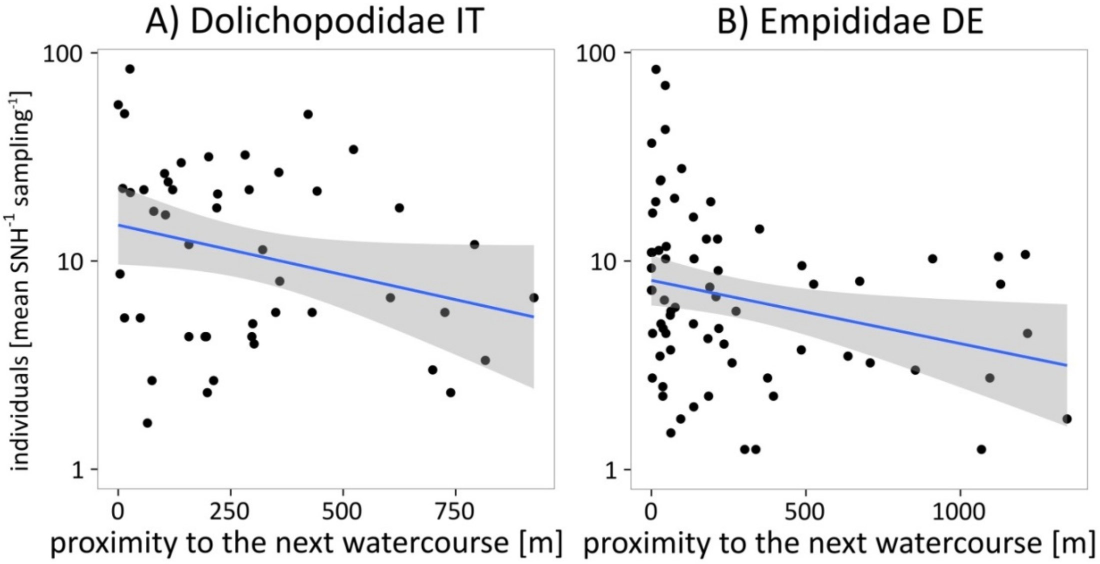

Figure 2.3 The proximity to the next watercourse [in meters] positively affected A) Dolichopodidae in Italy ($t_{43} = 2.4$, $p = 0.019$) and B) Empididae in Germany ($t_{61} = 2.6$, $p = 0.015$). 95% confidence intervals are shaded in grey.

2.3.3 SNH at the landscape scale

High proportions of SNH in the surrounding landscape positively affected abundance of predatory flies across all families in some countries, but not in all (only marginally significant for Syrphidae; Tab. 2.1). Over all countries the abundance of Dolichopodidae was influenced by the surrounding landscape in interaction with the local seminatural habitat type (Tab. 2.1). Abundances of Dolichopodidae in grass margins (HL) and hedgerows (WL) increased with increasing proportion of SNH in 1 km radius, while this relationship was not significant for grasslands (HA) and forests (WA) (Fig. 2.4A-D). A similar pattern was found in Germany (HA: $t_{14} = 2.1$, $p = 0.057$; HL: $t_{16} = 1.6$, $p = 0.13$; WA: $t_{15} = -0.026$, $p = 0.98$; WL: $t_{16} = 2.2$, $p = 0.039$). In Switzerland the interaction differed: the abundance of Dolichopodidae in grasslands decreased with increasing SNH in 1 km radius ($t_{14} = -2.5$, $p = 0.024$), whereas Dolichopodidae tended to be more abundant in hedgerows with more SNH in 1 km radius ($t_{16} = 1.8$, $p = 0.084$). In Italy, Dolichopodidae were not related to SNH at the landscape scale.

Over all countries increasing proportion of forests in 1 km radius tended to enhance the abundance of Empididae (Fig. 2.4E). Per country this pattern was only significant in Italy (Tab. 2.1). In Germany the abundance of Empididae tended to decrease with increasing proportion of hedgerows in 1 km radius (Tab. 2.1).

Over all countries Syrphidae were not significantly related to SNH at the landscape scale (Fig. 2.4F). In Switzerland the abundance of Syrphidae tended to be positively linked to the proportion of SNH in 1 km radius, whereas in Italy the abundance tended to be negatively related to the proportion of grasslands in 1 km radius (Tab. 2.1).

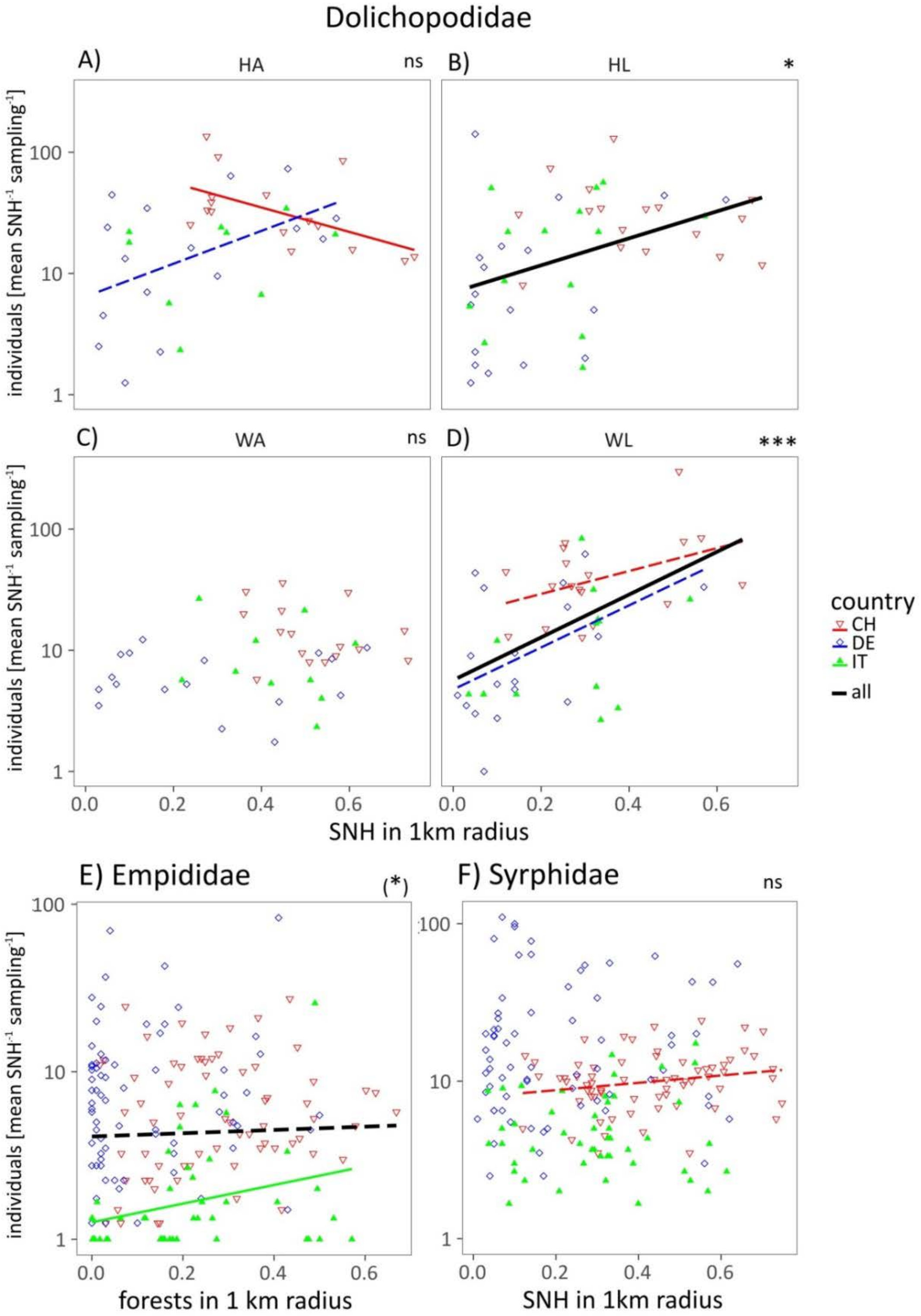

Figure 2.4 Influence of SNH at the landscape scale on the abundance of predatory fly families. For significant relations (solid lines) and trends (dashed lines) regression lines are shown per country (red, blank triangle = Switzerland; blue, blank rhombus = Germany; green, filled triangle = Italy) and for all countries together (black, bold). A - D) Abundance of Dolichopodidae increased with proportion of SNH in 1 km radius in B) grass margins (HL: $t_{29} = 2.2$, $p = 0.036$) and D) hedgerows (WL: $t_{48} = 3.5$, $p < 0.001$), but not in A) grasslands (HA: $t_{36} = 1.4$, $p = 0.16$) and C) forests (WA: $t_{41} = -0.54$, $p = 0.59$). E) Abundance of Empididae tended to increase with increasing proportion of forests in 1 km radius ($t_{136} = 1.8$, $p = 0.070$). F) And Syrphidae did not respond to any SNH at the landscape scale (SNH in 1 km radius: $t_{172} = 0.89$, $p = 0.37$).

Table 2.1 Local and landscape effects on predatory flies (Dolichopodidae, Empididae and Syrphidae): local SNH type, landscape composition (= proportion of SNH/ forests/ hedgerows or grasslands in 1 km radius; SNH_1km/ forests_1km/ hedgerows_1km/ grasslands_1km) and proximity to the next watercourse (proximity_water [m]). Predictors are given for all three countries together (all) and per country (CH = Switzerland, DE = Germany, IT = Italy). '*' mark interaction terms. Displayed are degrees of freedom (df) of n replicates, t-values for numerical variables, Chi-square values (χ^2) for factors, p-values for every variable and AICc of the model. Marginal R^2 values are displayed for all fixed factors of the total model (R^2_{tot}) and individually per fixed factor (R^2_{part}) to indicate the explained amount of variation. For interactive effects, only one marginal R^2 value for the whole interaction is given. All other models with delta AICc < 2 did not contain any additional significant variable. In most models including 'SNH_1km' or 'forests_1km' the respective other variable would have been slightly less significant, because the variables 'SNH_1km' and 'forests_1 km' are highly correlated (r = 0.94).

country	**predictors**	**df, n**	**t/χ^2**	**p**	**AICc**	**R^2_{part}**	**R^2_{tot}**
Dolichopodidae							
all	country	2, 183	18.3	< 0.001	159.9	0.21	0.32
	local SNH type* SNH_1km	3, 183	19.8	< 0.001		0.11	
	local SNH type	3, 183	29.5	< 0.001			
	SNH_1km	1, 183	0.11	0.91			
CH	local SNH type*SNH_1km	3, 67	11.2	0.011	36.4		0.38
	local SNH type	3, 67	23.1	< 0.001			
	SNH_1km	1, 67	-2.2	0.029			
DE.mod1	local SNH type*grasslands_1km	3, 69	9.9	0.020	86.4		0.16
	local SNH type	3, 69	13.4	0.0039			
	grasslands_1km	1, 69	2.4	0.021			
DE.mod2	local SNH type*SNH_1km	3, 69	12.7	0.0055	86.6		0.15
	local SNH type	3, 69	12.8	0.0052			
	SNH_1km	1, 69	1.3	0.20			
IT	proximity_water	1, 47	2.4	0.019	30.5		0.06
Empididae							
all	local SNH type*country	6, 183	17.2	0.0084	144.9	0.42	0.43
	local SNH type	3, 183	17.6	< 0.001			
	country	2, 183	79.5	< 0.001			
	forests_1km	1, 183	1.8	0.068		0.01	
CH	-				54.1		
DE	local SNH type	3, 69	28.2	< 0.001	58.7	0.27	0.35
	proximity_water	1, 69	2.6	0.015		0.07	
	hedgerows_1km	1, 69	-1.8	0.089		0.01	
IT	forests_1km	1, 47	2.5	0.015	20.2		0.14
Syrphidae							
all	local SNH type*country	6, 183	29.7	< 0.001	54.9		0.42
	local SNH type	3, 183	20.4	< 0.001			
	country	2, 183	49.1	< 0.001			
CH	local SNH type	3, 67	13.2	0.0043	-38.0	0.13	0.18
	SNH_1km	1, 67	1.9	0.056		0.05	
DE	local SNH type	3, 69	28.4	< 0.001	51.8		0.15
IT	grassland_1km	1, 47	-1.8	0.086	9.7		0.07

2.4. Discussion

2.4.1 Local habitat type

At the local scale, woody habitats harbored more Empididae and Syrphidae than herbaceous habitats, especially in Germany, but woody areal habitats (forests, woodlots) harbored less Dolichopodidae than woody linear and herbaceous habitats. Thus, predatory flies can especially be supported by woody (linear) habitats, such as hedgerows. Woody habitats might have the following advantages: first, they are shaded habitats with moist conditions. Many Dolichopodidae, Empididae and also some Syrphidae (f.e. *Episyrphus balteatus*) and their larvae are associated with moist conditions and are therefore often more abundant in shaded habitats, such as hedgerows and forests (Cauwer et al., 2006; Gelbič and Olejníček, 2011; Pollet and Grootaert, 1996; Röder, 1990). Especially in Germany Empididae and Syrphidae were more abundant in woody habitats. The different responses of different families across countries may be related to differences in climate, in properties of SNH types and in species composition (Hoback et al., 1999; Tscharntke and Brandl, 2004; Tscharntke et al., 2005). Maybe in Germany the contrast in moisture between herbaceous and woody habitats was stronger than in Switzerland due to higher temperatures and lower precipitation. The lack of a preference for woody habitats in Italy contradicts this explanation, but predatory fly densities were generally lower in Italy than in the two other countries. Second, although herbaceous habitats also harbor predatory flies (Bahrmann, 1993; Cauwer et al., 2006; Frouz and Paoletti, 2000), they are more disturbed (e.g. mowing of grasslands, crop harvesting) than woody habitats and predatory flies may use woody habitats as refuge (Boness, 1953). For example, Dolichopodidae of meadows often reside next to sheltering shrubs (Boness, 1953). Further, there are family-specific reasons for the preference of certain habitats. For example, Empididae use hedgerows for hunting and mating (Burel et al., 1998; Delettre et al., 1992). While, therefore positive relations of Empididae with hedgerows have been often reported in the literature (Burel et al., 1998; Delettre et al., 1997), we also found high densities of Empididae in forests.

The low abundance of Dolichopodidae in forests in our study is surprising, as Dolichopodidae hunt bark beetles in forests (Ulrich, 2004) and some use rotting wood and bark as larval habitat (Bickel and Dyte, 2013). Correspondingly, positive relations of Dolichopodidae to forests are reported (Bahrmann, 1993; Bortolotto et al., 2016; Pollet and Grootaert, 1991). A possible explanation for these divergent results is that although pan traps are the best method to collect the majority of dolichopodid species, our pan traps installed in the herb layer may be less suitable to sample species preferring forest canopies

(Gelbič and Olejníček, 2011; Pollet and Grootaert, 1994). A reason for the differences in Dolichopodidae occurrence between hedgerows and forests might be that Dolichopodidae are attracted by relatively short (1-5 m high) trees, but far less by higher trees (Peng et al., 1992). Still, although low densities of Dolichopodidae were observed in forests, the abundance of Dolichopodidae increased with increasing proportion of SNH in the surrounding landscape, consisting to a large part of forests (approximately 50% across countries). Thus, forests might be a larval or source habitat even for the Dolichopodidae that we caught in other seminatural habitats.

The preference for grass margins over grasslands by Syrphidae in Switzerland might be caused by the abundant perennial sown flower strips (7 of the 17 margins). These agro-environment schemes contain many floral resources and are very attractive for Syrphidae (Tschumi et al., 2016).

2.4.2 Watercourses

The proximity to watercourses increased predatory fly densities in two cases: the density of Dolichopodidae in Italy and the density of Empididae in Germany. Similarly to woody habitats watercourses offer moist conditions, which are important for many Dolichopodidae and Empididae (Cauwer et al., 2006; Gelbič and Olejníček, 2011; Pollet and Grootaert, 1996). Further, Dolichopodidae and Empididae hunt next to watercourses and feed on aquatic emergence such as black flies (Delettre et al., 1997; Wagner and Gathmann, 1996; Werner and Pont, 2003). In addition, most Dolichopodidae have aquatic or semi-aquatic larvae and stay close to their breeding sites as adults (Gelbič and Olejníček, 2011). Thus, at least in Italy the majority of Dolichopodidae was closely linked to aquatic habitats. Syrphidae were not related to watercourses, because they are dominated by species without aquatic larvae. The most abundant syrphid flies with aquatic larvae (Eristalinae) use small hypertrophic pools and are thus not necessarily associated with watercourses (Frank, 1999; Röder, 1990).

2.4.3 SNH at the landscape scale

As expected, the proportion of SNH at the landscape scale enhanced predatory fly densities, especially of Dolichopodidae and Empididae, and shaped the effects of the local SNH type on Dolichopodidae. This suggests a high mobility of some abundant species of Empididae and Dolichopodidae. Similarly, Burel et al. (1998) recorded a positive influence of landscape complexity on Empididae abundance and richness in France. The proportion of SNH in the surrounding landscape largely consisted of forests and grasslands.

Dolichopodidae were positively influenced by both, forests and grasslands, but Empididae mainly responded to the proportion of forests. In general, landscapes containing mainly open habitats consist of a more disturbed and short-lived vegetation that might therefore harbor less predatory flies than landscapes with more stable woody habitats (Grootaert et al., 2001). Given that the surrounding landscape mainly affected Dolichopodidae in linear SNH, our results further imply that linear habitats might be more vulnerable to landscape simplification than areal habitats, possibly due to their high border-to-area ratio and more pronounced edge effects (e.g. pesticide drift, microclimate).

Across countries abundance of Syrphidae was not significantly affected by seminatural habitats at the landscape scale, which is in line with findings of Jauker et al. (2009). There are several potential reasons for this. First, abundance patterns are driven by the most abundant species, which are usually well adapted to landscape intensification (Chaplin-Kramer et al., 2011; Haenke et al., 2009; Tscharntke et al., 2005). A species-level analysis of syrphid flies of the German and Swiss study regions (Schirmel et al., in prep.) revealed that landscape complexity in 1 km radius enhanced species richness and the abundance of all syrphid flies except *E. balteatus*. But the abundance relationships were blurred by the pattern of the most abundant, ubiquistic species, *E. balteatus* (Schirmel et al., in prep., chapter 3).

Second, Syrphidae could also be favored by anthropogenic land-cover types: e.g. crops hosting aphids can provide abundant food resources during certain times of the year for aphidophagous hoverflies (Haenke et al., 2009; Inclán et al., 2016; Meyer et al., 2009). Therefore, aphidophagous Syrphidae seem to be able to deal quite well with even simple agricultural landscapes with low proportions of SNH. In contrast non-aphidophagous Syrphidae seem to be more vulnerable to landscape simplification (Haenke, 2012; Inclán et al., 2016; Jauker et al., 2009; Meyer et al., 2009).

Third, well adapted abundant species are often more mobile and react to larger scales than specialists. Thus, landscape effects on Syrphidae can be found at relatively large spatial scales up to 4 km (Haenke et al., 2009; Power et al. 2016; Werling et al., 2011), but most syrphid species respond to the scale asessed in this study (Haenke et al, 2009; Kleijn and van Langevelde, 2006) and the 1 km scale proved to be predictive for Dolichopodidae and Empididae.

Fourth, Syrphidae use different habitats throughout the year and these high spatio-temporal dynamics in the distribution of Syrphidae in agricultural landscapes may lead to complex relationships with seminatural habitats (Alignier et al., 2014). Forests seem to be important habitats especially in winter and early spring, because many Syrphidae use them as overwintering refuge (Alignier et al., 2014; Sarthou et al., 2005). Similarly, forest cover tended to positively affect Syrphidae in Switzerland. Hedgerows offer floral resources and might be used as corridors during dispersal (Alignier et al., 2014; Haenke et al., 2014) and therefore can positively affect Syrphidae (Alignier et al., 2014; Burgio et al., 2015). In contrast, we did not find any positive effect of hedgerows in the surrounding on Syrphidae. Grasslands, which also offer floral resources, can also be important habitats for many syrphid species (Alignier et al., 2014; Meyer et al., 2009; Power et al., 2016; Speight 2010; Werling et al., 2011). However, our findings indicate that grasslands could also be negatively related to syrphid flies, because Syrphidae tended to be less abundant in landscapes with higher proportion of grasslands in Italy.

Switzerland was the only country, for which we found a positive trend of SNH at the landscape scale on total abundance of Syrphidae. Hereby, the higher shares of agro-environment scheme area in Swiss compared to German or Italian agricultural landscapes might have contributed to the landscape scale effects, e.g. by supporting a more diverse community of Syrphidae (Meyer et al., 2009).

2.4.4 Limitations of the family level

We are aware that the treatment at family-level had advantages and disadvantages. The family level enabled us to find general patterns despite the variation among species, to handle catches from three study regions covering different countries (in total 30527 individuals), and to analyse three families of predatory flies side by side. The families represent functional groups to some degree, because most taxa of these families are predators (Skevington and Dang, 2002) and total syrphid abundance is generally a good proxy for aphidophagous syrphids (~70% are aphidophagous; f.e. Frank, 1999; Haenke et al., 2014; Inclán et al., 2016). This is also confirmed by the significant responses of the families. On the other hand, we are aware that species within families may respond differently to the studied factors, even in opposite directions (see e.g. Schmidt et al., 2008). Such species-specific responses may blur the pattern at the family level and can be detected only when samples are analysed further, but species-specific analyses also complicate comparisons between countries.

2.5. Conclusions

At the local scale hedgerows were identified as a particularly important SNH type, which had positive effects on all studied predatory fly families. We also detected an important role of watercourses for Dolichopodidae and Empididae, suggesting that these structures should be considered more widely in landscape-scale studies on the ecology and functional role of insects. The proportion of SNH at the landscape scale enhanced predatory fly densities, especially of Dolichopodidae and Empididae, and shaped the effects of the local SNH type on Dolichopodidae. Thus, habitat-diverse, heterogeneous landscapes support high numbers of predatory flies across families. However, abundance of predatory flies and their response to local and landscape features differed between families and countries. Therefore, management strategies to promote predatory flies may need regional adaptation. The high abundance of Dolichopodidae and Empdididae in field-bordering seminatural habitats highlights the potential importance of these predator groups in European agricultural landscapes. However, to assess their importance as pest control agents further research is required.

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2.7 Supplementary Material

2.7.1 Appendix 1

Table S2.1 Information on sampling effort and explanatory variables, especially about the investigated SNH: Number of samplings, exact dates of the samplings (T1 to T4), number of landscape sectors (LS), and for each local SNH type (HA, HL, WA and WL) number (N), width (mean ± standard deviation) and % woody cover (mean ± standard deviation) and total number of local SNH in Switzerland (CH), Germany (DE), Italy (IT) and in total (all). Further ranges of landscape variables: proportion of SNH (%SNH_1km)/ grasslands (%grasslands_1km)/ forests (%forests_1km) and hedgerows (%hedgerows_1km) in 1 km radius as well as proximity to the next watercourse (proximity_water).

		CH	DE	IT	all
Samplings	N	4	4	3	
	T1	14. – 17.4.2014	7. – 13.4.2014	no	
	T2	10. – 13.5.2013	4. – 10.6.2013	18.6. – 9.7.2013	
	T3	8. – 11.7.2013	6. – 12.7.2013	18. – 29.7.2013	
	T4	19. –22.8.2013	21. – 30.9.2013	19. – 30.9.2013	
LS		17	18	15	50
HA	N	16 (14 LS)	16	9	38
	width	104 ± 14 m	60 ± 19 m	110 ± 138 m	95 m
	% woody	0	1 ± 5%	0	0.5%
HL	N	17 (16 LS)	18	14	48
	width	9 ± 6.6 m	6 ± 5.7 m	8 ± 4.9 m	8 m
	% woody	0	0.8 ± 2.5%	2 ± 6.7%	0.9%
WA	N	16	17	10	43
	width	457 ± 122 m	220 ± 245 m	428 ± 360 m	357 m
	% woody	72 ± 30%	83 ± 12%	81 ± 24%	78%
WL	N	18 (17 LS)	18	14	49
	width	11 ± 9 m	10 ± 5 m	12 ± 8 m	11 m
	% woody	75 ± 24%	86 ± 16%	81 ± 19%	82%
local SNH	N	67	69	47	183
SNH_1km	range	0.12 – 0.75	0.01 – 0.64	0.04 – 0.61	0.01 – 0.75
grasslands_1km	range	0.05 – 0.30	0 – 0.33	0.01 – 0.27	0 – 0.33
forests_1km	range	0.02 – 0.67	0 – 0.50	0 – 0.57	0 – 0.67
hedgerows_1km	range	0.003 – 0.04	0.01 – 0.06	0.003 – 0.10	0.003 – 0.10
proximity_water	range	0 – 1243	0 – 1345	0 – 924	0 - 1345

Table S2.2 Pearson rank correlation coefficients for all pairs of continuous explanatory variables (lower panel) and asymptotic p-values (upper panel).

	grasslands _1km	forests_1km	hedgerows_1km	SNH_1km	proximity_water
grasslands_1km	-	***	0.22	***	*
forests_1km	0.26	-	***	***	0.17
hedgerows_1km	-0.09	-0.25	-	*	0.08
SNH_1km	0.56	0.94	-0.16	-	*
proximity_water	-0.16	-0.10	-0.13	-0.16	-

Table S2.3 Overall abundance (N) and mean per sampling (S) and SNH of Dolichopodidae, Empididae and Syrphidae and sampling effort per country (CH = Switzerland, DE = Germany and IT = Italy).

Country	Sampling Effort	Dolichopodidae		Empididae		Syrphidae	
		N	mean	N	mean	N	mean
CH	67 SNH * 4 S * 4 days	9752	36	1678	6.3	2621	9.8
DE	69 SNH * 4 S * 4 days	4246	15	2684	9.7	6435	23
IT	47 SNH * 3 S * 4 days	2278	16	203	1.4	630	4.5
sum	2740 days	16276	23	4565	6.3	9686	13.5

2.7.2 Appendix 2

Best explaining spatial scale

To identify the best-explaining scale we compared models with the proportion of SNH (accounting for SNH type: HA, WA, WL) in 1 km radius with models accounting for the proportion of SNH at smaller scales. At scales < 1 km, the SNH in the surrounding landscape were weighed according to their proximity to the focal SNH with distance-weighted contact rates.

We decided to use distance-weighted contact rates, because we assume that SNH in the wider landscape support predatory flies in the local SNH and that proximity increases the probability that habitats have an influence. We furthermore assume that predatory flies have an equal probability to move in any direction. We decided to use the unweighted proportion in 1 km radius as variable for the maximum scale model. First, because with a kernel of 1 km half of the contact rate would lie outside of the measured area. Second, the larger the length scale of a kernel is, the less the habitats are differently weighted per distance. Thus, the larger the scale, the more the calculated contact rate approaches the calculated unweighted proportion.

We calculated contact rates with the kernel approach for different kernel lengths (50, 100, 200, 300, 400 or 500 u) (Clark et al 1999; Robinet et al. 2012; Lof 2016 in prep.). The kernel approach assumes that proximity increases the probability that habitats have an influence. Therefore it weighs the influence of the area of a habitat by the distance between this habitat and the sampling point. The kernel contact rate (K_{2Dt}(r)) is calculated using a 2Dt-distribution with two parameters, a length scale u in m and a shape parameter ν (ν = 25).

$$K_{2Dt}(r) = \frac{1}{u^2 \pi \nu} \frac{\Gamma\left(\frac{\nu+1}{2}\right)}{\Gamma\left(\frac{\nu-1}{2}\right)} \left(1 + \frac{1}{\nu}\frac{r^2}{u^2}\right)^{-\frac{\nu+1}{2}}$$

We set the shape parameter ν = 25 (the largest value that can be used in R), because this was identified as the optimal value to calculate contact rates with agricultural landscapes by Lof 2016 (in prep.). ν = 25 indicates, that the model approaches a normal distribution. The contact rate is the product of the area of the SNH type in the landscape sector and the dispersal kernel integrated over the whole landscape sector. The maximum value is 1, when the whole landscape would consist of this SNH type. 50 % of the contact rate lies in the radius of the kernel length scale u. To calculate the kernel contact rates the shape files were converted into raster files with 2.5 m resolution.

The model selection was done for each scale separately (procedure described in Statistical analyses). To compare the models of different kernel lengths with each other and with the model including proportion of (certain) SNH in 1 km radius, we calculated models at all scales with the explanatory variables of the best model, if landscape variables were included in this best model. The models containing the unweighted proportion of SNH in 1 km radius were always the best models (with the lowest AICc, Tab. S2.4).

In addition we tested how much the calculated landscape scale parameters were related to the local SNH type. The local habitat affected the proportion/ contact rate of this habitat type at the landscape scale. Especially local WA influenced the proportion of WA in the landscape, up to the 1 km scale. The effect of local HA usually wore off in a 400 m kernel. Effects of local WL were no longer detected in 300 m kernels (Tab. S2.5).

Not surprisingly, kernel contact rates at smaller scales were more influenced by the local habitat than at larger scales and the unweighted proportion was influenced the least. Because the models using the unweighted proportion as explanatory variable always were the best models and because contact rates were more biased by the local SNH type, we only used the local SNH type and the unweighted proportion of SNH in 1 km radius as variables in the manuscript. Even so, there is still a bias of local forests on the proportion of WA in 1 km radius, but nevertheless the proportion of (certain) SNH in 1 km radius added information to the local SNH type (Tab. 1).

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Table S2.4 Comparison (AICc) of the best models including landscape variables (_scale) calculated at different scales (kernel lengths 50 u, 100 u, 200 u, 300 u, 400 u, 500 u; and proportion in 1 km). Models for the different families (fam): Dolichopodidae (Dol), Empididae (Emp), Syrphidae (Syr), and countries (cty: all, CH = Switzerland, DE = Germany, IT = Italy).

fam	**predictors**	**country**	**scale**						
			50 u	**100 u**	**200 u**	**300 u**	**400 u**	**500 u**	**1 km**
Dol	snh_scale * SNH+country	All	165.3	162.9	162.4	160.8	160.1	159.9	159.9
Dol	snh_scale * SNH	CH	40.1	41.0	40.7	39.4	38.4	38.0	36.4
Dol	snh_scale * SNH	DE	88.0	89.1	90.4	89.1	88.2	87.7	86.6
Emp	forests_scale+SNH +country +SNH:country	All	147.5	147.3	147.2	147.0	146.6	146.3	144.9
Emp	forests_scale	IT	26.1	25.5	24.0	23.1	22.3	21.7	20.2
Emp	forests_scale + SNH	IT	31.3	27.2	26.3	26.8	26.5	26.2	25.2
Emp	hedgerows_scale + SNH + proximity_water	DE	61.6	61.5	61.1	60.0	59.7	59.6	58.7
Syr	snh_scale + SNH	CH	-35.9	-37.0	-36.7	-36.3	-36.1	-36.0	-38.0

Table S2.5 Effect of the local habitat (SNH: Ha, Wa, WL) on the contact rate (u = 50, 100, 200, 300, 400 or 500 m)/ proportion (in 1 km radius) of this habitat type a the different scales per country. Significant differences are marked with stars.

Country	**SNH**	**U= 50**	**100**	**200**	**300**	**400**	**500**	**1 km**
all	Ha	Ha > ***	Ha > ***	Ha > ***	Ha > **- ***	Ha > *-***	Ha > Wa (*), Wl**, Hl ***	no
	Wa	Wa > ***	Wa > ***	Wa > ***	Wa > ***	Wa > ***	Wa > ***	Wa > Ha **, Hl, Wl ***
	Wl	Wl > ***	Wl > ***	Wl > Hl, Wa ***	Wl > Hl *, Wa ***	Wl > Hl (*),Wa **	Wl > Wa **	Wl > Wa (*)
CH	Ha	Ha > ***	Ha > ***	Ha > *- ***	Ha > Hl**, Wa*	Ha > Hl*	Ha > Hl*	No
	Wa	Wa > ***	Wa > ***	Wa > ***	Wa > ***	Wa > **-***	Wa > *-***	Wa > Wl**
	Wl	Wl > ***	Wl > *- ***	Wl > Wa*	no	no	no	no
DE	Ha	Ha >***	Ha > ***	Ha > Hl, wl**,wa(*)	Ha > Hl, wl(*)	No	no	no
	Wa	Wa >***	Wa > ***	Wa > Hl, Wl ***, ha(*)	Wa > Wl**, Hl *	Wa > Wl*, Hl	Wa > Wl*, Hl	Wa > Wl(*)
	Wl	Wl >***	Wl > Hl, wa**	Wl > Wa*	No	No	No	no
IT	Ha	Ha >***	Ha > ***	Ha > Hl, Wl *	Ha > Hl*, Wl (*)	no	No	no
	Wa	Wa >***	Wa > ***	Wa > ***	Wa > *-***	Wa > Hl, Wl **, Ha(*)	Wa > Hl**, Wl *, ha(*)	Wa > Hl*, Wl (*)
	Wl	Wl > *-**	no	No	no	No	No	no

Chapter 3 Semi-natural habitats in the surrounding landscape promote hoverflies in agroecosystems of two European countries

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Summary

1. Semi-natural habitats (SNH) provide essential resources for many organisms in agricultural landscapes and can increase biodiversity at the local and landscape scale. For the management of ecosystem services, it is crucial to understand how local characteristics of SNH and the surrounding landscape complexity affect beneficial species.

2. We investigated this for hoverflies (Diptera: Syrphidae), an important functional group providing both pest control and pollination services, in a total of 138 SNH in 35 agricultural landscapes in Switzerland and Germany. SNH differed in type (woody, herbaceous), shape (areal, linear) and availability of food resources (floral resources and aphids). They were located along a gradient of landscape complexity (1-75 % SNH in a 1 km radius).

3. In total 9,030 hoverflies belonging to 89 species were collected. The hoverfly species compositions were, consistently across the two countries, mainly driven by SNH type, SNH shape and landscape complexity, and in Germany additionally by aphid density. Species richness and abundance increased with increasing amounts of SNH at the landscape scale, except for the ubiquitous aphidophagous *Episyrphus balteatus* which was indifferent to landscape composition.

4. Linear and areal SNH had similar species-rich hoverfly assemblages, but non-aphidophagous hoverflies were more vulnerable to landscape simplification in linear than areal SNH. Effects of the SNH type differed between the two countries. In Germany, aphidophagous species preferred woody over herbaceous SNH, while no difference was found in Switzerland.

5. Local richness and abundance of floral resources were, in contrast, poor predictors for hoverfly abundance, richness or community composition.

6. *Synthesis and applications*: Across study regions, large-scale conservation and restoration of complex agricultural landscapes with a high proportion of different SNH types is key for the conservation of hoverfly diversity and high densities of most aphidophagous and non-aphidophagous species, and thus likely promote pest control and pollination services provided by them. In contrast, local improvement of SNH to promote hoverflies has to consider regional differences in habitat characteristics.

Keywords

aphids, beneficial arthropods, ecosystem service providers, *Episyrphus balteatus*, field margins, landscape composition, Syrphidae

3.1 Introduction

Agricultural landscapes are composed of cultivated fields, anthropogenic infrastructures (e.g. roads and tracks) and semi-natural habitats (SNH) *(*Marshall & Moonen 2002). SNH are usually defined as all uncropped, non-commercial, vegetated features of the agricultural landscape such as hedgerows, field margins and forest patches (García-Feced *et al.* 2014).

SNH provide important resources (e.g. food, shelter, overwintering and nesting sites), and thus often positively affect the abundance and diversity of many organisms on the local scale (Marshall & Moonen 2002; Holland *et al.* 2016). At the same time, on the landscape scale, a high proportion of SNH (hereafter landscape complexity) can boost beta and gamma diversity through an enhanced and more heterogeneous resource pool (e.g. diversity of suitable microhabitats) and increased connectivity of habitats (Hendrickx *et al.* 2007). Favourable effects of SNH have been reported for a variety of beneficial arthropods for agriculture including spiders, hoverflies, and wild bees (Schmidt & Tscharntke 2005; Hänke *et al.* 2009; Diekötter *et al.* 2014). With respect to the conservation of biodiversity and associated ecosystem services, SNH gained much attention in ecological research during the last decades (Burel 1989; Frank 1999; Carré *et al.* 2009; Staley *et al.* 2016, Fußer *et al.* 2016, Schirmel *et al.* 2016). The ability of an organism to successfully persist in its environment is largely determined by the availability of resources within its home range, which in turn is largely driven by its mobility and dispersal capacity (e.g. Schweiger *et al.* 2007). Consequently, species are influenced by SNH characteristics determining resource availability at different spatial scales depending on their life-history traits (Schmidt *et al.* 2007; Meyer, Jauker & Steffan-Dewenter 2009; Woodcock *et al.* 2010).

Hoverflies (Diptera: Syrphidae) are a ubiquitous and diverse arthropod group that provides both pollination and pest predation services to agriculture (Jauker & Wolters 2008; Chaplin-Kramer *et al.* 2013). The conservation of hoverflies is therefore important to maintain regulatory ecosystem services sustaining crop production. With regard to ecological intensification (e.g. Bommarco *et al.* 2013) and agri-environmental schemes, a better knowledge of how local and landscape characteristics of SNH drive the abundance, diversity and community composition of hoverflies is essential to optimize the effectiveness of measures and to support management decisions of farmers and other stakeholders.

In a highly replicated field study we therefore investigated hoverflies in different SNH in agricultural landscapes in Central Europe (Switzerland and Germany). In particular, we analysed the effects of different SNH types (woody or herbaceous) and shapes (linear or areal), and their habitat characteristics as well as landscape complexity on two functional groups of hoverflies (aphidophagous and non-aphidophagous). We addressed the following research questions: (i) How do local SNH characteristics (i.e. type, shape and food resource availability) drive hoverfly community assemblage, abundance and species richness? (ii) How does SNH amount at the landscape scale affect hoverfly community composition, species richness and abundance and how does it interact with local SNH effects? (iii) How do drivers of abundance and species richness of aphidophagous hoverflies differ from those of non-aphidophagous hoverflies and what is the relative importance of drivers across these functional hoverfly groups?

3. 2 Methods

3.2.1 Study regions and site selection

The study was conducted in 35 agricultural landscapes in Switzerland and Germany, in which a total of 138 different semi-natural habitats (SNH) were studied. In Switzerland, the 69 studied SNH were located in 17 landscapes in the northern part of the central Swiss plateau (cantons Zurich and Aargau, N: 47°36’, S: 47°21’, W: 8°17’, E: 8°38’), a region characterized by a small-scaled mosaic of arable crops, grasslands and forest fragments. The climate is temperate with a mean annual temperature of 9.4 °C and precipitation of 1053 mm (Meteoschweiz 2014). In Germany, 69 SNH in 18 landscapes in the Upper Rhine

Valley, Rhineland-Palatinate, between the towns of Kandel and Ludwigshafen (S: 49°4’, N: 49°27’, E: 8°28’, W: 8°6’) were studied. The region is characterized by intensive agriculture dominated by cereals, maize and vegetables (Statistical Office of Rhineland-Palatinate 2014). The climate is temperate with a mean annual temperature of 10 °C and precipitation of 650 mm (DLR 2016).

We defined SNH as uncropped features of the agricultural landscape with more than 30 % vegetation, a minimum width of 1.5 m, a minimum length of 50 m and a minimum area of 150 m^2 (Holland *et al.* 2014, Fußer *et al.* 2016). SNH were distinguished in two types (woody or herbaceous) and two shapes (areal or linear). SNH with more than 30% cover of trees or shrubs counted as woody and SNH wider than 25 m as areal.

In each landscape we selected all combinations of SNH type and SNH shape, i.e. one woody areal, woody linear, herbaceous areal and herbaceous linear, respectively. These four focal SNH within one landscape had a minimum distance of 200 m from each other. In four landscapes it was not possible to find all four type-shape combinations that fulfilled the criteria outlined above. In Germany, two landscapes therefore miss some combinations while in Switzerland two missing combinations were instead studied in two of the other landscapes (thus five SNH were studied in the latter two landscapes). We calculated landscape complexity as the total proportion of SNH in a radius of 1 km around each focal SNH using aerial images (Switzerland: official satellite images provided by the Swiss Federal Office of Topography [SWISSIMAGE, swisstopo, Wabern]; Germany: satellite images provided by Google Earth [Google Earth 2013]) and a geographical information system (GIS) (Switzerland: ESRI, ArcMap 10.1; Germany: QGIS 1.8.0 (QGIS Development Team 2012). Because herbaceous linear SNH were not clearly visible on aerial images, only woody (areal and linear) and herbaceous areal SNH were taken into account for the calculation of landscape complexity.

3.2.2 Sampling

Hoverflies and aphids (as potential key driver of aphidophagous hoverflies) were sampled during four study periods (June, July and September 2013 and April 2014) with standardized pan traps according to Westphal *et al.* (2008). Per SNH two sets of pan traps (each containing a blue, white and yellow pan) were filled with 300 ml of water and a drop of detergent, and left active for four successive days per period (16 days in total). The collected specimens were stored in 70 % ethanol. In each SNH the flower abundance (total number of flowers) and flower richness (number of flowering plant species) was recorded in twenty 1 x 1 m^2 plots (up to a height of 2 m) randomly distributed along two 50 m transects ─ each of them containing one of the two sets of pan traps in the centre. Flower abundance of each plant species was calculated as the total floral area as follows: for species with circular flower morphologies (individual flower, flower head, corolla, corymb, umbel) diameter or radius was converted to the area of a circle; for other flower morphologies (spadix, cyme, flowered stem, capitulum, panicle, raceme, spike), the flowering surface was derived as the surface of a cylinder. Inflorescence dimensions were compiled from the following sources: PlantNET (Royal Botanic Gardens and Domain Trust 2016), Naturegate (NatureGate Promotions 2016), E-Flora BC (Klinkenberg 2015), and Pignatti (1982). In areal SNH half the sampling points (i.e. one set of pan traps and ten 1 m^2 plots for flower sampling) were located at the edge in 0.5 m distance to the adjacent field and the other half in the interior of the SNH (12.5 m from the edge). In linear SNH sampling points were placed at both edges.

Hoverflies were determined to species level according to van Veen (2004) and Merz & Bächli (1998). As it was not possible to distinguish the females of *Eumerus sogdianus*, Stackelberg 1952 from those of *E. strigatus*, Fallén 1817, both species were combined to one single group (*Eumerus spec*). Hoverflies were classified into the functional groups ‘aphidophagous’ and ‘non-aphidophagous’ according to Speight (2014), Röder (1990) and Maibach *et al.* (1992) (section 3.7 Supplementary Material).

3.2.3 Data analysis

All statistical analyses were performed using the open source software R version 3.2.5 (R Core Team 2016). A p-value < 0.05 was considered as statistically significant. Data of subsamples per SNH (repetition in time and space) were summed for statistical analyses.

3.2.3.1 Species composition

We assumed that hoverfly species compositions would differ between Switzerland and Germany. Hence, we first related the total hoverfly species composition to ‘country’ (factor with the two levels Switzerland and Germany) with a permutational multivariate analysis of variance (PERMANOVA) based on 999 permutations (command ‘adonis’ in R Package vegan: Oksanen *et al.* 2016). To reduce the influence of very abundant species a log(x+1)-transformation was performed on the species data. We then related the species compositions to local characteristics of SNH and landscape complexity separately for the two countries with PERMANOVA. The variables ‘SNH type’ (factor with the two levels woody and herbaceous), ‘SNH shape’ (factor with the two levels areal and linear), ‘landscape complexity’ (continuous proportion of SNH in 1km radius), ‘flower abundance’ (continuous), ‘flower richness’ (continuous), and ‘aphid density’ (continuous) were used as explanatory variables. To reduce the impact of outliers a log(x+1)-transformation was performed on the variables flower abundance and aphid density. Because of our nested design with four SNH located within one landscape, we used the landscape ID (‘LS’) as strata in the multivariate models. Non-metric multidimensional scaling (NMDS) on Bray-Curtis distances was performed to visualize the results (R Package vegan).

3.2.3.2 Effects of local and landscape effects on species richness and abundance

Local and landscape effects on hoverfly species richness and abundance were analysed with linear mixed models (LMM) on log(x+1)-transformed data to meet the assumption of normality and homoscedasticity of the residuals (‘lmer’ function in the R package lme4; Bates *et al.* 2015). LMMs were conducted for (1) total species richness of hoverflies, (2) species richness of aphidophagous hoverflies, (3) abundance of aphidophagous hoverflies (without *Episyrphus balteatus*, De Geer 1776), (4) abundance of *E. balteatus*, (5) species richness of non-aphidophagous hoverflies, and (6) abundance of non-aphidophagous hoverflies. We analysed *E. balteatus* (aphidophagous) separately from their *functional* group because the species was very dominant (Appendix S1), and leaving *E. balteatus* within their *functional* group would result in models that explain abundance patterns mainly driven by this species rather by the entire *functional* group. Predictor variables in all full models were SNH type, SNH shape, landscape complexity, flower abundance (log-transformed), flower richness, and country. For the models explaining aphidophagous hoverflies further aphid density (log-transformed) was included as a predictor. To test if the effects of SNH type and SNH shape depend on the landscape complexity, we included these interaction terms (SNH type × landscape complexity, SNH shape × landscape complexity) in all models. Additionally, we included interactions of all predictor variables with country to test whether effects vary between the two countries. The landscape ID was included as a random effect. For model simplification we used an information-theoretic approach to multi-model inference (Burnham & Anderson 2002). We standardized the regression predictors using the ‘standardize’ function (R package arm, Gelman & Su 2015). Collinearity in the predictor variables were assessed calculating variation inflation factors (VIF). In all models predictor variables had VIF values < 2.0 indicating low collinearity. For automated model selection we used the ‘dredge’ function (R package MuMln, Bartón 2013) and selected those top-ranked models within Δ AICc < 2. We used the AICc for small sample sizes. We then produced averaged parameter estimates from this top set of models using the ‘model.avg’ function. The appropriateness of all mixed models was assessed by visual checking of diagnostic plots (residuals vs. fitted values and normal Q-Q plots).

3.3 Results

In total 89 hoverfly species and 9,030 individuals were collected during the four study periods (Tab. S3.1). We found about 2.5 times more individuals in Germany (6,423) than in Switzerland (2,607), but slightly more species in Switzerland (69) than in Germany (62). The aphidophagous species *Episyrphus balteatus* was by far the most abundant species in both countries (Switzerland 35% and Germany 69% of all individuals).

3.3.1 Species composition

Both countries showed distinct hoverfly species compositions (PERMANOVA: $F = 26.2$, $R^2 = 0.16$, $P < 0.001$, Fig. 3.1a). In both countries, the hoverfly community composition was driven by SNH type, SNH shape and landscape complexity (Tab. 3.1, Fig. 3.1b,c). In Germany, the hoverfly composition was additionally related to aphid density (Tab. 3.1, Fig. 3.1b). In both countries neither flower abundance nor flower richness had a significant effect on the hoverfly composition (Tab. 3.1).

3.3.2 Species richness and abundance

Total species richness of hoverflies significantly increased with increasing landscape complexity (% SNH in 1 km radius) (Tab. 3.2, Fig. 3.2a). Species richness of aphidophagous hoverflies similarly increased with landscape complexity in both countries, while effects of SNH type varied across country (Tab. 3.3): aphidophagous species richness was similar between woody (6.3 ± 0.4) and herbaceous (6.4 ± 0.4) SNH types in Switzerland, while it was higher in woody (5.2 ± 0.4) than herbaceous (3.6 ± 0.2) SNH types in Germany (Tab. 3.3, Fig. 3.3a). Both species richness and abundance of aphidophagous hoverflies significantly increased with increasing landscape complexity (Tab. 3.3, Fig. 3.2b,c). Abundance of *E. balteatus* was significantly influenced the interaction between country and SNH type: in Switzerland, *E. balteatus* abundance was generally lower than in Germany and did not significantly differ between woody (13.8 ± 1.3) and herbaceous (12.6 ± 1.9) SNH types. In contrast, *E. balteatus* abundance was higher in Germany and more than three times higher in woody (97.9 ± 19.6) than in herbaceous (30.3 ± 8.7) SNH types (Tab. 3.3, Fig. 3.3b). *Episyrphus balteatus* abundance was significantly positively correlated with aphid density (Tab. 3.3).

Species richness of non-aphidophagous hoverflies significantly increased with increasing landscape complexity (Tab. 3.4, Fig. 3.2d). The abundance of non-aphidophagous hoverflies was significantly higher in Germany (19.8 ± 3.1) than in Switzerland (12.2 ± 1.3) and significantly increased with increasing flower richness (Tab. 3.4). The abundance of non-aphidophagous hoverflies in linear SNH significantly increased with increasing landscape complexity, while this increase was not significant in areal SNH (Tab. 3.4, Fig. 3.2d).

Table 3.1 Effects of the SNH type, SNH shape, landscape complexity (landscape), flower abundance, flower richness and aphid density on the hoverfly species composition in semi-natural habitats in a) Switzerland and b) Germany. Relationships were tested with permutational multivariate analysis of variance (PERMANOVA). Significant p-values are in bold.

Predictors	**F**	**R^2**	**P**
a) Switzerland			
SNH type	7.20	0.09	**< 0.001**
SNH shape	3.26	0.04	**0.002**
Landscape	4.40	0.06	**< 0.001**
Flower abundance	0.41	0.01	0.857
Flower richness	0.01	0.01	0.681
Aphid density	0.01	0.01	0.842
b) Germany			
SNH type	6.03	0.08	**< 0.001**
SNH shape	1.75	0.02	**0.012**
Landscape	4.86	0.06	**0.034**
Flower abundance	1.23	0.02	0.134
Flower richness	0.48	0.01	0.938
Aphid density	1.70	0.02	**0.025**

Table 3.2 Model-averaging results of the top-ranked models (delta AICc < 2) for total species richness of hoverflies in semi-natural habitats. Significant results ($P < 0.05$) are shown in bold.

	Predictor(s)	Estimate	Adjusted SE	z	P
Species richness	Country	-0.061	0.033	1.846	0.065
	SNH type	0.041	0.022	1.867	0.062
	Landscape	0.127	0.031	4.07	**< 0.001**
	Country : SNH type	0.065	0.045	1.434	0.151
	Country : landscape	-0.101	0.061	1.655	0.090
	SNH type : landscape	-0.056	0.047	1.201	0.230
	Flower richness	0.030	0.025	1.201	0.230

Table 3.3 Model-averaging results of the top-ranked models (delta AICc < 2) for aphidophagous hoverflies in semi-natural habitats. Significant results ($P < 0.05$) are shown in bold.

Dependent variable	Predictor(s)	Estimate	Adjusted SE	z	P
Species richness	Country	-0.087	0.039	2.215	**0.027**
	SNH type	0.053	0.022	2.378	**0.017**
	Landscape	0.094	0.033	2.837	**0.005**
	Country : SNH type	0.101	0.046	2.189	**0.029**
	Country : landscape	-0.078	0.066	1.214	0.225
	SNH type : landscape	-0.069	0.054	1.286	0.199
	Aphid density	0.030	0.036	0.828	0.408
	Flower abundance	0.026	0.035	0.749	0.454
	Flower richness	0.015	0.025	0.593	0.553
Abundance*	Landscape	0.178	0.072	2.461	**0.014**
	Country	-0.129	0.090	1.424	0.154
	Country : landscape	-0.163	0.141	1.162	0.245
	SNH shape	0.035	0.047	0.743	0.457
E. balteatus	Country	0.259	0.136	1.914	0.056
	SNH type	0.362	0.057	6.360	**< 0.001**
	Aphid density	0.320	0.101	3.165	**0.002**
	Flower abundance	-0.143	0.089	1.596	0.110
	Country : SNH type	0.521	0.111	4.699	**< 0.001**
	Country : aphids	0.267	0.207	1.292	0.196
	Landscape	-0.097	0.096	1.012	0.312
	SNH shape	-0.021	0.057	0.363	0.717
	Country : SNH shape	-0.205	0.112	1.826	0.068

* without the dominant aphidophagous species *E. balteatus*

Table 3.4 Model-averaging results of the top-ranked models (delta AICc < 2) for non-aphidophagous hoverflies in semi-natural habitats. Significant results (P < 0.05) are shown in bold.

Dependent variable	Predictor(s)	Estimate	Adjusted SE	z	P
Species richness	Landscape	0.172	0.043	4.052	**< 0.001**
	Flower richness	0.046	0.037	1.244	0.213
	SNH shape	0.029	0.036	0.798	0.425
Abundance	Country	0.382	0.112	3.400	**< 0.001**
	SNH shape	0.035	0.057	0.617	0.537
	SNH type	0.067	0.054	1.228	0.219
	Landscape	0.474	0.093	5.085	**< 0.001**
	Flower richness	0.141	0.065	2.173	**0.030**
	Country : SNH type	0.199	0.106	1.883	0.060
	SNH shape : SNH type	-0.183	0.112	1.636	0.102
	SNH shape : landscape	0.336	0.147	2.291	**0.022**
	Country : SNH shape	-0.252	0.150	1.679	0.093
	Country : landscape	-0.278	0.185	1.497	0.134
	Country : flower richness	0.153	0.126	1.220	0.222
	SNH type : landscape	-0.134	0.113	1.184	0.237

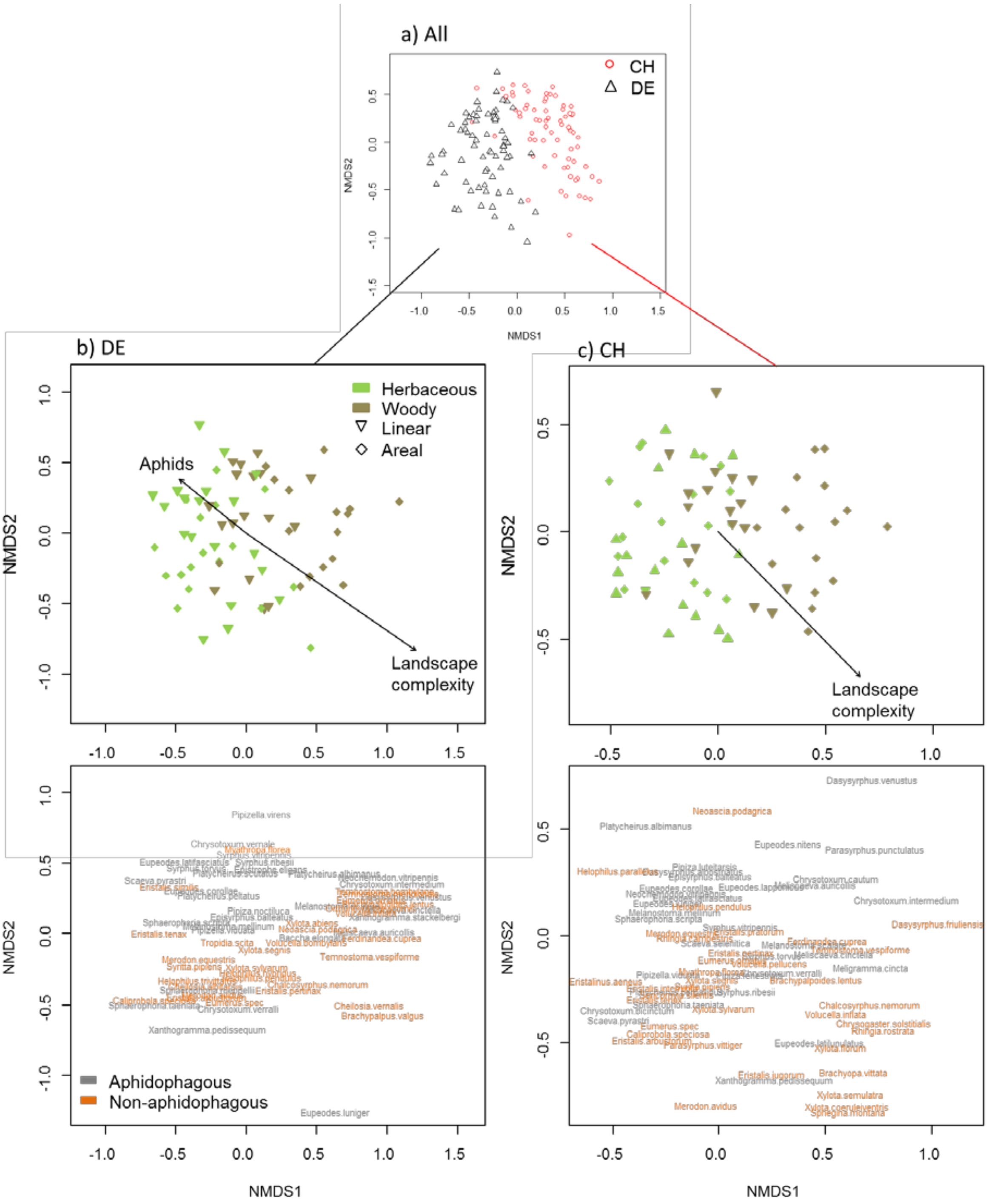

Figure 3.1 Relationships of a) overall hoverfly species composition to country (CH = Switzerland, DE = Germany), and the hoverfly species compositions of b) Germany (DE) and c) Switzerland (CH) to environmental variables. In b) and c) the upper panel show the sites (69 SNH, respectively) and significant environmental variables, the lower panel show the hoverfly species distribution. For statistics see Table 3.1.

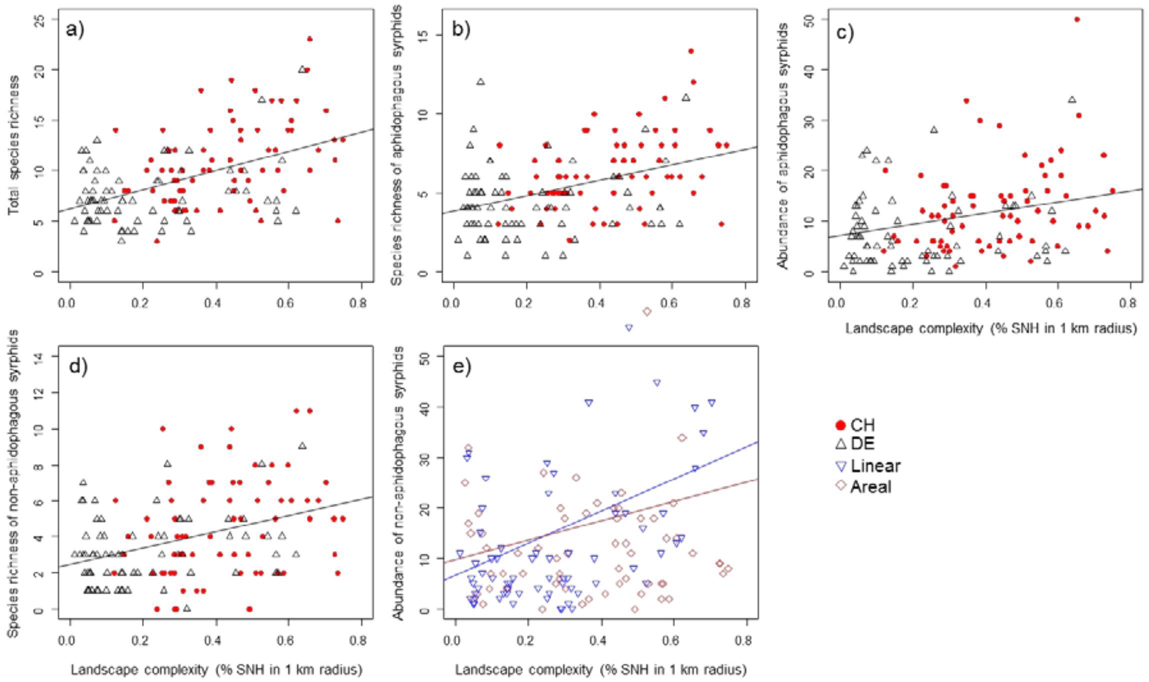

Figure 3.2 Positive effects of landscape complexity (% SNH in 1 km radius) on a) total species richness of hoverflies, b) species richness of aphidophagous hoverflies, c) abundance of aphidophagous hoverflies (without E. balteatus), d) species richness of non-aphidophagous hoverflies, and e) abundance of non-aphidophagous hoverflies (significant only for linear SNH) over all investigated SNH (35 landscapes, 138 individual habitats).

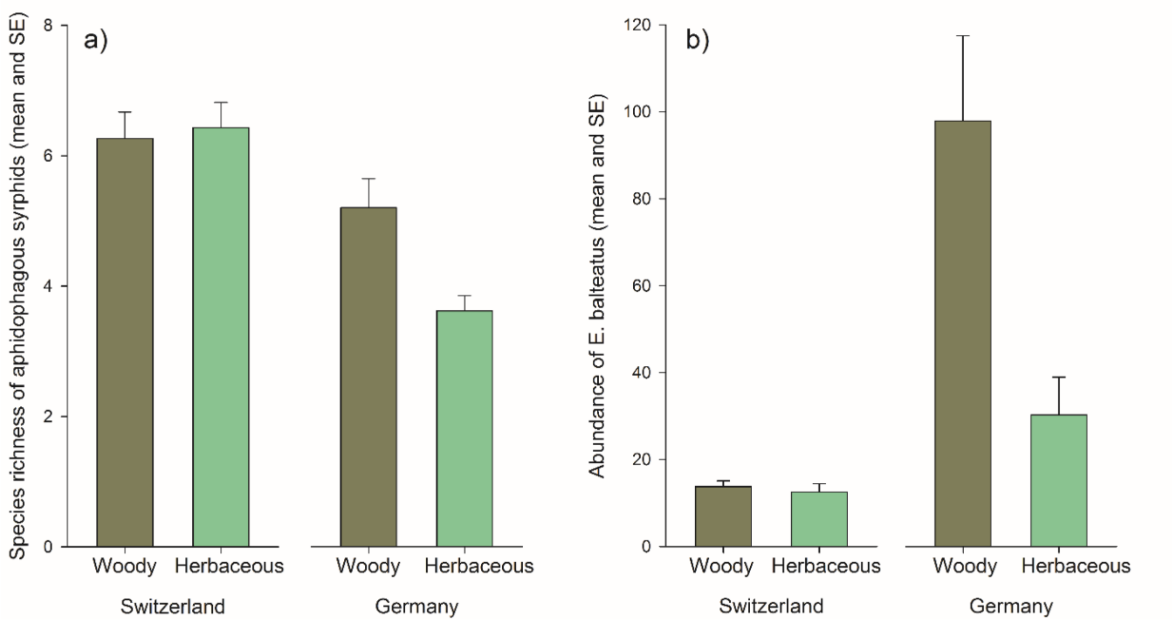

Figure 3.3 Interactive effects of SNH type and country for a) species richness of aphidophagous hoverflies and b) abundance of the dominant species Episyrphus balteatus. For statistics see Table 3.2.

3.4 Discussion

3.4.1 SNH at the landscape and local scale influence hoverfly species compositions

The hoverfly species compositions in Switzerland and Germany were driven in a similar way by SNH type, SNH shape and landscape complexity. As expected, the four investigated SNH types – areal woody, linear woody, areal herbaceous, and linear herbaceous – were characterised by distinct hoverfly assemblages. This reflects the occurrence of habitat specialists within both functional groups preferring either woody habitats (e.g. *Temnostoma spec.* and *Meliscaeva spec.*) or open habitats (e.g. *Eumerus spec*. and *Eupeodes spec*.). Moreover, hoverfly assemblages in both countries were influenced by the surrounding landscape complexity, indicating that complex landscapes host different and more species-rich (see below) assemblages than simple landscapes (e.g. Burgio & Sommaggio 2007; Schweiger *et al.* 2007). Thereby, a large number, in particular of non-aphidophagous species, were more abundant in complex landscapes (Fig. 1). In Germany, we also found aphid density as a determinant of the hoverfly composition. SNHs offering a high amount of aphids, may favour the occurrence of aphidophagous species (for example *E. baltetatus*, see below) and can therefore drive hoverfly assemblages.

However, although the effects of SNH type, SNH shape and landscape complexity were highly significant in our multivariate analysis, the R^2 values were rather low indicating a considerable species overlap among SNH and landscapes. Most hoverfly species in agricultural landscapes are highly mobile and generalist species can exist in various habitats (*Bańkowska 1980; Franke & Zucchi 1996;* Schweiger *et al.* 2007; *Speight 2014*). Moreover, most of these species are considered polylectic (Branquart & Hemptinne 2000; Speight 2014), which may explain why we did not found any significant effect of flower abundance and richness on hoverfly assemblages.

3.4.2 Effects of the semi-natural habitat type and shape can vary between countries

Total hoverfly species richness and species richness of non-aphidophagous hoverflies did not significantly differ between the SNH types and shapes. This may reflect on the one hand the high ecological tolerance of the mostly generalist hoverfly species with broad ecological niches occurring in agricultural landscapes. On the other hand, this indicates that, at least for non-aphidophagous species, a similar number of species preferred either woody or herbaceous habitats. One might have expected that linear SNH generally contain a lower species richness and abundance of hoverflies than their areal counterparts, due to the smaller area, disproportionally larger edge habitat and often associated reduced resource availability and heterogeneity. However, habitat quality is not sufficiently described by habitat size alone *(*Kleijn & van Langevelde 2006*)*, and small patches offering a large number of flower resources might favour hoverflies more than large patches with low flower resources *(*Meyer, Jauker & Steffan-Dewenter 2009*;* Hänke et al. 2009).

In contrast, the species richness of aphidophagous hoverflies was affected by the SNH type, but only in Germany. Here, more aphidophagous species occurred in woody than herbaceous SNH. Woody SNH might therefore provide shelter from harsh weather conditions and predators or more suitable resting sites for aphidophagous hoverflies than herbaceous SNH (Sutherland et al. 2001). Moreover, aphidophagous hoverflies often use woody habitats as overwintering sites (Hondelmann & Poehling 2007). Like in other studies in Central European agricultural landscapes, the aphidophagous species *E. balteatus* was the dominant hoverfly (Tenhumberg & Poehling 1995; Hänke *et al.* 2009; Meyer, Jauker & Steffan-Dewenter 2009; Trzciński & Piekarska-Boniecka 2013). Similar to species richness of aphidophagous hoverflies, we found *E. balteatus* to prefer woody SNH types in Germany, while we found no such preference in Switzerland. The preference of *E. balteatus* to hover in open patches near woody habitats (e.g. hedgerows, forest edges, paths in woodland) has been reported by Röder (1990), Sarthou *et al.* (2005), and Speight (2014). The unequal importance of SNH types between Switzerland and Germany may be explained by at least two reasons. First, the drier weather conditions in Germany compared to Switzerland (~ 40% more precipitation in CH) might be especially pronounced in open herbaceous habitats (e.g. short vegetation cover). Thus, in Germany woody habitats can offer shelter from these conditions and may explain the preference of many aphidophagous hoverflies for woody SNH. Several species depend on a humid environment for oviposition and larval development and, such as *E. balteatus*, are weakly sclerotized and have to avoid dehydration (Röder 1990). Second, swiss herbaceous SNH are more suitable for aphidophagous hoverflies than herbaceous SNH in Germany. Since flower abundance ($\chi^2 = 0.373$, $P = 0.542$) as well as flower richness ($\chi^2 = 1.095$, $P = 0.295$) of herbaceous SNH were not significantly different between the two countries, and, according to our findings do not play a major role driving aphidophagous hoverflies in the study regions (see below), possibly varying vegetation composition could be a further explanation. In fact, herbaceous SNH in Switzerland are, in contrast to those in Germany, often extensively managed grasslands or sown wildflower habitats part of agri-environmental schemes (AES), possibly offering less disturbed habitat or more suitable resource plant species (e.g. Apiaceae) for hoverflies. This explanation is corroborated by our finding that species richness in particular of aphidophagous hoverflies was considerably higher in Swiss compared to German herbaceous habitats.

3.4.3 Effects of local resources (flower abundance, flower richness, aphid density)

We found no positive effects of flower abundance and richness on hoverfly species richness, neither for total hoverflies nor for the two functional groups. We expected flower resources to have a positive effect, since adult hoverflies depend on nectar for energy and pollen for sexual maturation (Schneider 1948; Hickman, Lövei & Wratten 1995; Irvin *et al.* 1999; Branquart & Hemptinne 2000), and it has indeed been found that provisioning of flower resources can promote local hoverfly abundance and diversity in agricultural landscapes (Meyer, Jauker & Steffan-Dewenter 2009; Hänke *et al.* 2009; Tschumi *et al.* 2015). However, most ‘anthropophilic’ hoverflies inhabiting human dominated landscapes are generalists with high dispersal capacities and polylectic species, which are able to utilize a broad range of plant species (Branquart & Hemptinne 2000; Speight 2014). They are therefore able to exploit resources over large distances (Speight 2014), which may explain the low importance of local flower resources within SNH for hoverflies in our study. In contrast to species richness, the abundance of non-aphidophagous hoverflies was positively related to flower richness. Hence, the occurrence of individuals within this functional group can be favoured by the conservation or creation of flower rich SNH. High flower richness can contribute to a continuous and extended flowering period (through staggered phenologies of plant species) throughout the year, resulting in temporally more stable resource availability (Ebeling *et al.* 2008).

Specialized natural enemies are predicted to be positively related to the density of their prey or host taxa (e.g. Freier *et al.* 2007). In agreement with this prediction, we found a positive association of the dominant aphidophagous *E. baltatus* with aphid density. The larvae of this species are often among the most important predators of aphids (e.g. Tenhumberg & Poehling 1995). In conclusion, our findings suggest that aphidophagous hoverflies such as *E. balteatus* are locally more strongly driven by habitats supporting high densities of aphids as larval food source than by habitats providing high amounts of flower resources.

3.4.4 Hoverflies benefit from complex landscapes

Our results provide evidence that complex agricultural landscapes favour species richness of hoverflies in SNH. Importantly, this is consistent for both functional groups across countries. Non-aphidophagous species may benefit from higher landscape complexity, because they require multiple resources for larval development (e.g. microhabitats like dead wood, litter, sap runs, host plants, standing water and damp tree-holes). These resources are generally not provided by crop fields (Rotheray 1993) and oviposition sites of non-aphidophagous hoverflies in agricultural landscapes are therefore mostly restricted to SNH (Raymond *et al.* 2014). The abundance of non-aphidophagous hoverflies was also positively related to landscape complexity, however, only in linear SNH. This indicates that linear SNH can be more vulnerable to landscape simplification than areal SNH, where abundances of non-aphidophagous hoverflies can be high even in simple landscapes. A similar pattern was found for the abundance of long-legged flies (Dolichopodidae) (unpublished own data).

Our findings refine the hypothesis from Hänke (2012) and Inclán *et al.* (2016) that some very abundant aphidophagous species (i.e. *E. balteatus*) can cope to some extent with landscape simplification, but that most aphidophagous species similarly to non-aphidophagous ones benefit from landscape complexity. The high aphid densities in crop fields often provide an important larval food resource for aphidophagous hoverflies in agroecosystems (Tenhumberg & Poehling 1995; Raymond *et al.* 2014; Meyer, Jauker & Steffan-Dewenter 2009). We found many abundant crop-aphidophagous species in our study (e.g. *Episyrphus spec.*, *Eupeodes spec.*, *Melanostoma spec.*, *Sphaerophoria spec.* and *Syrphus spec.*; Röder 1990; Speight 2014) that may cope with or even benefit from a low landscape complexity due to a larger area of crops as larval feeding habitat (Jauker *et al.* 2009). Indeed, *E. balteatus* was not affected by landscape complexity. However, our results suggest that (except for *E. balteatus*) aphidophagous hoverflies strongly benefit from SNH at the landscape scale.

3.5 Conclusions and management implications

We recommend that management for the conservation and restoration of diverse hoverfly communities, and the promotion of their key role in natural aphid pest control in agroecosystems, should focus on the conservation and creation of complex landscapes characterised by a high proportion of different SNH types. Based on data from 138 semi-natural habitats, our results provide evidence that complex landscapes favour, consistently across countries, species richness and abundance of non-aphidophagous and ahidophagous hoverflies. The strongly enhanced species richness and abundance of aphidophagous hoverflies in complex landscapes are likely associated with increased aphid pest control services in complex agricultural landscapes. Many of the enhanced common aphidophagous and non-apidophagous species play also a significant role as pollinators of a series of important crops such as oilseed rape. Hoverflies in areal habitats were less affected by landscape simplification than in linear habitats, supporting the hypothesis that wide SNH sustain populations of beneficial insects better than narrow SNH. Our findings indicate that habitat management to foster hoverflies regulating crop aphids in agroecosystems should not only consider improved floral resource provisioning, but also the promotion of alternative aphid preys in SNH, e.g. through the conservation and restoration of their preferred host plant communities. Such management guidelines have to consider regional differences in SNH characteristics in order to promote the most promising SNH for hoverflies. Woody SNH, for example, seemed to be most suitable in favouring aphidophagous hoverflies in Germany, while herbaceous SNH were equally important in Switzerland. Hence, to support diverse hoverfly assemblages and associated regulatory ecological services, agricultural landscapes should consist of a high amount of different types of SNH.

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Data accessibility

The data used in this study are available from the Dryad Digital Repository [*will be inserted in case of acceptance*].

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3.7 Supplementary Material

Table S3.1 Species list of hoverflies observed in semi-natural habitats in Switzerland and Germany during four study periods in 2013-2014.

Species	Functional group	Switzerland	Germany
Baccha elongata	aphidophagous	0	32
Brachyopa vittata	non-aphidophagous	1	0
Brachypalpoides lentus	non-aphidophagous	15	5
Brchypalpus valgus	non-aphidophagous	0	1
Caliprobola speciosa	non-aphidophagous	4	1
Chalcosyrphus nemorum	non-aphidophagous	2	25
Cheilosia albitarsis	non-aphidophagous	0	4
Cheilosia vernalis	non-aphidophagous	0	2
Chrysogaster solstitialis	non-aphidophagous	1	0
Chrysotoxum bicinctum	aphidophagous	1	0
Chrysotoxum cautum	aphidophagous	4	0
Chrysotoxum intermedium	aphidophagous	1	1
Chrysotoxum vernale	aphidophagous	0	1
Chrysotoxum verralli	aphidophagous	2	6
Dasysyrphus albostriatus	aphidophagous	3	0
Dasysyrphus friuliensis	non-aphidophagous	1	0
Dasysyrphus venustus	aphidophagous	1	2
Epistrophe eligans	aphidophagous	0	2
Episyrphus balteatus	aphidophagous	909	4455
Eristalinus aeneus	non-aphidophagous	2	0
Eristalis arbustorum	non-aphidophagous	17	39
Eristalis interrupta	non-aphidophagous	31	0
Eristalis jugorum	non-aphidophagous	1	0
Eristalis pertinax	non-aphidophagous	55	58
Eristalis similis	non-aphidophagous	3	2
Eristalis tenax	non-aphidophagous	220	4
Eumerus ornatus	non-aphidophagous	3	1
Eumerus strigatus(sogdianus)	non-aphidophagous	15	95
Eupeodes corollae	aphidophagous	244	100
Eupeodes lapponicus	aphidophagous	51	0
Eupeodes latifasciatus	aphidophagous	9	6
Eupeodes latilunulatus	aphidophagous	1	0
Eupeodes luniger	aphidophagous	5	2
Eupeodes nitens	aphidophagous	3	0
Ferdinandea cuprea	non-aphidophagous	92	31
Species	Functional group	Switzerland	Germany

Helophilus hybridus	non-aphidophagous	0	10
Helophilus pendulus	non-aphidophagous	21	970
Helophilus trivittatus	non-aphidophagous	8	20
Meligramma cincta	aphidophagous	7	0
Meliscaeva auricollis	aphidophagous	87	18
Meliscaeva cinctella	aphidophagous	21	1
Melanostoma mellinum	aphidophagous	115	182
Melanostoma scalare	aphidophagous	17	20
Merodon avidus	non-aphidophagous	2	3
Merodon equestris	non-aphidophagous	7	12
Myathropa florea	non-aphidophagous	96	2
Neoascia podagrica	non-aphidophagous	6	26
Neocnemodon vitripennis	aphidophagous	2	5
Orthonevra brevicornis	non-aphidophagous	0	1
Parasyrphus punctulatus	aphidophagous	1	0
Parasyrphus vittiger	non-aphidophagous	1	0
Pipiza fenestrata	aphidophagous	1	0
Pipiza luteitarsis	aphidophagous	1	0
Pipiza noctiluca	aphidophagous	0	4
Pipizella viduata	aphidophagous	2	2
Pipizella virens	aphidophagous	0	1
Pipizella spec	aphidophagous	0	2
Platycheirus albimanus	aphidophagous	5	13
Platycheirus peltatus	aphidophagous	0	4
Platycheirus perpallidus	aphidophagous	1	0
Platycheirus scutatus	aphidophagous	0	5
Rhingia campestris	non-aphidophagous	27	0
Rhingia rostrata	non-aphidophagous	4	0
Scaeva pyrastri	aphidophagous	16	3
Scaeva selenitica	aphidophagous	19	0
Sericomyia silentis	non-aphidophagous	1	0
Sphaerophoria rueppellii	aphidophagous	0	2
Sphaerophoria scripta	aphidophagous	158	109
Sphaerophoria taeniata	aphidophagous	4	1
Sphegina montana	non-aphidophagous	1	0
Syritta pipiens	non-aphidophagous	13	6
Syrphus ribesii	aphidophagous	22	30
Syrphus torvus	aphidophagous	20	5
Syrphus vitripennis	aphidophagous	32	32
Species	Functional group	Switzerland	Germany

Temnostoma bombylans	non-aphidophagous	0	8
Temnostoma meridionale	non-aphidophagous	0	2
Temnostoma vespiforme	non-aphidophagous	13	9
Tropidia scita	non-aphidophagous	0	12
Volucella bombylans	non-aphidophagous	0	6
Volucella inflata	non-aphidophagous	6	1
Volucella pellucens	non-aphidophagous	3	0
Xanthogramma pedissequum	aphidophagous	2	3
Xanthogramma stackelbergi	aphidophagous	0	7
Xylota abiens	non-aphidophagous	0	1
Xylota coeruleiventris	non-aphidophagous	1	0
Xylota florum	non-aphidophagous	2	0
Xylota segnis	non-aphidophagous	153	9
Xylota semulatra	non-aphidophagous	2	0
Xylota sylvarum	non-aphidophagous	10	1
Total individuals		2607	6423
Total species		69	62

Chapter 4 Aphids and their natural enemies in pumpkin fields respond differently to management, local and landscape features

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Highlights

- Natural enemies were best supported by enhancing flower resources in field margins
- Aphids and their enemies differed little between conventional and organic management
- Landscape complexity had no clear effect on pest control in pumpkin

Abstract

Natural enemies of agricultural pests can be limited by high farming intensity and the scarcity of important resources such as flowers and alternative prey. Thus, organic farming and the presence of seminatural habitats adjacent to crop fields or in the surrounding landscape may enhance pest control. However, studies in vegetable crops investigating combined effects of field management, adjacent habitats and landscape complexity are still rare. We measured natural field densities of aphids and their enemies in 18 pumpkin fields in Southwest Germany. Increasing flower abundance in field margins tended to decrease aphid densities and significantly increased densities of natural enemies, especially of lady beetles, parasitoids, lacewings and aphid gall midges. Organic management and landscape complexity (measured as proportion of agriculture in 1 km radius) had no clear effect on pest control. Our results indicate that abundant flower resources in field margins are the most promising tool to enhance natural aphid control in pumpkin.

Keywords

Aphid; biological control; flower resources; *Cucurbita maxima;* landscape, management

4.1 Introduction

Today, 40% of the worldwide land area is used for agriculture (FAOSTAT 2013). During the last decades, seminatural habitats in many agricultural landscapes were converted to cropland and the use of agrochemicals and mechanical input increased (Tscharntke et al., 2005). This intensification can disrupt ecosystem services including pollination and natural pest control which are important regulating services for agriculture (Tscharntke et al., 2012). Benefits of natural pest control are especially high in organic farming systems, where the use of pesticides is limited, and can deliver a monetary value of about US \$ 50 ha^{-1} (Sandhu et al., 2008). However, integrated pest management (US \$ 33 ha^{-1}, Landis et al., 2008) and even intensive conventional management benefit from natural pest control (~US \$ 12 ha^{-1}, Losey and Vaughan, 2006), too.

Environmentally friendly farming (or ecological intensification) replaces anthropogenic inputs (such as pesticides, inorganic fertilizers, energy) by ecosystem service management (Bommarco et al., 2013). By managing the service-providing organisms environmentally friendly farming can also be very productive while minimizing negative environmental impacts (Bommarco et al., 2013; Tscharntke et al., 2012). Environmentally friendly farming includes management practices, such as reduced pesticide use or organic management, whereby pest control agents such as parasitoids are favoured and natural pest control can be enhanced (Bengtsson et al., 2005; Tuck et al., 2014; Lu et al., 2015). In addition, the use of cover crops and diversified crop rotations can contribute to the avoidance of insect pest outbreaks and provide natural enemies with a higher diversity of resources than landscapes that are highly dominated by single crop types (Bommarco et al., 2013). Environmentally friendly farming also includes the management of seminatural habitats in the surrounding landscape. Seminatural habitats promote pest control by offering shelter, overwintering sites and alternative food resources to beneficial organisms (Holland et al., 2016). For example, Tschumi et al. (2015) and Tschumi et al. (2016a) recently showed that flower strips adjacent to wheat fields can strongly enhance pest control services resulting in 10% higher crop yield. Complex landscapes with a higher proportion of seminatural habitats enhance the abundance of natural enemies and can increase pest control services (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Rusch et al., 2016). However, evidence for this is mainly based on studies with cereals (64% Bianchi et al., 2006; 53% Rusch et al., 2016). In contrast, studies regarding natural enemies and pest control in vegetables are rare, especially those considering simultaneous effects of field management and seminatural habitats at the local and landscape scale.

Pumpkin (*Cucurbita maxima*) is a well-suited vegetable to apply conservation pest control of aphids. First, compared to other vegetables pumpkin has a relatively long residence time on the field (12 – 21 weeks). Thus, there is sufficient time to build up natural enemy populations. Second, there is a potential to reduce insecticide applications that are used by farmers to control aphids and viruses transmitted by them. Third, the marketable pumpkin fruit is not infested with aphids or beneficial organisms. Thus, the use of natural enemies for aphid suppression in pumpkin therefore does not result in problems with consumer acceptance.

The aim of our study was to investigate how aphids and their natural enemies in pumpkin fields respond to local management such as organic farming, to adjacent seminatural habitats and to the proportion of agriculture in the surrounding landscape. Our hypotheses are:

1. Natural enemies: Aphids on pumpkin are reduced at high densities of natural enemies (top-down control).
2. Management: Organic farming favours aphid enemies more than aphids, thereby reducing aphid densities.
3. Adjacent habitat: Seminatural habitats adjacent to pumpkin fields enhance natural aphid control.
4. Floral resources: Aphid control increases with the abundance of flowers in adjacent habitats.
5. Landscape: Aphid control decreases with increasing proportion of agriculture in the surrounding landscape.

4.2 Material and methods

4.2.1 Study sites

The study was done in the Upper Rhine Valley between Kandel and Ludwigshafen, Germany (N: 49°4’ to 49°27’, E: 8°28’ to 8°6’), a region characterized by intensive agriculture (cereals, maize, vegetables). The region has a temperate climate with an annual mean temperature of 10.5 °C and precipitation of 667 mm (station Landau, German Weather Service). The elevation ranges from 90 to 150 m a.s.l.

In 2014, we selected 18 commercial pumpkin fields (*Cucurbita maxima* Duchesne cv. Hokkaido) with a size of 3 ± 2.6 ha and a minimum width of 52 m. Six fields were each bordered either by a herbaceous seminatural habitat (SNH), a woody SNH or another crop field (Fig. 1). Seminatural habitats (SNH) were defined as any habitat containing a community of non-crop plant species with a minimum width of 1.5 m, a minimum length of 50 m and a minimum size of 150 m^2 (Holland et al., 2014). Woody SNH had at least 30% shrub/tree canopy cover. Half of the pumpkin fields were managed organically (EU-Eco regulation 834/2007) and the other half conventionally. In addition, the pumpkin fields were located in landscapes differing in the proportion of agriculture in 1 km radius around the focal field (28-91%). A radius of 1 km was identified as an important scale for natural enemies and biological control patterns (Rusch et al., 2013; Rusch et al., 2016). Habitats around the focal field were mapped and classified in SNH, agriculture (annual herbaceous, perennial herbaceous and woody crops), urban areas, water bodies and other habitats. Land use classifications were ground-truthed at every site. The proportion of agriculture in 1 km radius was calculated using GIS. The minimum distance between fields was > 1.75 km avoiding overlap of the landscape sectors (only marginal overlap for one pair). Management, adjacent habitat and landscape complexity (measured as proportion of agriculture in 1 km radius) varied independently of each other.

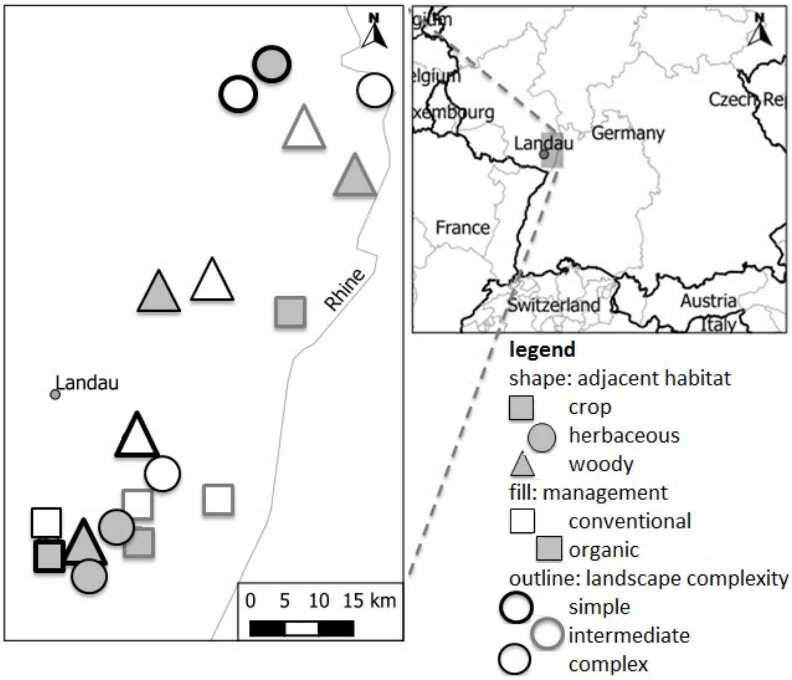


Figure 4.1 Location of the 18 pumpkin fields in the Upper Rhine Valley, Germany.

4.2.2 Sampling

We recorded the density of aphids (Hemiptera: Aphididae) and their natural enemies, which were aphid gall midges (Diptera: Cecidomyiidae, *Aphidoletes* sp.), lacewings (Neuroptera: Chrysopidae), lady beetles (Coleoptera: Coccinellidae), parasitic wasps (Hymenoptera: Braconidae, Aphidiinae), spiders (Araneae) and syrphid flies (Diptera: Syrphidae). Counts were performed along four transects per field at distances of 2, 10, 18, and 26 m from the edge to the field centre. The sampling effort was adapted to the aphid infestation (Ragsdale et al., 2007). When aphids were found on < 50% of the leaves, the density of aphids and natural enemies was sampled on 80 randomly selected leaves (20 per distance). When 50-80% of the leaves were infested, 40 leaves (10 per distance) and when infestation was > 80%, 20 leaves (5 per distance) were sampled. Leaf sampling was standardized by using mature leaves (which are usually the most infested) of a similar size (ca. 300 cm^2). Fields were investigated six times in 2014 (calendar week 22, 24, 25, 26, 28, 30) between the start of the growing season of pumpkin in May until the natural aphid population on the pumpkin plants vanishes by the end of July. We are aware that numbers of natural enemies are underestimated by these counts, because many natural enemies are mobile, acting at larger scales and many of them are nocturnal. We included all life-stages (eggs, larvae, adults and for spiders also spider webs) for natural enemy quantification. Parasitized aphids (mummies) were used to measure parasitism.

Flower abundance was estimated as the total number of flowers of all flowering plant species at a specific date. Flower abundance was measured three times (calendar week 22, 26, 29) in 20 plots per adjacent SNH. Each sampling plot for flower abundance had a surface of 1 x 1m, and flowers up to 2m above ground were considered.

4.2.3 Statistical Analyses

The data were analyzed in R 3.3.1 (R Core Team, 2015). Arthropod densities were standardized as mean number of individuals per leaf, field and sampling. Flower abundance was standardized to a mean number per plot and sampling. In order to determine how management (factor: organic vs. conventional), adjacent habitat type (factor: crop, herbaceous, woody), flower abundance in the adjacent habitat (continuous) and proportion of agriculture in 1 km radius (continuous) influenced the density of aphids and natural enemies we fitted linear models to the data. Density data was log-transformed to normalize the data distribution. We analyzed densities separately for each sampling time, wherever possible, because Chaplin-Kramer et al. (2013) found that seasonal averages may mask relations of pests to natural enemies and SNH. Therefore we used total aphid density per leaf, aphid density per sampling and changes in aphid density *delta* (Eq 1) between samplings as response variables for aphids.

Changes in aphid density from one sampling to the next sampling (*delta*, Eq1) were calculated based on Chaplin-Kramer et al. (2013).

$$delta = \frac{\ln(\mathrm{Ay})}{\ln(\mathrm{Ax})} \qquad \text{Eq 1}$$

The aphid densities per sampling were natural log-transformed and then the changes in aphid density, *delta*, was calculated by the division of the aphid density A_y at the later sampling divided by the aphid density of the previous sampling A_x.

Except for spiders, we sampled too few natural enemies to analyze them separately per sampling. In models for natural enemies the total aphid density was included as an explanatory variable to analyze relationships between aphids and natural enemies. We performed an automated model selection (dredge function) based on Akaike´s information criterion for small sample sizes (AICc) (package “MuMIn”, Barton, 2015). Models were checked visually for normality and homoscedasticity of residuals and outliers. Models containing variables with p-values > 0.1 were not chosen, unless these variables were also part of an interaction term. Outliers were identified visually by the Cook´s distance (>1). The significance of the effects of factors was tested with F-tests (package “car”, Fox and Weisberg, 2010) and post-hoc Tukey tests (package “multcomp”, Hothorn et al., 2008). Pearson correlation was checked for all possible pairs of explanatory variables (Table S4.1). The explanatory variables included in the best models were not significantly correlated with each other ($r < 0.6$, Table S4.1).

4.3 Results

Overall we found 78331 aphids (mainly *Aphis fabae* Scopoli, *Aphis gossypii* Glover), 376 lacewings (mainly eggs; mainly *Chrysoperla carnea* agg. Stephens), 353 spiders (2/3 spiders, 1/3 webs; mainly Linyphiidae such as *Tenuiphanthes tenuis* Blackwall, *Phylloneta impressa* L. Koch (Theridiidae) and some Araneidae), 209 lady beetles (eggs, adults and larvae; mainly *Coccinella septempunctata* Linnaeus and *Harmonia axyridis* Pallas), 207 parasitized aphids, 114 gall midges (mainly larvae; *Aphidoletes* sp.) and 70 syrphid flies (eggs and larvae).

4.3.1 Relationships of aphids and natural enemies

The total natural enemy density and densities of aphid gall midges, lady beetles, parasitic wasps, spiders and syrphid flies were positively correlated to aphid density (Table 4.2, Fig. 4.2). Only lacewings were not significantly correlated to aphid densities (Table 4.2, Fig. 4.2). Spiders most strongly responded to the abundance of aphids at the beginning and end of the infestation period (Table 4.2).

4.3.2 Management

Management had significant effects only on aphids, while natural enemies were not influenced (Tables 4.1 and 4.2). Aphid populations in mid and end of June stagnated or declined more strongly in conventional than in organic fields (Table 4.1, Fig. 4.3). The slower changes of aphid density at the end of June in organic fields (Table 4.1) lead to four times higher aphid abundances at the end of July (Table 4.1) in organic compared to conventional fields ($t_{16} = 3.7$, $p = 0.002$, $R^2 = 0.43$).

4.3.3 Adjacent habitat

Adjacent habitat type was only selected once in the best models (Tables 4.1 and 4.2). Spider density at the end of May was lower in fields next to woody habitats than in field-field situations ($t_{10} = -2.9$, $p = 0.03$, Fig. S4.1). Flowers tended to be more abundant in herbaceous SNH than in crops ($t_{10} = 2.0$, $p = 0.061$). Flower abundance in the adjacent SNH tended to reduce the aphid density within pumpkin fields (Table 4.1, Fig. 4.4A). Further, increasing flower abundance increased the total natural enemy density (Fig. 4.4B), and in particular, densities of lacewings (Fig. 4.4C), lady beetles (Fig. 4.4D), parasitized aphids (= parasitsm, Fig. 4.4E) and aphid gall midges (Fig. 4.4F; Table 4.2).

4.3.4 Landscape

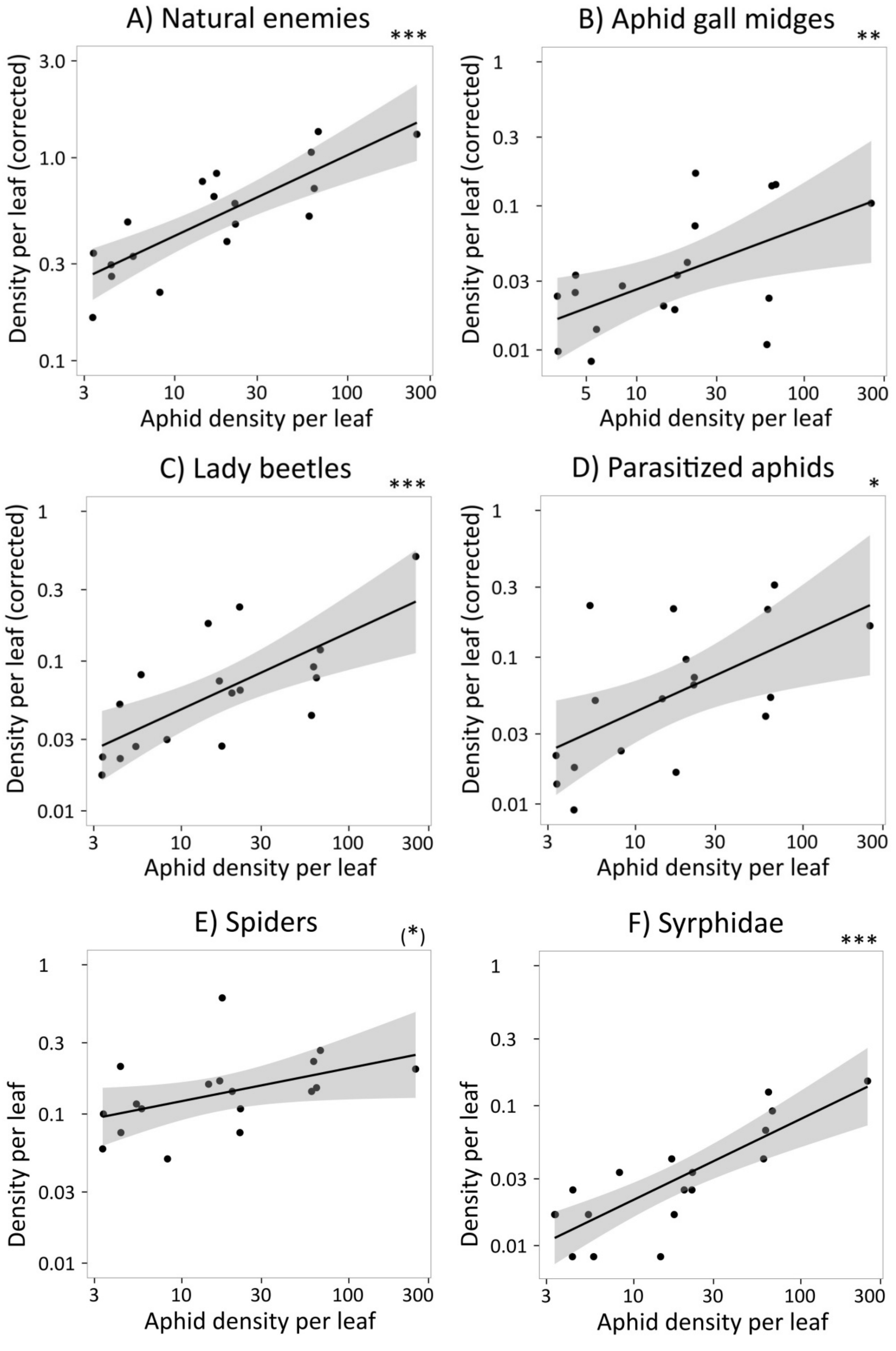
Fields with a higher proportion of agriculture in the surrounding landscape had lower densities of aphids (Fig. 4.5A) and were less infested by aphids early in the growing season at the end of May (Fig. 4.5B; Table 4.1). Densities of aphid gall midges (Fig. 4.5C) and lacewings (Fig. 4.5D) also decreased with increasing proportion of agriculture in the surrounding landscape, whereas lady beetles were more abundant in fields with more agriculture in the surroundings (Fig. 4.5E; Table 4.2).

Table 4.1 Effects of local (management, adjacent SNH type, flowers in this SNH) and landscape variables (% agriculture in 1 km radius) on aphid density per leaf and on changes of aphid densities from one sampling to the next. All models with delta AICc < 2 are shown, that are better than the null model and contain predictors with $p < 0.1$ in addition to the predictors included in the best model. For the aphid density in the 2nd to 5th sampling, the null model had the lowest AICc (not shown). For the changes of aphid densities from the 1st, 4th and 5th sampling, the null model had the lowest AICc (not shown).

Response	**Reference period**	**Explanatory**	**t/ F**	**value**	**p**	**R^2**	**AICc**
Aphid density	Whole season	%Agriculture	t_{15}	-2.5	0.023	0.22	32.2
		Flowers in SNH	t_{15}	-2.1	0.054		
	1st sampling	%Agriculture	t_{16}	-2.4	0.031	0.21	33.8
	6th sampling	Management	$F_{1,16}$	2.2	0.044	0.18	44.8
Changes of aphid densities	2nd sampling	Management	$F_{1,16}$	7.7	0.014	0.28	34.7
	3rd sampling	Management	$F_{1,16}$	3.1	0.096	0.11	13.9

Table 4.2 Effects of local (in-field aphid density, management, adjacent SNH type, flowers in this SNH) and landscape variables (% agriculture in 1 km radius) on natural enemy densities per leaf. All models with delta AICc < 2 are shown, that are better than the null model and contain predictors with $p < 0.1$ in addition to the predictors included in the best model. For aphid gall midges and lacewings, two competing models are shown. For other enemy groups, the best model was distinctly superior to the 2nd best model. All models refer to the whole sampling period, except for spider where numbers were sufficient for analyses per sampling date (but null models had lowest AICc from 3rd to 5th sampling period). The number e.g. in "Aphid_1st" indicates the number of the sampling.

Response	**Reference period**	**Alternative models**	**Explanatory**	**t/ F-value**		**p**	**R^2**	**AICc**
Natural enemies	whole season	none	Aphid_total	t_{15}	5.8	< 0.001	0.70	-8.4
			Flowers in SNH	t_{15}	3.7	0.0024		
spiders	whole season	none	Aphid_total	t_{16}	2.1	0.051	0.17	4.5
	1st sampling	none	Aphid_1st	t_{14}	2.7	0.017	0.42	4.0
			SNH type	$F_{2,14}$	4.1	0.039		
	2nd sampling	none	Aphid_1st	t_{16}	2.7	0.014	0.28	3.3
	6th sampling	none	Aphid_5th	t_{16}	3.6	0.0027	0.41	3.2
Aphid gall midges	whole season	mod1	Aphid_total	t_{15}	3.0	0.0091	0.51	20.9
			%Agriculture	t_{15}	-2.1	0.055		
		mod2	Aphid_total	t_{15}	4.2	< 0.001	0.50	21.2
			Flowers in SNH	t_{15}	2.0	0.064		
Lacewings	whole season	mod1	%Agriculture	t_{15}	-1.9	0.070	0.14	11.3
		mod2	Flowers in SNH	t_{15}	1.9	0.082	0.13	11.6
Lady beetles	whole season	none	Aphid_total	t_{14}	6.6	< 0.001	0.76	11.8
			Flowers in SNH	t_{14}	4.8	< 0.001		
			%Agriculture	t_{14}	2.4	0.033		
Parasitized aphids	whole season	none	Aphid_total	t_{15}	2.9	0.010	0.41	25.8
			Flowers in SNH	t_{15}	2.7	0.016		
Syrphid flies	whole season	none	Aphid_total	t_{16}	5.7	< 0.001	0.65	3.1


A) Natural enemies
***
Density per leaf (corrected)
3.0
1.0
0.3
0.1
3
10
30
100
300
Aphid density per leaf
B) Aphid gall midges
**
Density per leaf (corrected)
1
0.3
0.1
0.03
0.01
5
10
30
100
300
Aphid density per leaf
C) Lady beetles
***
Density per leaf (corrected)
1
0.3
0.1
0.03
0.01
3
10
30
100
300
Aphid density per leaf
D) Parasitized aphids
*
Density per leaf (corrected)
1
0.3
0.1
0.03
0.01
3
10
30
100
300
Aphid density per leaf
E) Spiders
(*)
Density per leaf
1
0.3
0.1
0.03
0.01
3
10
30
100
300
Aphid density per leaf
F) Syrphidae
***
Density per leaf
1
0.3
0.1
0.03
0.01
3
10
30
100
300
Aphid density per leaf

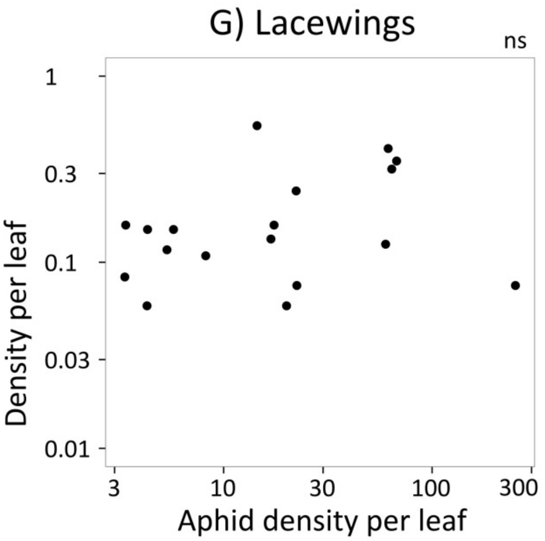


Figure 4.2 Density of natural enemies and aphids per leaf. All natural enemies of aphids were positively related to the total abundance of aphids (A-F), except for lacewings ($t_{16} = 1.1$, $p = 0.30$; G). Confidence intervals are marked in grey. (*) $p < 0.1$, '*' $p < 0.05$, '**' $p < 0.01$, '***' $p < 0.001$. Densities were corrected for the residuals of other significant explanatory variables. For detailed statistics, see Table 4.2.

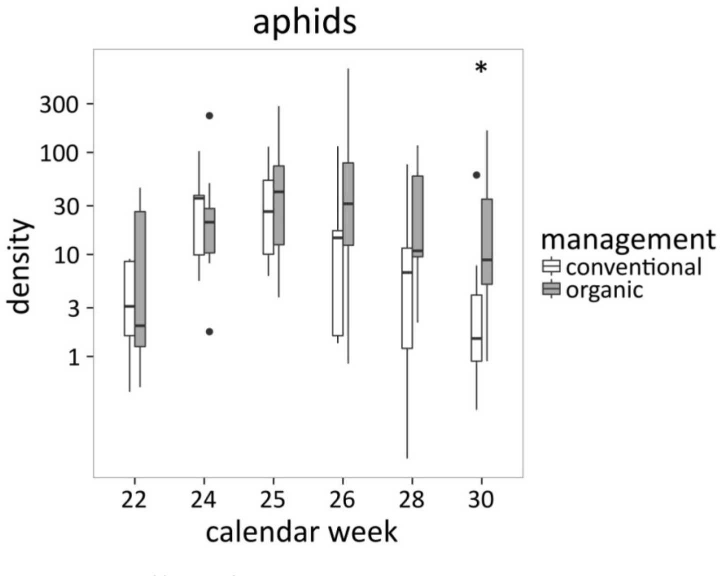


Figure 4.3 Effect of management on aphid densities. Aphid densities per leaf were significantly higher in organic compared to conventional fields at the end of July (calendar week 30).

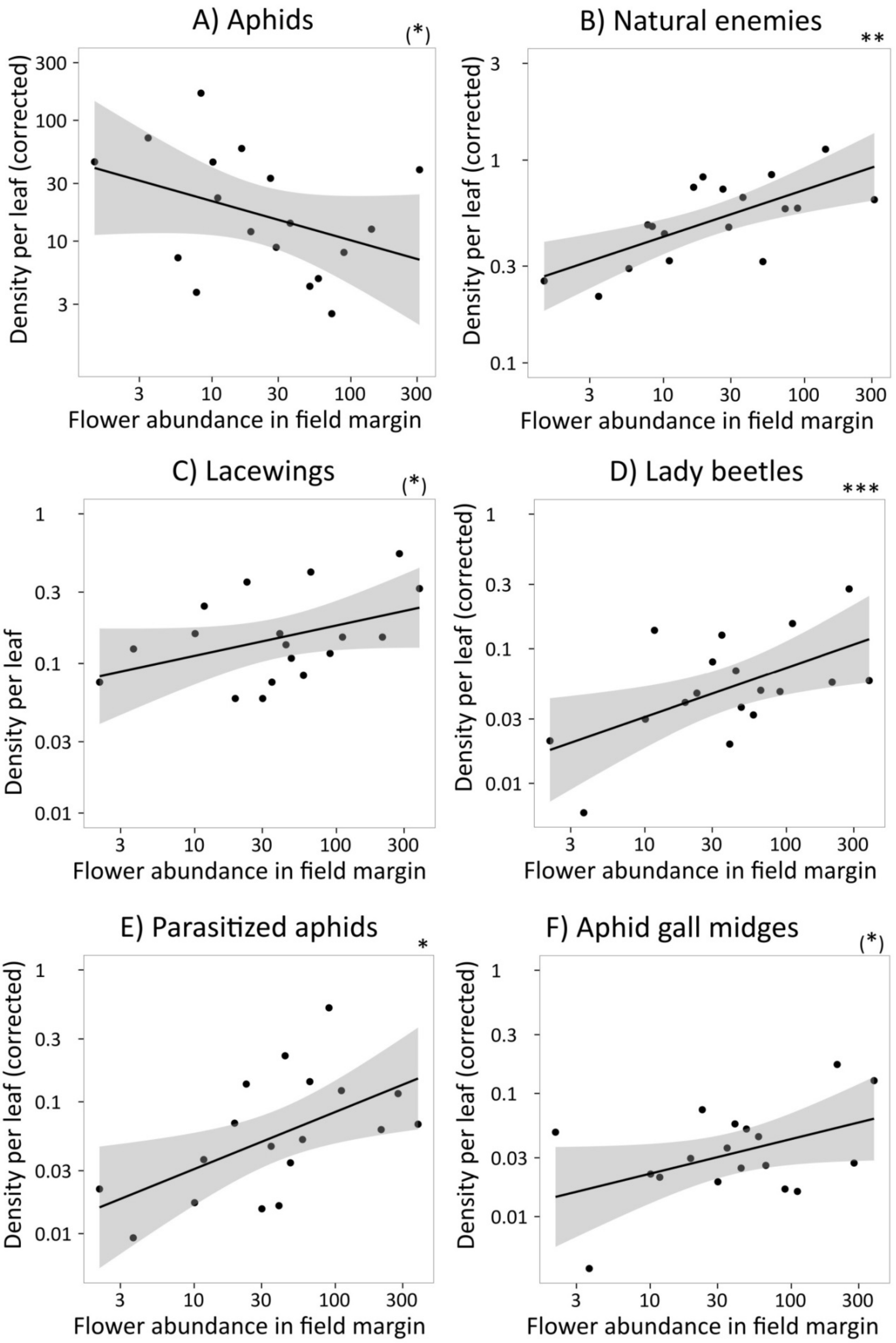


Figure 4.4 Flower abundance in field margins (per m^2) tended to reduce density per leaf of aphids (A) and enhanced density per leaf of natural enemies in the field (B), especially of lacewings (C), lady beetles (D), parasitized aphids (E) and aphid gall midges (F). (*) $p < 0.1$, ‘*’ $p < 0.05$, ‘**’ $p < 0.01$, ‘***’ $p < 0.001$. Densities were corrected for the residuals of other significant explanatory variables. For detailed statistics, see Tables 4.1 and 4.2.

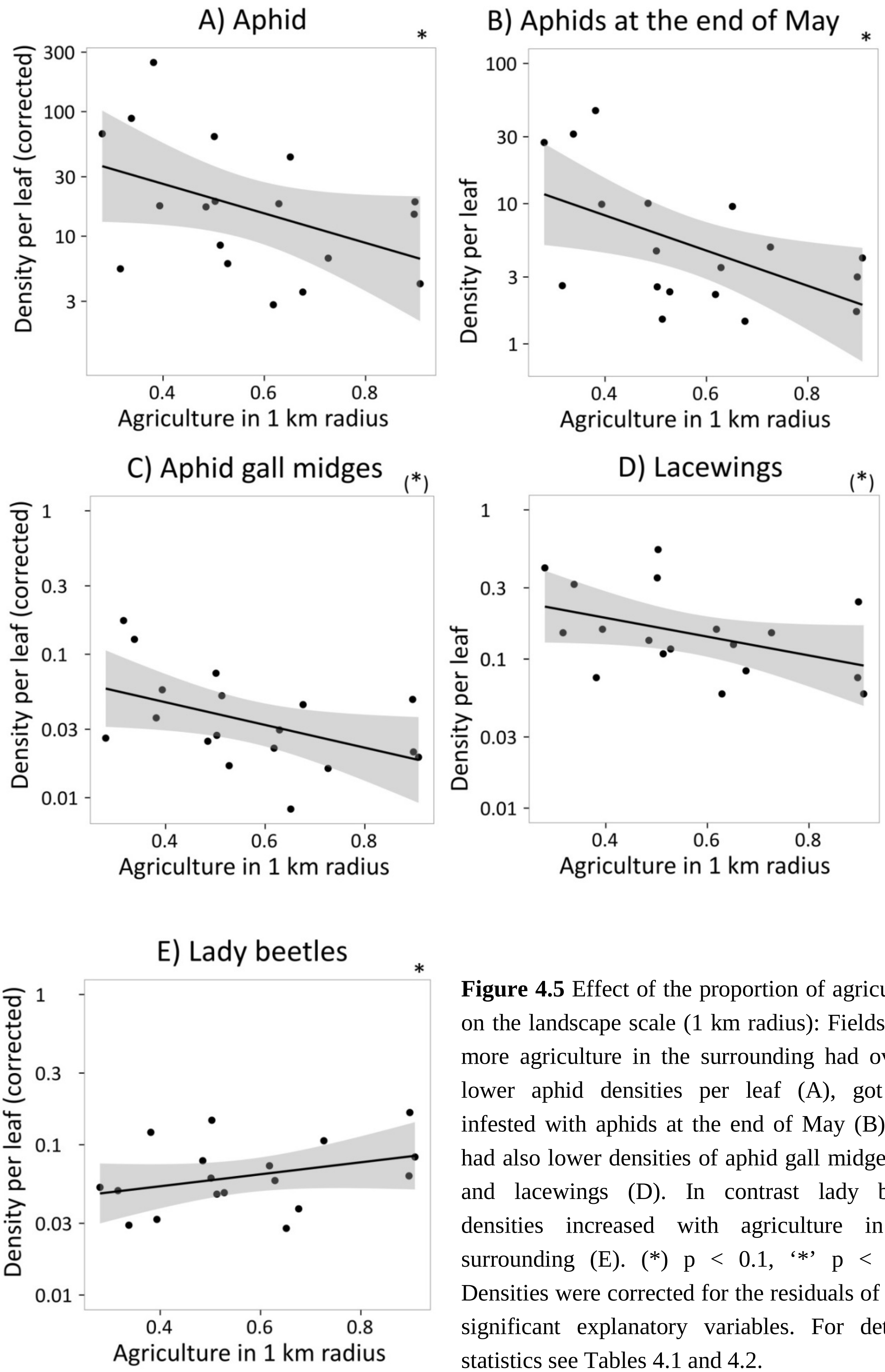


Figure 4.5 Effect of the proportion of agriculture on the landscape scale (1 km radius): Fields with more agriculture in the surrounding had overall lower aphid densities per leaf (A), got less infested with aphids at the end of May (B), and had also lower densities of aphid gall midges (C) and lacewings (D). In contrast lady beetle densities increased with agriculture in the surrounding (E). (*) $p < 0.1$, '*' $p < 0.05$. Densities were corrected for the residuals of other significant explanatory variables. For detailed statistics see Tables 4.1 and 4.2.

4.4. Discussion

4.4.1 Relationships of aphid and their natural enemies

In contrast to our expectations, aphid densities were not reduced at high densities of natural enemies (top-down control). Conversely, natural enemies were positively correlated to aphid densities, suggesting bottom-up control of aphid enemies by their prey (Costamagna and Landis, 2006; Raymond et al., 2015). This was likely the case because natural enemy densities were too low to affect aphid populations. For example, the parasitism rate of 0.6% (±1.3%) was substantially below the values of 15 to 36% above which effective control of aphids has been observed (Hawkins and Cornell, 1994; Thies et al., 2011; Plećaš et al., 2014). Population densities of aphidophagous predators, such as aphid gall midges and host-specific parasitoids (Rand and Tscharntke, 2007), syrphid flies (Freier et al., 2007; Alignier et al., 2014) and lady beetles (Elliott et al., 2002; Freier et al., 2007), are often positively related to aphid densities, because they can localize aphid colonies and deposit their eggs there. Surprisingly, lacewings, also aphidophagous predators, were not related to aphid density, which contrasts findings of e.g. Freier et al. (2007). On the other hand, aphids are often poor food for generalist predators like spiders (Toft, 2005). Nevertheless, aphids can make up a large proportion in the diet of spiders such as *Phylloneta impressa* (73%, Pekár, 2000), and these spiders locate their webs related to clusters of hemipteran prey (Jurczyk et al., 2012). Thus the positive relation between spiders and aphids found in our study, especially at the beginning and end of infestation, is likely due to spiders settling preferably near aphid populations, including *P. impressa*, which is one of the most abundant spiders in fields in our region. Especially at the beginning of aphid infestation generalist predators can be important aphid antagonists. Due to their feeding on non-aphid prey, they can already be present in the fields before aphids colonize and therefore can reduce aphid population growth (Evans, 2008). However, aphids in our study showed no negative response to spider density, even in the early season. This is in line with the more frequent control of herbivores on exotic plants in cultivated habitats by parasitoids rather than by predators (Hawkins et al., 1999).

4.4.2 Management

In contrast to earlier studies, we did not find higher densities of natural enemies in organic compared to conventional fields (Bengtsson et al., 2005; Krauss et al., 2011; Lu et al., 2015), which would be required for higher pest suppression in organic farming. After development of similar aphid densities in organic and conventional fields in the early season, organic fields even retained higher aphid densities towards the end of the season in July. At this time, aphids are seen to be unproblematic, because then the aphid density is already in decline. Maybe conventional management had no negative effects on natural enemies in our study, because weed density and diversity in the field were not reduced by conventional management (data not shown), and due to the generally low use of insecticides (Table S4.2; in contrast to the studies mentioned above). Insecticides were applied in only three conventional and two organic fields, with no significant effects on arthropod abundance. The aphid densities observed in the study year were unlikely to affect yield, as no relationship between pumpkin production and pest infestation was observed in experiments with up to 374 aphids per leaf (data not shown).

4.4.3 Adjacent habitat

In contrast to our expectations adjacent seminatural habitats did not directly support natural aphid control. The adjacent habitat type only influenced spiders, while in-field densities of the other natural enemies and aphids were not affected. Spiders were less abundant in fields with woody margins at the end of May. This could be triggered by *Phylloneta impressa*, a tangle-web spider (Theridiidae) which is known to have reduced densities along woody field margins, possibly due to predation by *Trypoxylon* Latreille wasps (Coudrain et al., 2013; Pfister et al., 2015).

Importantly, flower abundance in the adjacent field margins increased the densities of natural enemies, especially of lady beetles, parasitoids, aphid gall midges and lacewings. This in turn might be the reason for the negative trend of reduced aphid-densities with increasing flower abundance in the adjacent field margins. In line with many other studies we found that field margins, which offer floral resources, can support natural enemies (f.e. Chaplin-Kramer and Kremen, 2012; Tschumi et al., 2015; Tschumi et al., 2016a). Floral resources can enhance the abundance of natural enemies by attracting them and by increasing the fecundity and longevity of natural enemies, especially of parasitic wasps (Lu et al., 2012). Tschumi et al. (2016b) have shown that flower strips next to potato fields increased the in-field abundance of adult syrphid flies, lacewings and lady beetles and that the reproduction of lacewings and syrphid flies resulted in a reduction of aphids by 75%. Our results point in the same direction, although the effects on aphids were less pronounced than in the studies using flower strips tailored for natural enemy enhancement.

4.4.4 Landscape

Overall, fields in landscapes dominated by agriculture were less infested with aphids at the beginning of the vegetation period of pumpkin and had in total lower aphid densities. However, natural enemies in total did not react to landscape complexity and lady beetles showed contrasting responses to aphid gall midges and lacewings. In contrast to earlier studies (see reviews of Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Rusch et al., 2016), we found surprisingly little landscape effects on natural enemies. However, we observed negative effects of the proportion of agriculture on aphids, aphid gall midges and lacewings and positive effects on lady beetles. We expect that seminatural habitats contribute to the negative responses of aphid gall midges and lacewings. Aphid gall midges are known to react positively to landscape complexity (Chaplin-Kramer and Kremen, 2012; Rand and Tscharntke, 2007). Landscape complexity usually refers to the proportion of agriculture (or inverted proportion of non-crop habitat; e.g. Rusch et al., 2016) or of seminatural habitats in the surrounding (e.g. Chaplin-Kramer et al., 2011). Both are highly correlated, nevertheless in our study the proportion of agriculture in the surrounding was the better explanatory variable than the proportion of seminatural habitats. There are several possible reasons for this (Tscharntke et al., 2016): First, agriculture dominated landscapes could have lower insect populations not only owing to the smaller amount of suitable seminatural habitats, but also owing to negative effects of the use of pesticides (Geiger et al., 2010; Jonsson et al., 2012; Bianchi et al., 2013; Roubos et al., 2014). These might be the reasons for the negative responses of aphid gall midges and lacewings towards the proportion of agriculture. Second, crops can be important habitats for pests and natural enemies, especially when there is a mosaic of asynchronous crops (Tscharntke et al., 2016). Thus, landscapes with a higher proportion of agriculture might contain more attractive crops for aphids, so that the aphids move less into the pumpkin fields. As a vegetable and fruit growing area, our study region offers numerous alternative host plants for the studied aphid species. Except for cereals almost any other crop grown in our study region (e.g. sugar beet, potato, or even maize and wine) is a potential host of the aphid species, that we found on pumpkin (mainly *Aphis fabae* and *Aphis gossypii*) (Blackman and Eastop, 2000; Lampel and Meier, 2007). As pumpkin is a relatively late crop, aphids and their enemies may immigrate from other crops rather than from seminatural habitats. Especially the melon aphid *Aphis gossypii* is likely not related to seminatural habitats in our region, because it overwinters in greenhouses (Blackman and Eastop, 2000; Lampel and Meier, 2007). In addition, lady beetles (mainly *Coccinella septempunctata* Linnaeus and *Harmonia axyridis* Pallas) were positively related to agriculture as well, similar to findings of Rand and Tscharntke (2007). We assume that they build up populations on aphids in other surrounding crops and then move into pumpkin (Bianchi and van der Werf, 2004; Caballero-López et al., 2012). Thus, the observed lower aphid densities in crop-rich landscapes are likely not caused by a higher predation pressure, but by other effects of agriculture. Considering natural enemies, there is no indication in our study that landscape complexity would be a promising management tool to enhance pest control owing to the few and contrasting responses.

4.4.5 Specialists vs. generalists

Specialist natural enemies are expected to react more at the local scale, whereas generalists react more at the landscape scale (Chaplin-Kramer et al., 2011). However, we found local and landscape effects on both specialists and on generalists. While the highly specialized parasitic wasps were, indeed, affected only on the local scale by the flower abundance in the field margin, aphid gall midges - also specialists with a low mobility (Rand and Tscharntke, 2007; Maisonhaute and Lucas, 2011) - were also negatively affected by a high proportion of agriculture in the landscape. The generalist lady beetles and lacewings were also affected on the local scale (flower abundance) and on the landscape scale. Surprisingly, the generalist syrphid flies were neither influenced by the proportion of agriculture in the landscape nor by the adjacent habitat type. This may have been due to the dominance of *Episyrphus balteatus* De Geer, which is ubiquitous and highly mobile and thus able to build up large densities also in landscapes dominated by agriculture (Jauker et al., 2009; Röder, 1990). We found that the abundances of aphidophagous syrphid flies in seminatural habitats - except for *E. balteatus* - were positively related to landscape complexity (Schirmel et al. in prep; same study region).

4.4.6 Conclusions

We found that high proportions of agriculture in the surrounding landscape reduce overall aphid densities in pumpkin, but the underlying mechanisms are unclear. In contrast to earlier studies, our results do not indicate positive effects of organic farming or landscape complexity on pest control. However, we also found no severe negative effects indicating that they can be applied to support other ecosystem services like pollination without fearing tradeoffs. From our results, it seems most promising to enhance the flower abundance in the field margins to enhance natural enemies in pumpkin, especially lady beetles, parasitic wasps, lacewings and aphid gall midges.

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4.6 Supplementary Material

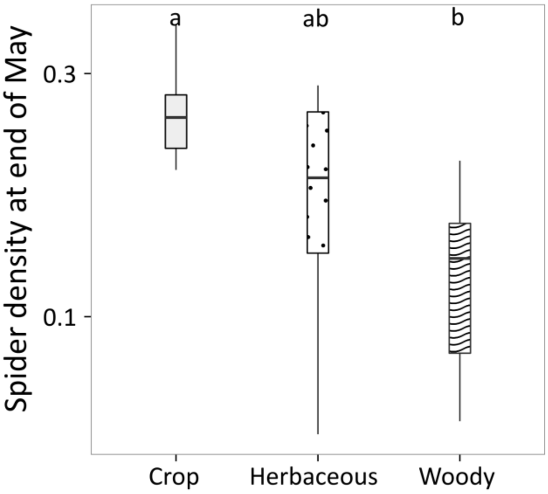

Figure S4.1 Spider density at the end of May was lower in fields next to woody habitats than in field-field situations (t_{10} = -2.9, p = 0.03). Different letters indicate significant differences. The density was corrected for the effects of aphids.

Table S4.1 Pearson rank correlation coefficients for all pairs of continuous explanatory variables (lower panel) and asymptotic p-values (upper panel). Pearson correlations with r ≥ │0.5│ (p ≤ 0.1) are marked in bold. Variables with r > 0.6 are not included in the same model. Owing to correlation between variables we used the following explanatory variables in the models: First, we only used the proportion of agriculture and not the proportion of seminatural habitats. Second, we either used the total abundance of aphids or the abundance of aphids at a certain sampling.

	Management	%SNH	%Agriculture	Aphid_ total	Aphid 1. Sampling	Flower abundance in the field margin
Management	-	0.49	0.94	0.32	0.18	0.35
%SNH	-0.17	-	**	0.54	0.17	0.75
%Agriculture	0.02	**-0.66**	-	0.16	*	0.052
Aphid_total	0.25	0.16	-0.35	-	***	0.85
Aphid 1. Sampling	0.33	0.34	-0.54	**0.86**	-	0.36
Flower abundance in the field margin	0.23	-0.08	-0.47	-0.05	0.23	-

Table S4.2 Management type (conventional vs. organic), number of insecticide applications and type of insecticides applied are given for the 18 investigated pumpkin fields. The information is based on farmer´s questionaires.

Field No.	**Management**	**N Insecticide applications**	**Type of insecticides**
1	conventional	1	Karate Zeon (Lambda-Cyhalothrin)
2	organic	0	
3	organic	0	
4	organic	0	
5	organic	0	
6	organic	0	
7	conventional	1	Karate Zeon (Lambda-Cyhalothrin)
8	conventional	1	Karate Zeon (Lambda-Cyhalothrin)
9	conventional	0	
10	conventional	0	
11	organic	0	
12	conventional	0	
13	organic	0	
14	organic	5	Neem Azal (2), Neodosan (potassium salts, 3)
15	conventional	0	
16	conventional	0	
17	organic	4	Neem Azal (3), Neodosan (potassium salts, 1)
18	conventional	0	

Chapter 5 Sensitivity of commercial pumpkin yield to potential decline among different groups of pollinating bees

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Abstract

The yield of animal-pollinated crops is threatened by bee declines, but its precise sensitivity is poorly known. We therefore determined the yield dependence of Hokkaido pumpkin in Germany on insect pollination by quantifying: (1) the relationship between pollen receipt and fruit set; and (2) the cumulative pollen deposition of each pollinator group. We found that approximately 2500 pollen grains per flower were needed to maximize fruit set. At the measured rates of flower visitation, we estimated that bumble bees (21 visits/ flower lifetime, 864 grains/ visit) or honey bees (123 visits, 260 grains) could individually achieve maximum crop yield, whereas halictid bees are ineffective (11 visits, 16 grains). The pollinator fauna was capable of delivering twenty times the necessary amount of pollen. We therefore estimate that pumpkin yield was not pollination-limited in our study region and that it is currently fairly resilient to single declines of honey bees or wild bumble bees.

Keywords

Bombus, *Apis*, *Cucurbita*, ecosystem services, Halictidae, pollination effectiveness

5.1 Introduction

Pollination is a valuable ecosystem service, especially for crops requiring animal pollination such as pumpkin [1,2]. Worldwide, 75% of our leading food crops benefit from animal pollination, mainly by bees [1]. Pollination services from wild insects are important, even in the presence of honey bees *Apis mellifera*, because they ensure and enhance pollination through spatial and temporal complementarity, behavioural interactions and higher effectiveness [3–5]. For example, wild bees can be more effective pollinators than honey bees and can increase the fruit set of a wide variety of important cash crops such as almond, spring rape, strawberry, watermelon, cucumber and squash [6]. While numbers of honey bees and wild bees have declined in some areas during the past decades, the demand for insect-pollinated crops has grown [2,7]. Potentially, this may lead to pollination deficits and increases in yield variability [8,9]. In temperate regions, mainly honey bees are used for managed crop pollination outdoors. Reliance on just honey bees increases the risk of uneconomic yields, because it utilizes only a single species. Furthermore, honey bees are likely to be more susceptible than indigenous wild bees to stressors such as diseases, because the human breeding reduced their genetic diversity [10]. Consequently, a diverse community of wild pollinators can be important for insuring crop yield [11] and it is therefore important to establish whether unmanaged pollinators are alone capable of sustaining pollination services.

We therefore investigated the contributions of different pollinators to fruit set in commercial fields of the pumpkin *Cucurbita maxima* Duchesne ex Poir cv Hokkaido. Insect pollination is essential in pumpkin because all cultivated *Cucurbita* species have unisexual flowers requiring pollen transfer from male to female flowers for fruit set [12]. Although cucurbits have a long flowering period (on average 72 - 80 days), the single flowers of pumpkin remain open from between six hours to one day. Rapid and effective pollinator visits are therefore vital to maximize yields. To attract pollinators, the *Cucurbita* flowers offer relatively rich rewards of pollen and nectar [13,14]. In Europe, the specialized pumpkin bees (*Peponapis, Xenoglossa*) do not exist [15,16], thus pumpkin flowers could be pollinated by honey bees, bumble bees and halictid bees [13,14,17]. However, the knowledge about the performance of these pollinators has been largely restricted to honey bees [13,18,19] and wild bees in other parts of the world [20–22], and there are no previous studies on Hokkaido pumpkin.

Two main components are required for a quantitative understanding of the relationship between crop yield and the composition of the flower-visiting fauna: (1) the cumulative pollen deposition of each pollinator taxon during the flower´s lifespan (further: "cumulative pollen deposition"); and (2) the relationship that links pollen receipt to seed/fruit set [23-25]. Floral visitors vary in cumulative pollen deposition because of variation in both visitation rates and the amount of pollen transferred during a visit [23,26]. By knowing this relationship, the impact of pollinator declines can be predicted and the resilience of food security can be explored. Nevertheless, to our knowledge this relationship is only known for two economically important crops: cranberry [27] and canola [28]. Both cranberry and canola have bisexual flowers, each with fairly small numbers of ovules (less than 40). In the present study, by contrast, we investigated a crop with unisexual flowers and large numbers of ovules (400-700) [13,15]. The separation of male and female flowers confers a high degree of pollinator-dependence on the crop, because mechanisms of autonomous (within-flower) pollination such as seen in canola [28] are impossible, and the large number of ovules initially suggests a need for delivering numerous pollen grains to stigmas.

The aim of the present study was to analyze the cumulative pollen deposition of honey bees (*A. mellifera*) and two kinds of wild bee groups, namely bumble bees (mainly *Bombus terrestris agg.*, which include *B. terrestris*, *B. lucorum* and rarely *B. cryptarum*) and halictid bees (several species, mainly of the genus *Lasioglossum*), as pollinators of pumpkin. Cumulative pollen deposition was characterized by combining pollen deposition per single flower visit with flower visitation rates [25]. We used controlled hand-pollinations to determine the relationship between a stigma's receipt of pollen and the likelihood that the flower set a harvestable pumpkin and the fruit's mass. Based on these data, we modelled the contribution of each pollinator group to crop yield and investigated the potential impact of reductions in bee abundance. The objectives were as follows: (1) to determine the pollination requirements of Hokkaido pumpkins; (2) to determine the most effective pollinators of Hokkaido pumpkin; (3) to determine if there is a pollination deficit in the current pollination system; and (4) to investigate the sensitivity of crop yield to declines of the three bee groups.

5.2 Methods

5.2.1 Study region

We conducted our studies in 2012, 2014 and 2015 in 26 commercial *Cucurbita maxima* cv. Hokkaido fields (3 ± 2.6 ha) in the Upper Rhine Valley between Kandel and Ludwigshafen, Germany (49°4 N, 8°6 E; 49°27 N, 8°28 E). The area has a temperate climate with annual mean temperatures around 11 °C and 700 mm of annual precipitation on average.

5.2.2 Single visit pollen deposition

According to Ne’eman et al. [24] pollinator effectiveness is the contribution of the pollinators to pollen deposition independently of resources spent or available. We measured per visit pollination effectiveness via single visit pollen deposition (SVD). SVD was investigated in three different fields between 8th July and 23rd August 2015. SVD on the stigma was measured for honey bees *A. mellifera* (n = 43), bumble bees *B. terrestris* agg. (n = 42) and halictid bees (Halictini, size: 5-10 mm, > 50% *Lasioglossum malachurum*, n = 33). These three groups of bees were chosen, because they are the main flower visitors of pumpkin in our region. Honey bees most likely originated from apiaries in the region, but no hives were found within 70 m of the pumpkin fields. Flowers were bagged prior to anthesis and again after the single visit with a synthetic mesh bag (mesh size ≈ 1 mm^2) to exclude further pollinator visits. For each replicate, one single bee was allowed or engineered to visit one virgin bagged female flower. Flowers were left on the plants and the observer waited for a bee to visit the flower (allowed) or caught a bee and released it at the flower’s corolla (engineered, halictids). Since few halictid bee visits occurred naturally in the studied fields, we performed additional replicates in August and engineered their visits by catching them from a male flower and transferring them to a virgin female flower. The duration and the time at which the visit occurred was noted. We tried to evenly space the observed visits over the approximately four hour interval of flower receptivity in our experiments between 6:45 and 10:45 am. After pollinating, the halictid bees were caught when they left the flower and later identified in the laboratory, where their length and intertegular span were measured. The stigmas of the experimental flowers were cut and frozen for later quantification of pollen numbers. In order to quantify pollen removal from anthers, we measured the number of pollen grains present in open and bagged flowers over daytime, which we used to estimate the overall efficiency of the pollen transfer system. In August 2012 and 2015, the anthers of eight bagged flowers

(2012) and of 44 open flowers (2012: 13; 2015: 31) were taken between 7:30 and 11:00 am for later quantification of pollen numbers.

5.2.3 Flower visitation rate and handling time

We studied flower visitors and their foraging behaviour in 18 fields in our study region in 2014. Each field was investigated at each one time period on three different days in July during the flowering period (2-6, 15-17, 23-25 of July 2014), once at 7:00, 8:30 and 10:00 am. On each occasion, we recorded four 15 minute-long videos each surveying a different female pumpkin flower. The camera, a digital HD video camera recorder (handycam Sony ® HDR-CX115E), was positioned ~50 cm above a female flower in order to monitor the mouth of the flower's corolla. Video recording is a suitable method to sample visitation rates in pumpkin [20,29], because the frequency of visits is high and relatively evenly distributed across female flowers. From the videos we extracted for each bee group the visitation rates and their flower handling time (H = the entire duration the bee spent on and in the flower, from landing until leaving). Three bee groups were distinguished: 1) honey bees *A. mellifera*, 2) bumble bees = *B. terrestris* agg. and *B. lapidarius* were identified from the videos, and 3) halictid bees. Halictid bees could be distinguished only into two size-defined groups (length ≈ 6 mm and length ≈ 8 mm), each containing several halictid species. Additionally, we recorded for each visit the time of day, the elapsed time spent at the nectaries and whether or not the insect contacted the flower's stigma.

5.2.4 Relation of fruit set and yield to pollen deposition

To determine the relation of fruit set and yield (seed set and fruit mass) to pollen deposition, we conducted controlled hand-pollination experiments for three reasons. First, the pollen loads delivered by bees can vary greatly. Second, the single-visit pollen deposition of a single bee may not be sufficient for fruit set. Third, potential fruit and seed set can be highly reduced through abortion, especially in plants with floral overproduction like pumpkins [24,30,31]. Hand-pollination experiments were conducted in one field per year (2014, 2015). Female flowers were bagged the day before anthesis with a synthetic mesh bag (mesh size ≈ 1 mm^2). At anthesis, they were hand-pollinated and re-bagged. Hand-pollination was done between 7:00 and 11:00 am to ensure pollen viability and stigma receptivity. Stigmas are normally receptive until 13:30 [18] and although pollen viability decreases during anthesis, we predict it to be 75% at 13:00 based on a previous study [13]. We always pollinated the first female flower of a plant to avoid enhanced abortion rates through first-fruit dominance, thereby maximizing the chance of measuring seed set. Each pumpkin plant produces several consecutive female flowers during the flowering period. The first female flower is the flower that blooms as the first in the flowering period. In 2015, we removed non-experimental fruits from the treated plants at intervals of one day, three days and six or seven days after the pollination of our focal flower in order to minimize abortions among the hand-pollinated fruit [31].

For transferring different amounts of pollen to the stigma, we initially (2014) created five levels of pollen deposition by dissecting single anthers into parts of different sizes (Table S5.1). Given the high variability of pollen numbers in deposits obtained with this method, we changed the method in 2015, when we used a metal wire (tip diameter 1 mm) or a nail head (diameter 2.4 mm) in several repetitions and combinations to transfer seven levels of pollen to stigmas (Table S5.1). Experimental pollinations at each level were replicated 20 times in 2014 and around 30 times in 2015. At the beginning of September, the pumpkins were harvested from the experimentally-pollinated flowers and the fruit mass plus the number of fully developed seeds were measured. Our main measure of crop yield is the proportion of fruit set, but we also investigated fruit mass because Hokkaido pumpkins are sold for human consumption. After consultation with local farmers, fruits with a minimum weight of 800 g were defined as marketable.

5.2.5 Quantification of pollen numbers

In order to quantify pollen deposition, we extracted the pollen from each stigma by acetolysis following Jones [32]. After acetolysis, glycerol 50% was added to the extracted pollen to a total volume of 0.5 mL. All pollen from the stigmas from the single visit experiments was counted under ×65 magnification.

In order to determine the amount of pollen in anthers, the pollen was washed off the anthers with 70% ethanol. After the pollen grains had sedimented by centrifugation, the supernatant was removed with a micropipette and glycerol 50% was added to the pollen pellet to make up 5 mL (in 2012) and 1 mL (in 2015) (based on Vidal et al. [33]). To evenly re-suspend the pollen, the vials were shaken by a vortex mixer prior to counting the pollen in 10 (bagged anthers) or five (open anthers) subsamples of 20 µL in 2012. In 2015 the pollen was counted in three to 9 subsamples of 50 µL (depending on the standard deviation of the counted pollen). The total pollen load of each male flower was estimated volumetrically from the mean of the subsamples.

5.2.6 Data analyses

All statistical analyses were conducted in R 3.2.2 [34]. In order to determine whether per visit pollination effectiveness varied among the pollinator groups we used multiple pairwise comparisons using the method of Herberich et al. [35] to account for the heterogeneous variances and unbalanced group sizes (R packages “multcomp”, “sandwich”). For each bee group, we tested the following potential explanatory variables for SVD: length (only for halictid bees), handling time, time of day of visit, and their interactions and we dropped non-significant terms ($p > 0.1$) from final models. The SVD data were log-transformed to reduce the heterogeneity of variance. To account for non-normality, we checked the p-values with permutation tests (R package “pgirmess”). Best models were selected using Akaikes Information Coefficient (AIC) (R package “MASS”). In the SVD dataset, one outlier (likely a technical anomaly, bumble bee, Fig. 5.1) was removed prior to data analysis.

In order to determine whether cumulative pollen deposition varied among pollinator groups due to differential rates of flower visitation, we tested whether the response variables of the video data, i.e. handling time (log-transformed) and visitation rate, varied among bee groups using multiple pairwise comparisons. For the comparison of the handling times we used the method of Herberich et al. [35] to account for the unbalanced group sizes (see above). In the comparison of the visitation rates we included ‘field’ as random factor.

To test whether the amount of pollen available at the anthers of flowers declined during anthesis, we used a linear mixed-effect model on a combined dataset with ‘year’ (levels of 2012, 2015) as a random factor (R packages: ‘nlme’, ‘piecewiseSEM’).

In order to relate crop performance to pollen deposition (D), we used the data from the hand-pollination experiments to describe the dependence of fruit set of harvestable (i.e. not aborted) pumpkins on pollen deposition (log-transformed), which was tested by fitting a non-linear three-parameter (a,b, and c) logistic model with the following form:

$$F = \frac{a}{100*(1+\exp[\frac{-\log 10(D)+b}{c})])} \qquad \text{(Eq 1)}$$

In Eq 1, F denotes the proportion of harvestable fruit. As fruit set is a binary variable, we used a binomial distribution to model the statistical error in the proportion of harvestable pumpkins. In order to further investigate the basis for variation in fruit mass among the fruits that were set, we used the data obtained from hand-pollinations to evaluate whether fruit mass depended on the estimated deposition of pollen (log-transformed) and the numbers of fully developed seeds.

5.2.7 Modelling the contribution of bee groups to crop yield

We assume that the probability that a flower produces a marketable pumpkin depends on the amount of pollen accumulated on its stigma. In order to model the cumulative pollen deposition of a certain bee group *i*, let v_i denote the visitation rate of bee group *i* (visits flower^{-1} h^{-1}) during the flower lifetime of *R* h. Let each single visit by bee group *i* deposit d_i pollen grains. The contribution to pollen accumulation of bee group *i*, D_i, is therefore given by:

$$D_i = v_i \, R \, d_i \qquad \text{(Eq 2)}$$

We relate crop performance (i.e. the proportion of marketable pumpkins), *F*, to the expected total pollen accumulation *D* using the sigmoidal relationship described above (Eq 1). To model the effect of a specified pollinator decline, we introduce a proportional change in the visitation rate of bee group *i* in Eqs 1 and 2. In the analyses below we assume that the flower is receptive to pollination for $R = 4$ h.

In order to estimate the expected rate of pollen deposition due to each pollinator group, we had to account for the following four circumstances (see Results): (a) the magnitude of SVD (of bumble and honey bees) decreased as the flowers aged; (b) for bumble bees the magnitude of SVD increased with the time spent handling the flower, denoted *H*, and the handling times were much shorter in realistic situations ($H = 12 \pm 23$ s) than in the single visit experiments ($H = 151 \pm 64$ s; $t = -29.5$, $p < 0.001$); (c) for halictid bees the SVD varied with length of the individual bee, denoted *l*; and (d) only a proportion of floral visits result in contact with the flower's stigma, denoted *s*. For modeling purposes, we therefore calculated the expected pollen deposition for a single pollinator visit in Eq 2, $d_{i,}$ as a weighted average for each pollinator group using only significant terms from statistical analyses (see Results) as follows.

Bumble bees:

$$\overline{d_B} = s_B \sum_T \left[V_T \left(10^{(\alpha - \beta T + \gamma H)} \right) \right] \qquad \text{(Eq 3)}$$

In Eq 3, $\overline{d_B}$ denotes the expected number of pollen grains delivered to a flower's stigma by a bumble bee visit, s_B denotes the proportion of floral visits in which bumble bees contacted the flower's stigma, *H* indicates the time spent handling the flower, *T* indicates that we separately treated the c. 4 h lifetime of the flowers (between 7 and 11 am) as five sequential segments (each of 48 minutes, so that the values of *T* are the decimalized times:

0.31, 0.34, 0.38, 0.41 and 0.44). Values for the unsampled second and fourth intervals (i.e. T = 0.34 and T = 0.41) were calculated as mean of the two adjacent segments, either the first and third or the third and fifth, respectively. V_T denotes the proportion of bumble bee visits that occurred in time interval T in the video data (from T_1 to T_5: 0.08, 0.15, 0.21, 0.26, 0.31). Fitted constants from statistical analyses (see Results) are denoted by α, β, and γ.

Honey bees:

$$\overline{d_A} = s_A \sum_T \left[\overline{V}_T(10^{(\alpha-\beta T)})\right] \qquad \text{(Eq 4)}$$

In Eq 4, $\overline{d_A}$ denotes the expected number of pollen grains delivered to a flower's stigma by a honey bee (*Apis*) visit, with symbols annotated as for Eq 3.

Halictid bees:

$$\overline{d_H} = \sum_l [s_l V_l d_l] \qquad \text{(Eq 5)}$$

In Eq 5, the proportion of visits due to each of two length classes, l = 1 and l = 2, are denoted by V_l, the size-specific probability of stigma contact is denoted s_l, and the per visit pollen deposition of each size class is denoted by d_l. Specifically, the halictid bees were separated into two length classes as follows: l = 1, comprising individuals ≈ 6 mm long (i.a. *Lasioglossum morio*, *L. pauxillum* and *L. politum*); and l = 2, comprising individuals ≈ 8 mm long (mainly *L. malachurum*). The small halictid bees (l_1) deposited only eight pollen grains per visit (SD ± 8.2 , n = 10), whereas larger halictid bees (l_2) deposited around 46 pollen grains (SD ± 56.5 , n = 15).

We estimated the mass of fruit produced per hectare of crop using the following model:

$$Y = FNMP \qquad \text{(Eq 6)}$$

In Eq 6, Y denotes the yield of Hokkaido pumpkins in tonnes per ha, F is the probability that a flower sets a harvestable pumpkin (related to pollen deposition using Eq 3), N denotes the number of female flowers per plant, M denotes the mass of a single Hokkaido pumpkin (tonnes), and P denotes the number of plants (individuals per ha). For our calculations, we assumed: N = 6 female flowers per plant based on field observations on 30 plants; M = 0.001 t per fruit because 1 kg is the optimal weight for the market; and P = 10000 plants per ha based on responses to farmer questionnaires (n = 35 fields, data not shown). Further, we assume that the same number of female flowers bloom each day.

5.3 Results

5.3.1 Cumulative pollen deposition

a) Single visit pollen deposition

Bumble bees deposited almost six times more pollen grains per single visit (mean ± SD, SVD = 3369 ± 2473, n = 41) than honey bees (SVD = 582 ± 752, n = 43; t = 9.11, $p < 0.001$) and 75 times more than halictid bees (SVD = 45 ± 76, n = 33; t = 16.8, $p < 0.001$). Honey bees deposited 13 times more pollen than halictid bees (t = 8.96, $p < 0.001$) (Fig. 5.1). The pollen deposition that resulted from a bumble bee visit (*grains* = 10^(3.906 + 0.0027*H* - 2.565*T*); $R^2 = 0.24$) increased with handling time ($t_{38} = 3.34$, p = 0.0019) and tended to decrease as the day progressed ($t_{38} = -1.85$, p= 0.072; Fig. S5.1a). The pollen deposition of a honey bee visit decreased significantly over the course of the morning (*grains* = 10^(4.44 - 5.54*T*)*;* $t_{41} = -3.4$, p = 0.0015, $R^2 = 0.20$) (Fig. S5.1a). The pollen deposition of a halictid bee visit tended to increase with body size (*grains* = 10^(0.168 + 0.170*l*) - 1*;* $t_{27} = 2.0$, p = 0.052, $R^2 = 0.10$).

Bagged male *C. maxima* flowers contained on average 37000 pollen grains (SD = 6900, n = 8). In open male flowers, the number of pollen grains remaining on the anthers decreased to c. 600 by 11:00 *(grains* = 10^(6.9 - 9.0*T*); $t_{41} = -11.0$, $p < 0.001$; $R^2_{marginal} = 0.53$) (Fig. S5.1b), which implies that 98% of pollen was removed before flowers senesced.

b) Flower visitation rate and handling time

In 54 hours of video footage, we observed a total of 2100 individual flower-visitors, of which 79% were honey bees *A. mellifera*, 14% bumble bees (mainly *B. terrestris agg.*, some *B. lapidarius*) and 7% halictid bees. The rate of flower visits by honey bees (123 visits/ flower lifetime) was significantly higher than by bumble bees (21 visits/ flower lifetime; *t* = 18.5, $p < 0.001$) and halictid bees (11 visits/ flower lifetime; *t* = 20.2, $p < 0.001$). The handling time at individual flower visits was very variable, but differed significantly among bee groups. Bumble bee visits (mean ± SD, *H* = 12 ± 23 s) were more than ten times shorter than visits of honey bees (*H* = 144 ± 252 s; *t* = 22.4, $p < 0.001$) and of halictid bees (*H* = 191 ± 225 s; *t* = 15.8, $p < 0.001$). Virtually all visits by bumble bees (*s* = 99%) and honey bees (95%) resulted in contacts with the stigma. We could not visually verify the contact with the stigma by halictid bees while they were descending and ascending the flower, but we assume that they did make contact if they reached the nectaries. Overall, 82% of all halictid bees reached the nectaries during their visit.

5.3.2 Relation of fruit set and yield to pollen deposition

The likelihood that a flower produced a harvestable pumpkin increased sigmoidally with pollen deposition (Eq 1: $a = 40.52$, $t_9 = 7.53$, $p < 0.001$; $b = 2.96$, $t_9 = 36.5$, $p < 0.001$; $c = 0.15$, $t_9 = 1.77$, $p = 0.111$; $R^2 = 0.79$; Fig. 5.2) and the relationship saturated at a fruit set of 41%. When c. 2500 pollen grains were deposited, 95% of this maximum fruit set was obtained (Fig. 5.2). Marketable fruits, which weigh > 800 g, contained at least 140 fully developed seeds and were pollinated with more than 500 pollen grains. Fruit mass (g) increased with the number of fully developed seeds ($mass = 424.8 + 1.503 seeds$; $t_{36} = 3.7$, $p < 0.001$, $R^2 = 0.25$) and tended to increase with increasing pollen deposition ($mass = 311.8 + 122.3 * \log_{10}(pollen\ grains)$; $t_{36} = 1.8$, $p = 0.077$, $R^2 = 0.06$).

5.3.3 The contribution of bee groups to crop yield

During a single flower visit an average bumble, honey or halictid bee deposits an expected number of pollen grains of $\overline{d_B} = 864$, $\overline{d_A} = 260$ or $\overline{d_H} = 16$, respectively (Table S5.2). Using these as values for d_i and the current rates of flower visitation in Eq 2 yields the following estimates of the pollinating capabilities (grains deposited per flower lifetime) of the bee groups: honey bees, 31980 grains; bumble bees, 18144; and halictid bees, 183 (Table S5.2). Using these values in conjunction with the pollen-yield relationship (i.e. Eq 1 and Eq 6) indicates that reducing crop yield by 10% relative to current levels requires a cumulative pollen deposition equivalent to 11% of the extant bumble bee intensity (= 2 bumble bee visits/ flower lifetime) or 7% of the extant honey bee intensity (= 8 honey bee visits) or 1100% of the extant halictid bee density (= 123 halictid bee visits) (Fig. 5.3). Our model predicts that crop yield will be more sensitive to declines of bumble bee than honey bee visits, because a reduction of one bumble bee visit results in the delivery of 600 fewer pollen grains than the reduction of a single honey bee visit (Table S5.2). The model also predicts that the loss of any single pollinator group will not reduce crop yield in our study system. Based on our assumptions, our model predicts a maximum pumpkin yield of 24.3 tonnes per ha (Eq 6), which closely matches the maximum value that is widely reported by farmers in our study area (25 tonnes/ ha). The system's potential transfer efficiency is c. 17% ($100 \times 50307/(8 \times 37000)$), when the following values are used: the model's predicted pollen deposition by the extant pollinator fauna (50307 grains; Table S5.2); the number of pollen grains eventually removed from a male flower's anthers (37000); and the eight-fold preponderance of male flowers in our study area [S.C.P. 2012, 2014, 2015, personal observation].

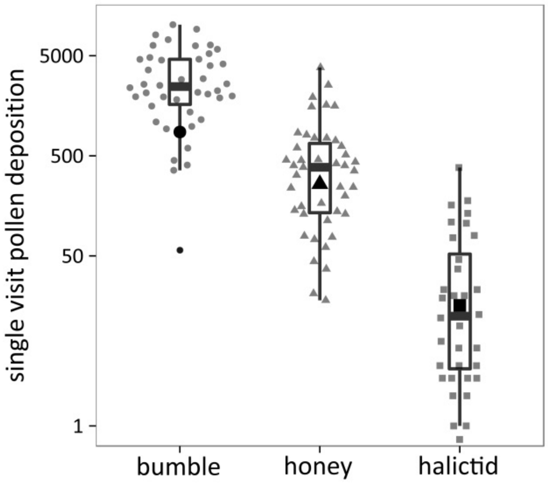

Figure 5.1 The number of pollen grains deposited in single visits to flowers by the pollinator groups in our study, or ‘single visit deposition’ (SVD). For each bee group, the box plots present the median, quartiles and range in the conventional style and the accompanying scatter depicts the individual observations. For realism in our model, we calculated weighted averages, denoted $\bar{d}$, to account for variation in handling times, in size, in stigmatic contact and in pollen transfer over the flowering interval. For each pollinator, the values of $\bar{d}$ are shown as a large circle (bumble bees), a triangle (honey bees) and a square (halictid bees). The small black circle below the data for bumble bees marks an outlier that we excluded from our analyses.

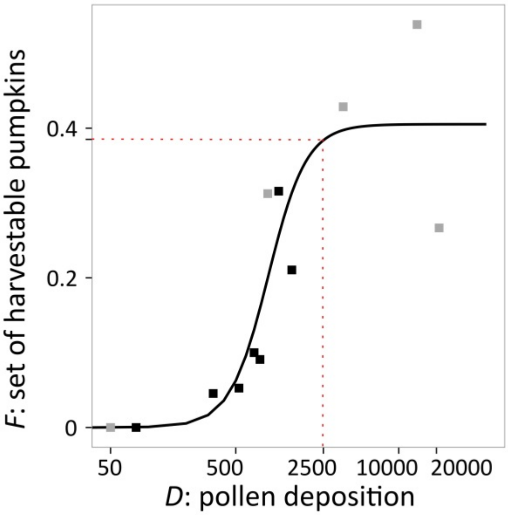

Figure 5.2 The probability of fruit set of harvestable Hokkaido pumpkins (y-axis: F) increased with the number of pollen grains deposited on a flower’s stigma (x-axis: D) based on the hand-pollination results from 2014 (grey squares) and 2015 (black squares). The fitted relationship is based on Eq 1 (see text). According to this relationship, the 95% of the maximum level of fruit set (a = 41%) occurs when approximately 2500 pollen grains have been deposited on a flower’s stigma (dashed lines).

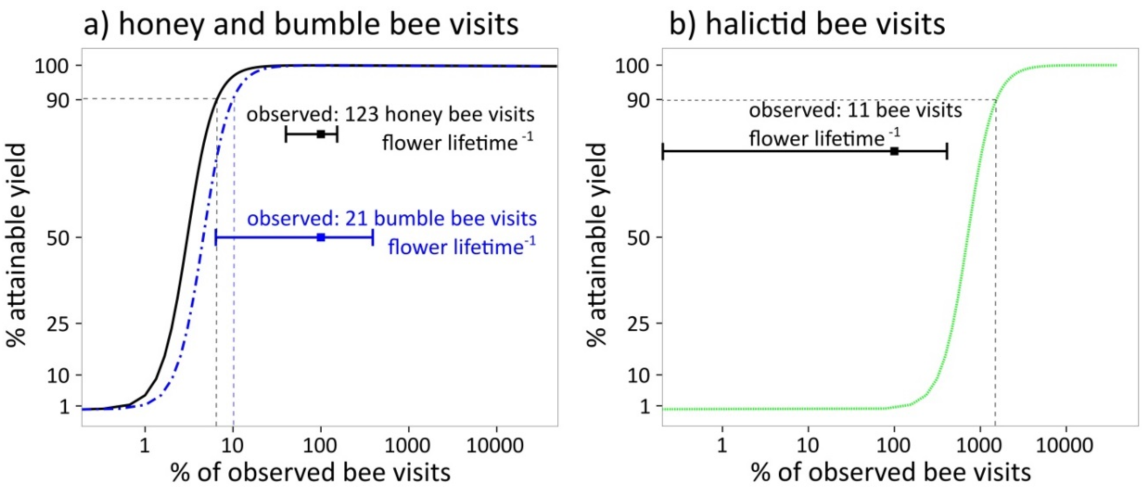

Figure 5.3 The impact of pollinator decline or increase on yield in Hokkaido pumpkin.

a) The estimated attainable yield (*y*-axis: percentage of harvestable pumpkin fruits relative to extant levels) in relation to the rate of flower visits per flower lifetime (x-axis: rate of visits as a percentage of extant intensity) by either honey bees (black, solid line) or bumble bees (blue, dot-dashed line).

b) As for (a) except the relationship is for halictid bees.

In both panels, a horizontal bar shows the range of the observed visitation rate and the associated filled square indicates the mean. The number of visits corresponding to 100% of the observed visits in the x-axis differs per bee group and is displayed above the horizontal bars. Dashed lines indicate the percentage of the extant visit rate that is required to produce 90% of the currently attainable yield (i.e. 7% for honey bees, 11% for bumble bees and 1100% for halictid bees).

5.4 Discussion

We found bumble bees to be the most effective pollinators per flower visit of Hokkaido pumpkins in Germany and crop yield is therefore most sensitive to declines in bumble bee visits. However, based on our model, honey bees deposited overall more pollen per flower owing to their greater rates of flower visitation, and pumpkin yield was not pollination-limited in our study region at the extant abundance of bees.

5.4.1 Pollination requirements of Hokkaido pumpkins

We established that the minimum pollination requirements of each flower in *C. maxima* Hokkaido pumpkin were 500 pollen grains for a marketable fruit and that the likelihood of fruit set reached 95% of the maximum with around 2500 pollen grains present on the stigma. Thus for maximum seed set, approximately four pollen grains per ovule are necessary, which corresponds fairly closely with Cruden´s Rule [16,36]. Further, *C. maxima* Hokkaido pumpkins have higher thresholds for fruit set than *C. pepo* (minimum for fruit set 70 pollen grains, maximum rate of fruit set ~1300 pollen grains; [19–21] and

C. foetidissima (minimum 50 pollen grains, maximum > 900 pollen grains; [16,37] and in contrast to other *Cucurbita* species, fruit set does not reach 100% even under optimal pollination [38]. Unlike smaller cucurbit fruits like squash, Hokkaido pumpkins and other larger pumpkins may have higher pollination requirements, but fail to achieve a fruit from every flower even when these are met, because the individual plants lack sufficient resources to invariably produce a marketable fruit [39]. The high pollination requirements of Hokkaido pumpkin relative to other cucurbits underline the need for abundant and stable pollinator populations in their production areas.

5.4.2 Cumulative pollen deposition

Similar to other crops pollinated by honey and bumble bees [6,11], bumble bees were the most effective pollinators of pumpkin per flower visit, probably for three reasons. First, bumble bees transfer the most pollen owing to their large body size [4,21] and densely hairy coat [40]. Second, the faster handling of bumble bees relative to the other pollinator groups increased their relative effectiveness: in the same time a honey bee visits one pumpkin flower a bumble bee could visit 12 flowers [similarly 20,41]. In general, smaller bee species have longer handling times, likely because of their lower nectar extraction rate owing to the shorter proboscis length and the lower body mass [26]. Third, bumble bees, like the specialized squash bees (tribe *Eucerini*) that pollinate pumpkin in the Americas, and in contrast to honey and halictid bees reliably touch the reproductive parts of the flower with their ventral side as they handle the flowers, thereby avoiding the attachment of pollen to the head and eyes, which apparently otherwise slows a bee's progress [20,42]. We also observed that pollinator visits were most effective early in the morning when more pollen was available at the anthers for transfer by bees ([19], Fig. S5.1). Further, all investigated pollinators only collected nectar, but did not harvest pollen in male flowers. Despite the eight-fold preponderance of male flowers in our study area, our analysis indicates that the extant pollinator fauna was capable of generating a transfer efficiency of approximately 17%. Previously, estimates in systems with friable pollen have reported transfer efficiencies in the region of 1% [43]. In our case, however, we are dealing with an extraordinarily high level of flower visitation with rates in the range of one visit by a honey or bumble bee every two minutes (Table S5.2). This high flower visitation results in our high modelled potential for pollen deposition. It is likely that real pollen deposition is somewhat more limited, however, because the stigma's surface becomes eventually saturated with pollen. Thus, when the cumulative pollen deposition is high enough to cause stigma clogging, pollen transfer per bee visit may become increasingly poor later in the flower's life, which is later in the morning in our case. Taken together, these findings are consistent with our observation that fruit production in our Hokkaido pumpkin system was very far from pollen-limited.

5.4.3 Sensitivity of pumpkin yields to bee declines

Our model reveals the relative importance of the components of the bee fauna as follows: 90% of the attainable yield is reached with two bumble bee visits per female pumpkin flower or eight honey bee visits. Thus, in our region bumble bees provide a substantial ecological service by playing a key role in pumpkin pollination despite their lower densities relative to honey bees. As individuals, bumble bees are also more effective pollinators than honey bees owing to their faster handling of flowers. However, at the measured visitation rates honey bees deposit more pollen per flower than bumble bees. Halictid bees do not appear to be capable of pollinating *C. maxima* effectively. It is likely that the pollen deposition of halictid bees is limited by their size [4,22] and hairiness [40] and that their cumulative pollen deposition was actually low. However, our findings must be treated with caution,because our handling of the bees during engineered visits may have affected measurements of pollen deposition. For example, although the handling times of halictid bees were similar in natural and engineered visits (data not shown), the handling during 'engineered' visits might have dislodged pollen from the bees. In any case, even a two-fold error in our estimate of single visit deposition would not affect our conclusion that halictids barely contributed to the pollination of pumpkin in our study area and that only a many-fold increase (*c*. 10 fold) in their abundance would satisfy the pollination requirements of pumpkin. Thus, our findings suggest that social bees are essential for pumpkin pollination in the study region.

Our model predicts realistic values of yield in pumpkin, which suggests that it can be plausibly used to investigate the consequences of changes to the pollinator fauna. On this basis, we predict that current crop yields are sustainable even in the event that any single pollinator group is lost. Consequently, pumpkin could continue to be a profitable crop at our study area despite a catastrophic loss of only honey bees or bumble bees, for example. Thus, our cropping system demonstrates a high level of 'attack tolerance' [44] and that wild bumble bees provide ecological insurance [11]. However, even if the causes for the decline of one group of bee would not directly affect other groups of bees as well, removing one type of bee could alter the visitation rate and therefore pollen deposition by other bees.

Bumble and honey bees are clearly the key to pollination success of pumpkins in Germany, underlining that crop pollination is often delivered by a few common species in intensified agricultural landscapes [45]. However, we recognise that functional group diversity of bees might nevertheless be important elsewhere. For example seed set of *C. moschata* in Indonesia only increased with functional group diversity (25 species, eight functional groups) and not with the number of bee visits [4]. Furthermore, flower-visitor richness increases yields in pollinator-dependent crops worldwide [46].

Our model's predictions should be considered alongside some caveats. For example, our model did not include the pulsed bloom that characterizes most crops. Thus, it is possible that more bees may be needed to successfully pollinate all flowers at the peak flowering time than our model predicts. Secondly, we have not considered how the probability of fruit set may vary with plant age. In general, the probability of setting a harvestable pumpkin in the first female flower of a pumpkin plant is higher, because pumpkins produce at least twice as much female flowers than fruits, which means that the successful pollination of the first pollinated female flowers reduces the plant's pollination requirements [30]. Based on observations of 30 non-manipulated plants the probability of setting a harvestable pumpkin in the first female flower of a plant (80%) could be twice as high as the probability of fruit set in all flowers (41%). Third, the threshold of fruit set in the manipulated yield experiments (41%) was much lower than could be expected given the use of the first female flowers and removal of other flowers. Most likely because the plants in this experiment received less water than the flowers of the non-manipulated plants, but other differences between fields and Hokkaido cultivars might also have contributed to the differences between fruit sets. On the other hand the similarity of the calculated threshold of fruit set derived from our yield-experiment and the overall probability of fruit set in non-manipulated plants in another field enabled us to combine the probability equation of fruit set derived from our manipulated plants with field-data from non-manipulated plants to estimate yield per hectar. Nevertheless, our yield estimates are not precise owing to the possible variation of all input variables. While these additional complexities could be incorporated in future models if desired, we do not anticipate that they would qualitatively change the outcome of our analysis.

5.4.4 Management implications

Importantly, pumpkin received more than enough visits of honey and bumble bees in our region. Thus, the system is currently resilient to the decline of either honey bees or bumble bees, but not to the decline of both. However, it should be taken into account that in our region cucurbit crops are grown in moderate field sizes (3 ha), that they comprise only a small proportion of all cropping area (on average 9 ha pumpkin in 1 km radius) and that few other pollen and nectar resources were available to bees during the bloom of the pumpkin fields (S.C.P. 2012, 2014, 2015, personal observation). Thus, pollinators were likely attracted to the floral rewards in the pumpkin fields from a relatively large area. It is possible that more bees will be needed in other landscapes where the cultivation area of cucurbit crops or competing simultaneously flowering crops is larger. For crops with high pollinator dependence such as pumpkin, yield variability is quite high (~13.2%) [9]. Thus, high pollination levels must be ensured to increase yield stability [9]. Therefore, we recommend a management strategy for pumpkin that supports and sustains high densities of bees. Especially bumble bees should be supported, because their abundance depends on undisturbed natural land offering nesting sites and year-round floral resources, which are not always available near crops in agricultural settings [5,47]. In intensively farmed areas, the pollinator fauna could be supported by both a high frequency of interstitial semi-natural habitats and areas of organic farming, which can benefit bees by providing flower resources and suitable nesting habitats [7,48].

Finally, we encourage the adaptation of our quantitative approach to other pollinator-dependent crops such as almonds, citrus and apple in order to determine their resilience to potential pollinator decline in different regions. If widely adopted, these techniques could provide mechanistically supported inferences about food security in pollinator-dependent crops worldwide. Overall, studies like ours could become increasingly important for directing stewardship efforts involving habitat management, landscape modification and the protection of bee habitats within the agricultural landscape.

Research ethics

The study followed the laws and ethical guidelines of Germany.

Animal ethics

Wild bee capture and field experiments were approved by the regional nature conservation administration (Struktur- und Genehmigungsdirektion Süd, Neustadt).

Permission to carry out fieldwork

We obtained the permissions of the farmers to conduct fieldwork in their fields.

Data Availability

All data and code to reproduce this analysis are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.fh078

Competing interests

We declare we have no competing interests.

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5.6 Supplementary Material

Table S5.1 Methods used in 2014 and 2015 to transfer fixed pollen loads to the stigma in the yield experiment. Pollen loads were transferred by different methods: a metal wire (= clip, diameter 1 mm), a nail head (diameter 2.4 mm) and pieces of anthers. Pollen loads were measured on extra flowers, not used for the yield experiment, but treated with the same hand-pollination methods. Given are the replicates of pollen measures and separately replicates of the different levels of pollen numbers in the yield experiment and the mean and standard deviation (SD) of pollen deposited on the stigma. For levels, where we have not measured the transferred pollen, we estimated it from the known data (indicated by “~”). Repetitions of the clip method exactly resulted in multiplicated amounts of transferred pollen, therefore estimates for repetitions and combinations with the clip method were calculated by simple addition and multiplication. Repetition of the nail head method did result in much lower transferred pollen amounts than would be estimated by the multiplication of the amount tranferred by using the nail head once, therefore estimates for the repeated use of the nail head (three and four times) were calculated by multiplication of the measured pollen amount transferred by using the nail head twice. Hand-pollinations for yield measurement were done on 6 days in 2014 (12.- 18.07.2014) and 7 days in 2015 (28.6.- 2.7.2015 and again 21.7. – 1.8.2015, because almost all fruits of the first pollination round in 2015 were aborted owing to heat and water stress independently of the treatment). Per day 10 – 40 plants were hand-pollinated, thus 2 to 6 replicates of each level of pollen numbers per day. If all fruits of all treatments, that were pollinated on the same date, aborted, the data was removed from the statistical analysis (data of 1 day in 2014 and of 2 days in 2015).

year	**method**	**Replicates**	**Transferred pollen**		**Replicates**
		Pollen measure	mean	SD	Yield experiment
2014	counting	4	50	0	13
2015	1x clip	5	82	22 (27%)	19
2015	3x clip	4	246	21 (9%)	0
2015	4x clip	0	~330		22
2015	1x nail head	16	528	75 (14%)	19
2015	2x nail head	5	702	167 (24%)	20
2015	1x nail+ 3x clip	0	~780		22
2015	3x nail	0	~1100		19
2015	4x nail	0	~1400		19
2014	1 mm of ¼ anther	4	888	549 (62%)	16
2014	4 mm of ½ anther	4	3575	585 (16%)	14
2014	1 anther	4	14038	4818 (34%)	13
2014	5 anthers	4	21088	12391 (59%)	15

Table S5.2 Performance indicators of the Hokkaido pumpkin pollination system and its component pollinators: bumble bees, honey bees, and two sizes of halictid bees. The figures show the taxon-specific contributions to the total estimated number of pollen grains (50,307) that are deposited on an average flower's stigma by 155 flower visits with annotation indicating model solutions or parameter values.

Name	Parameter	Bumble bee	Honey bee	Small halictid	Large halictid
Total deposition	D_i	18144	31980	48	135
Per visit deposition	d_i	864	260	6	45
Visits per flower lifetime	v_iR	21	123	8	3
Stigmatic contact	s	0.99	0.95	0.76	0.98
Handling time	H	12	144	153	298
No. of observations	n	282	1664	114	40

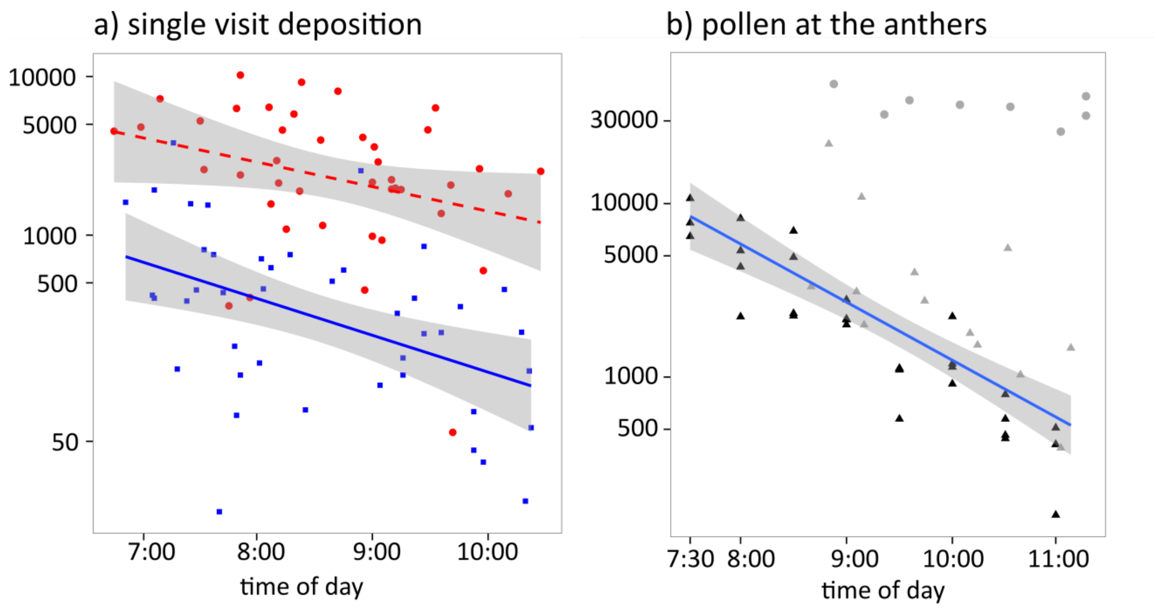

Figure S5.1 The availability of pollen in the anthers of male flowers and pollen deposition on the stigmas of female flowers decreased over the daily flowering interval.

a) Single visit pollen deposition on the stigma by honey (squares, solid line) and bumble bees (circles, dashed line) decreased in the course of the morning.

b) Number of pollen grains at the anthers in open male flowers decreased in the course of the morning (triangles). The initial amounts of pollen in closed male flowers (circles) did not vary over time and was c. 37000 pollen grains. Datasets collected in two separate years are distinguished by colour (2012: grey, 2015: black).

First visitors remove a high amount of pollen (see also a) pollen deposition), thus male flowers can loose a high amount of pollen very early in the morning. In 2015 male flowers were visited by around 3 bumblebees and 12 honeybees per hour.

Chapter 6 Dominance of agricultural land reduces crop pollination services from bumble bees

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Abstract

Wild bees deliver important crop pollination services whose sustainability may be affected by quality of habitat offered by farmland. We studied the effects of farming intensity in the landscape up to 1 km radius on pollinator visits and pollen delivery to pumpkin fields in Germany. We found that wild bumble bees were the key pollinators of pumpkin despite higher visitation frequency of honey bees and, critically, we observed that their pollination service declined strongly with increasing agricultural land cover in the landscape. Specifically, a 10% increase of the proportion of agricultural land reduced pollen delivery by 7%. Our findings suggest that habitat conversion to agricultural land is a driver of deteriorating pollination services. This underlines the importance to maintain sufficient areas of non-crop habitats in agricultural landscapes.

Keywords

Ecosystem services, landscape context, *Cucurbita maxima, Bombus* sp., landscape insecticide intensity, field management, field margin, *Apis mellifera,* seminatural habitat

6.1 Introduction

Pollination is an important ecosystem service, especially for pollinator-dependent crops such as pumpkin (Klein *et al.* 2007). Worldwide 75% of our leading food crops benefit from or even depend upon animal pollination (Klein *et al.* 2007), translating into an annual value of pollination services around 235- 577 billion US $ (Lautenbach *et al.* 2012; Potts *et al.* 2016). Pollinator-dependent crops are mainly fruits, nuts and vegetables, which contain essential micronutrients. Therefore pollination deficits can increase malnutrition (Chaplin-Kramer *et al.* 2014). Although their proportion of the global food volume is small (5-8%), the dependency of global food production on pollination is now twofold higher than fifty years ago (Potts *et al.* 2016). At the same time managed and wild bees declined globally owing to habitat loss, pesticides, mismanagement of bees, climate change, diseases and their interactions (Potts *et al.* 2010; Goulson *et al.* 2015; Potts *et al.* 2016). As a result, worldwide many pollinator-dependent crops suffer from pollination instability and deficit (Garibaldi *et al.* 2013; Garibaldi *et al.* 2016). By enhancing the visits of bees and especially of wild bees fruit set and yield of these crops can be increased (Garibaldi *et al.* 2013; Garibaldi *et al.* 2016). Pollination intensity is usually measured as fruit or seed set or yield (Ricketts *et al.* 2008; Garibaldi *et al.* 2011b; Garibaldi *et al.* 2013; Garibaldi *et al.* 2016). However, measures of natural pollen deposition should be better suited to distinguish among the potential drivers of pollination decline. First, it is more directly related to pollinator activity than fruit set and yield, which are influenced by many not-pollination related variables. Second, although pollinator activity is important, the amount of flower visits is not necessarily a good proxy for pollination, because flower visitors can vary largely in their effectiveness (Garibaldi *et al.* 2013). Nevertheless, there are few studies that relate actually measured, cumulative natural pollen deposition to landscape effects on pollination (Ricketts 2004; Phillips & Gardiner 2015).

Wild bees are important pollinators, even in the presence of honey bees *Apis mellifera*. They ensure and enhance pollination through spatial and temporal complementarity, behavioural interactions and higher efficiency (Greenleaf & Kremen 2006; Hoehn *et al.* 2008; Garibaldi *et al.* 2011b; Garibaldi *et al.* 2013). Further, the pollination services of wild bees are consistent across fields with a similar landscape context, over days and years (Rader *et al.* 2012). Therefore farming practices and landscape management need to safeguard pollinators and pollination (Potts *et al.* 2016). In general, wild bees need nesting sites and a continuity of abundant and diverse floral resources (Goulson *et al.* 2015). Thereby, primarily floral resources affect bees (Roulston & Goodell 2011) and both flower richness and floral cover enhance the number of bee visits and diversity (Ebeling *et al.* 2008). In addition, flower richness can contribute to a continuity of floral resources and thereby reduce temporal variability of bee visits (Ebeling *et al.* 2008). Therefore, the abundance and diversity of wild bees are positively influenced by organic farming (Batary *et al.* 2011; Tuck *et al.* 2014) and seminatural habitats at the local and landscape scale (Kennedy *et al.* 2013; Scheper *et al.* 2013), which usually contain abundant and diverse flower resources i.a. owing to the renunciation of herbicides (Holzschuh *et al.* 2007; Rundlöf *et al.* 2008). Seminatural habitats further provide nesting sites (Roulston & Goodell 2011). In consequence pollination is often more successful in organic than in conventional fields (Morandin & Winston 2005; Andersson *et al.* 2014) and in fields in proximity to seminatural habitats (Ricketts *et al.* 2008; Garibaldi *et al.* 2011b; Garibaldi *et al.* 2016). However, much less is known about the negative effects of pesticides at the landscape scale. Wild bees are exposed to multiple pesticides nowadays (Hladik *et al.* 2016; Botias *et al.* 2017) and especially neonicotinoids can have adverse effects on bees (Goulson & Kleijn 2013). Pesticides are frequently found in wild bumble bees, whereby more pesticides were found in bumble bees foraging in agricultural landscapes than in urban landscapes (Botias *et al.* 2017). In addition to pesticide applications, habitat conversion to agricultural land has other negative effects on pollinators (Goulson *et al.* 2015). Frequent soil disturbance and vegetation removal prohibit nesting of wild bees in annual crops (Roulston & Goodell 2011; Goulson *et al.* 2015). In addition, wind-pollinated crops such as cereals offer no floral resources to bees, especially if herbicides exclude wild flowering plants (Goulson *et al.* 2015). Even mass-flowering crops such as oilseed rape only offer monotonous resources for short time periods so that few, if any, bee species will be able to complete their life cycle on them (Goulson *et al.* 2015; Holzschuh *et al.* 2016). Thus, agricultural land is a largely hostile environment for wild bee species, and land use change into crops may trigger their persistence in farmed landscapes. Most existing studies do not distinguish among possible drivers of crop pollination at the landscape scale, namely the availability of seminatural habitats for nesting and alternative resources on the one hand, and potential negative drivers such as high proportions of agricultural land or the intensity of insecticide use in the surrounding landscape on the other (e.g. Garibaldi *et al.* 2011b; Garibaldi *et al.* 2016).

We addressed this gap of knowledge by studying pollinator activity and pollen delivery to pumpkin across replicated landscapes. We studied the combined effect of organic farming, field-bordering seminatural habitats, land-use composition and insecticide intensity in the surrounding landscape on pollinator visits and pollen delivery in 18 pumpkin fields. We chose pumpkin, because pumpkin has separate male and female flowers and heavy pollen grains, thus it is obligate cross-pollinated by insects (Hurd *et al.* 1971). In addition, pumpkin has a short flower lifetime (6 hours – 1 day) and needs a high pollinating intensity (ca. 2,500 pollen grains are needed to maximize fruit set) and therefore needs effective and rapid pollinator visits (Dmitruk 2008; Nepi & Pacini 1993; Pfister et al. subm.). We tested the following hypotheses:

1. Pollen delivery is positively related to the number of pollinator visits (honey and bumble bees).
2. The number of pollinator visits is higher in organic fields and in fields with adjacent seminatural habitats (local management).
3. The proportion of agricultural land and insecticide intensity in the landscape reduce the number of pollinator visits and thereby pollen delivery (landscape effects).

6.2 Material and methods

6.2.1 Study sites

Pollinator visits and pollen delivery were studied in 2014 in 18 commercial pumpkin fields *Cucurbita maxima* Duchesne ex Poir cv Hokkaido (mean field size 3 ± 2.4 ha) in the Upper Rhine valley between Ludwigshafen and Kandel, Germany (49°4 N, 8°6 E; 49°27 N, 8°28 E; 90 – 155 m a.s.l.) (see Fig. 4.1, p. 107). The area has a temperate climate with annual mean temperatures around 11 °C and 700 mm of annual precipitation on average (station Landau, German Weather Service). Each 9 fields were managed conventionally or organically (EU-Eco regulation 834/2007, European Commision 2007), respectively. Six fields were bordered by another crop field and 12 fields by a herbaceous or woody seminatural habitat (SNH). SNH were defined as any habitat containing a community of non-crop plant species and include herbaceous (e.g. field margins, fallows) and woody vegetation (e.g. hedgerows, forest fragments) with a minimum width of 1.5 m, a minimum length of 50 m and a minimum size of 150 m^2 (Holland *et al.* 2014). In addition, the pumpkin fields were located in landscapes differing in the proportion of seminatural habitats (5- 49%) and in the proportion of agricultural land in 1 km radius around the focal field (28- 91%). To calculate the proportions we mapped habitats around the focal field in 1 km radius. The habitats were classified into 56 categories that included 45 crops (e.g. annual and perennial crop types, orchards), SNH (e.g. forests, grasslands, hedgerows and grass margins), urban areas, water bodies and other habitats. Any mapped element had a minimum width of 1.5 m and at least 50 m length and a minimum size of 75 m^2. Land use classifications were confirmed with ground-truthing surveys at every site.

6.2.2 Insecticide intensity

We further used the landscape data of the 16 most abundant crop types to calculate an index of insectide use intensity for the landscape surrounding each field.

$$Ia = \left(\sum_{k=1}^{n} NI_k * \%A_k\right) / \%Aa \qquad Eq\ 1$$

The landscape insecticide index Ia ($Eq\ 1$) was calculated by summing up the insecticide applications per crop NI_k weighted by crop area $\%A_k$ divided by the proportion of agricultural land in the landscape sector $\%Aa$ to have a value independent from the proportion of agricultural land in the landscape sector. NI_k is the average number of insecticide applications on crop k in conventional management according to the reports from the Federal Research Centre for Cultivated Plants (Roßberg 2009, 2010; Roßberg *et al.* 2010; Roßberg & Hommes 2014; Roßberg 2016) and according to the regional extension service (Dienstleistungszentrum ländlicher Raum, pers. comm.) (Table S6.1). For the number of insecticide applications on pumpkin we used the average value that was applied in 2014 and 2015 on 18 conventional pumpkin fields in the case study region (farmer´s questionaires). $\%A_k$ is the proportion of the area occupied by crop k on the total area *A* of the landscape sector (314 ha).

6.2.3 Pollinator visits

Flower visitors and their foraging behaviour were documented by a digital HD video camera recorder (handycam Sony ® HDR-CX115E). Each field was investigated at each one time period on three different days in July during the flowering period (2-6, 15-17, 23-25 of July 2014), once at 7:00, 8:30 and 10:00 am. On each occasion, we recorded four 15-minute-long videos each surveying a different female pumpkin flower. The camera was positioned ~50 cm above a female flower in order to monitor the mouth of the flower's corolla. Weather conditions were comparable at all samplings (temperature at ground level 24 ± 5°C measured by HOBO ® Pendant temperature/light data logger UA-002-08, wind velocity at 1.5 m above ground 0.8 ± 0.7 m/s measured by cup anemometer PCE-A420). From the videos we extracted the visitation rates for each bee group. Video recording is a suitable method to sample visitation rates in pumpkin (Artz & Nault 2011; Phillips & Gardiner 2015), because the frequency of visits is high and relatively evenly distributed across flowers. Three bee groups were distinguished: 1) honey bees *A. mellifera* L., 2) bumble bees = *Bombus terrestris* L. agg. (including *B. terrestris* L. and *B. lucorum* L.) and

B. lapidarius L. and 3) halictid bees (several species, species could not be distinguished from the video data). Bee identification followed Schmid-Egger et al (1995) and Amiet (1996).

6.2.4 Pollen delivery

In order to quantify the pollen delivery by the collective pollinator fauna, we measured stigmatic pollen loads of open pollinated flowers corresponding to the first two samplings where we recorded the pollinator visits. In the 18 studied fields we harvested 16 stigmas per sampling and field (Σ 32/ field) after 14:00 pm, when pollination had finished, and stored them in a freezer. We extracted the pollen by acetolysis following Jones (2012). After the acetolysis, glycerol 50% was added to the extracted pollen to a total volume of 2 mL. To evenly re-suspend the pollen, the vials were shaken by a vortex mixer prior to taking three subsamples of 50 µL from the pollen suspension. Each subsample was pipetted on 1 cm^2 area and a picture (2560 x 1920 pixel) was taken by a microscope camera (Zeiss AxioCam ERc 5s). The pollen on this picture was counted by image analysis (ImageJ v. 1.48, defined particle size 225- 900 $Pixel^2$, circulartiy 0.7- 1.0). The total pollen load was extrapolated volumetrically from the mean of the subsamples.

6.2.5 Statistics

We performed structure equation models (package “lavaan”, Rosseel 2012; Shipley 2016) in order to determine the effects of management (factor: organic or conventional), adjacent habitat (factor: SNH or crop), landscape insecticide intensity (continuous), proportion of agricultural land in 1 km radius (continuous), and proportion of SNH in 1 km radius (continuous) on flower visitation and pollen delivery. The proportion of agricultural land in 1 km radius and the proportion of SNH in 1 km radius were correlated ($r = -0.65$). Hence, a model with both variables would not be multivariate normal. Thus, we calculated two models, with either the proportion of agricultural land or the proportion of SNH plus the remaining explanatory variables. All numeric variables were tested for multivariate normality (package “MVN”, Korkmaz *et al.* 2014). With the structure equation models we studied the direct effects of the above mentioned explanatory variables on the number of honey or bumble bee visits in 3 hours [sum of 12 videos per field] and their indirect effects on pollen delivery on female pumpkin flowers [mean pollen delivery on 32 stigmas per field] mediated by honey and bumble bee visits. Covariances between the predictors were fixed, when they were independent from each other (pearson correlation $r < 0.4$, see Table S6.2). The following three covariances were not fixed: adjacent habitat and landscape insecticide intensity, adjacent habitat and proportion of agricultural land in 1 km radius, and proportion of agricultural land in 1 km radius and landscape insecticide intensity. Owing to our small sample size we used the generalized least-squares chi-square statistic (Shipley 2016). Linear models relating bumble bee visits or pollen delivery with proportion of agricultural land were compared to models with proportion of seminatural habitats by Akaike´s information criterion for small sample sizes (AICc, package “AICcmodavg”, Mazerolle 2016). Data and R code are available from the Dryad repository (*link to be inserted*). All analyses were conducted in R 3.3.1 (R Core Team 2015).

6.3 Results

In total we observed 2,100 bee individuals, of which 79% were honey bees *Apis mellifera*, 14% bumble bees (mainly *Bombus terrestris agg.*, some *B. lapidarius*) and 7% halictid bees in 54 hours of video footage. At maximum 33,147 pollen grains were delivered to a female pumpkin flower, average delivery was 11,600 per flower (± 5,680, n = 551).

Pollen delivery significantly increased with the number of bumble bee visits, while the numerically dominant honey bees had no effect on pollen delivery (Fig. 6.1, Fig. 6.2 A+B, Table 6.1). The proportion of agricultural land in 1 km radius strongly reduced the number of bumble bee visits (Fig. 6.2 C, Table 6.1), with a corresponding decline in pollen delivery (Fig. 6.1, Fig. 6.2 D, Table 6.1). An increase of agricultural land in the surrounding landscape by 10% reduced the number of bumble bee visits by two and the number of delivered pollen grains by ca. 1,200 per female flower. The proportion of seminatural habitats tended to increase bumble bee visits and increased pollen delivery (second structure equation model see Table S6.3). The models with agricultural land explained more of the variance (AICc [pollen delivery ~ %agricultural land] = 343, AICc [pollen delivery ~%SNH] = 347; AICc [bumble bee visits ~ % agricultural land] = 148, AICc [bumble bee visits ~ %SNH] = 154). There were no significant effects of management, the adjacent habitat, and insecticide intensity on honey and bumble bees (Table 6.1).

Table 6.1 Direct effects of adjacent habitat (factor: crop or SNH), management (factor: organic or conventional), proportion of agricultural land in 1 km radius (% agricultural land, continuous), and insecticide intensity in the landscape (continuous) on visits of honey and bumble bees and direct and indirect effects of them on pollen delivery (hypothesised causal structure see Fig. 1). Indirect effects on pollen delivery are split in effects mediated by bumble bee visits or by honey bee visits. Results from the structure equation model (number of observations = 18, minimum generalized least-squares chi-square statistic = 9.3, df = 11) are displayed. For all predictors estimates, standard errors, z-values and p-values are given. R^2 is given per response.

response	**mediated by**	**predictor**	**estimate**	**Std.Err**	**z-value**	**P**	**R^2**
Honey bee visits		~					0.33
		Adjacent SNH	12.1	21.2	0.6	0.57	
		Organic	-19.8	10.2	-1.9	0.053	
		% Agricultural land	0.1	0.4	0.3	0.76	
		Insecticide intensity	-4.2	3.8	-1.1	0.26	
Bumble bee visits		~					0.61
		Adjacent SNH	4.6	11.1	0.4	0.68	
		Organic	8.5	5.0	1.7	0.090	
		% Agricultural land	-0.64	0.19	-3.5	0.001	
		Insecticide intensity	0.3	1.8	0.2	0.88	
Pollen delivery		~					0.67
		Honey bee visits	22	25	0.9	0.38	
		Bumble bee visits	183	40	4.5	< 0.001	
	Honey bee visits	Adjacent SNH	260	571	0.4	0.65	
		Organic	-425	523	-0.8	0.43	
		% Agricultural land	2	8	0.3	0.77	
		Insecticide intensity	-91	118	-0.8	0.45	
	Bumble bee visits	Adjacent SNH	829	2059	0.4	0.68	
		Organic	1566	973	1.6	0.11	
		% Agricultural land	-118	39	-3.0	0.003	
		Insecticide intensity	52	339	0.2	0.88	

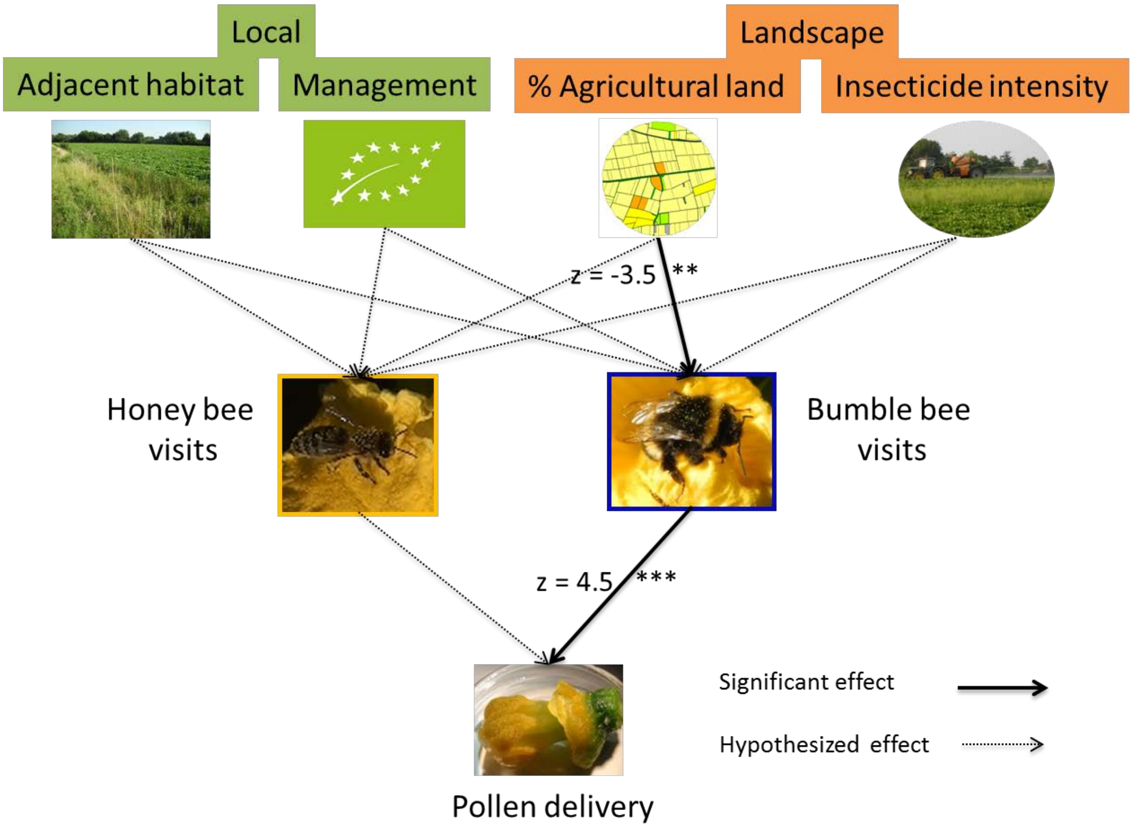

Figure 6.1 Effects on pumpkin pollination: Separation of the effects of adjacent habitat type (crop, SNH), management (organic, conventional), proportion of agricultural land in 1 km radius and insecticide intensity in the landscape on bumble bee and honey bee visits and the impact of all these variables on pollen delivery. Dotted arrows show hypothesised impacts, bold solid arrows show significant effects ($p < 0.05$) derived from the structure equation model. Proportion of agricultural land in 1 km radius decreased bumble bee visits. Pollen delivery only increased with bumble bee visits, but not with honey bee visits. Statistics see Table 6.1.

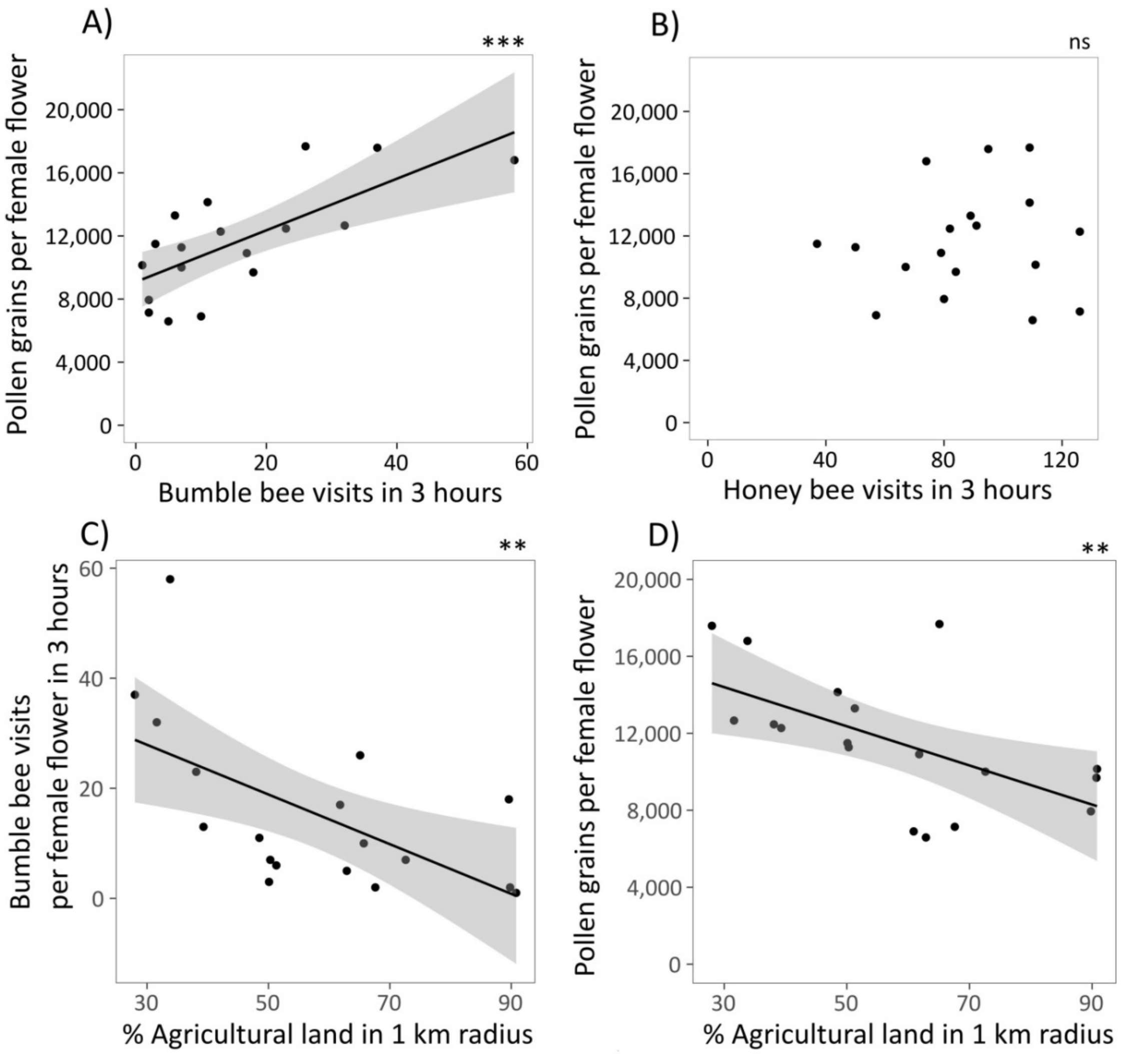

Figure 6.2 Pollen delivery increased with bumble bee visits (A), but was not related to the number of honey bee visits (B). The proportion of agricultural land in 1 km radius reduced the number of bumble bee visits (C) and pollen delivery (D). Statistics see Table 6.1.

6.4 Discussion

6.4.1 Pollination efficiency

Surprisingly, honey bee visits did not significantly contribute to pollen delivery in our pumpkin fields, although there were around five times more visits by honey bees than by bumble bees. This can partly be explained by the six times higher single-visit deposition of bumble bees compared to honey bees (Pfister et al. subm.). With on average 11,000 deposited pollen grains, around four times more pollen grains were deposited than needed to maximize fruit set (~2,500 pollen grains are needed, Pfister et al. subm.). Thus, there is no pollination deficit in pumpkin in our region. Only 3% of the investigated flowers received less than 2,500 pollen grains, half of them because the flowers were filled with water from overhead irrigation. Nevertheless, crops with lower visitation rates per flower, such as strawberry, may suffer yield losses in our study region.

6.4.2 Local management

In contrast to our expectations, local management (organic farming and field-bordering seminatural habitats) had no significant effects on pollinator visits and consequently on pollen delivery. This may be owing to the large foraging ranges of honey and bumble bees (Greenleaf *et al.* 2007) in combination with the high attractivity of pumpkin flowers. In late summer floral resources are scarce in agricultural landscapes (Persson & Smith 2013). Pumpkin flowers offer high nectar and sugar amounts (c. 290 µL nectar m^{-2} day^{-1} and 30 mg sugar m^{-2} day^{-1}; Dmitruk 2008: amounts per flower, combined with own flower density data). Consequently, pumpkin may attract honey and bumble bee populations from the wider landscape context. Further, although herbicides were applied in conventional fields, they had a higher weed cover than organic fields and two conventional fields had very high abundances of flowering weeds (Table S6.4). This is in contrast to other studies finding positive effects of organic farming on plants and pollinators (Batary *et al.* 2011; Tuck *et al.* 2014). Conventional farmers can tolerate a higher weed cover in pumpkin, because pumpkin outcompete the weed and the weed pressure in subsequent crops can be regulated by herbicides, whereas organic farmers depend more strongly on low weed pressures for the subsequent crops. Insecticide use did not differ significantly between organic and conventional management. However, management varied a lot within organic farming. Organic fields managed according to the EU-Eco regulation 834/2007 had more insecticide applications than conventional fields and organic fields managed by rules from organic associations, which ban insecticides completely (Table S6.4).

6.4.3 Landscape effects

In line with Petersen & Nault (2014), the landscape effects on pollination were mediated by bumble bees. Surprisingly, the negative effects of agricultural land on bumble bee visits and pollen deposition were stronger than the positive effects of seminatural habitats. Several studies report positive effects of seminatural habitats, such as grassland (Petersen & Nault 2014), forest (Julier & Roulston 2009) or both (Xie & An 2014), on bumble bee visits and on modelled pollen deposition in pumpkin in North America and China. Similar to our findings, bumble bee visits and pollen deposition were higher in landscapes dominated by seminatural habitats (forest and grassland) and urban habitats than in landscapes dominated by agricultural land in North America (Phillips & Gardiner 2015).

Existing studies of crop pollination in a landscape context did not distinguish between positive effects of seminatural habitats or negative effects of agriculture (e.g. Garibaldi *et al.* 2011b; Garibaldi *et al.* 2016). The dominant role of agricultural land cover in our study suggests that it should be included also in other studies of landscape management for ecosystem services. Surprisingly, the insecticide intensity in the surrounding landscape did not influence bee visits or pollen delivery. Thus, the hostility of agricultural landscapes seems to be mainly related to the lack of nesting sites and floral resources, which seem to be more important drivers than insecticide intensity. This can pose a dilemma to crop production if land use change into crops creates a negative feedback on productivity via the decline of pollinators (Garibaldi *et al.* 2011a). Hostility of agricultural land as the main limiting factor for pollination services implies that efforts of reducing farming intensity or adding small surfaces of ecological compensation areas may offer little prospect of sustaining this ecosystem service in landscapes dominated by agriculture. If confirmed by other studies, a dominant role of agricultural land cover for pollination services would imply that moving pollination-dependent crops to more complex landscapes is more realistic than enhancing pollinators within landscapes dominated by agriculture, at least as far as wild pollinators are concerned.

6.4.4 Conclusions

Our study demonstrates that honey bees, even at fivefold visitation frequency compared to bumble bees, have no measurable effect on pollen delivery to pumpkin. Thus, pumpkin provides a striking example for a dominant role of wild pollinators for pollination success of a crop. In addition, our study suggests that the dominance of agricultural land is the main limiting factor for the pollination of pumpkin through its negative effect on bumble bee visitation. Thus, sufficient areas of non-crop habitats need to be maintained in agricultural landscapes for pollination-dependent crops.

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6.5 References

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6.6 Supplementary Material

Table S6.1 Average number of insecticide treatments of the 16 dominant crops in our study area (proportion of total area in the landscapes, LS = number of landscapes, where the crop was present) according to the cited literature.

crop	**% of total area (range)**	**LS**	**N insecticide treatments**	**literature**
apple	0 – 10%	9	7.5	Roßberg 2009
asparagus	0 – 5%	10	1.1	Roßberg & Hommes 2014
cabbage	0 – 4%	10	4.9	Roßberg & Hommes 2014
carrot	0 – 7%	11	1.7	Roßberg & Hommes 2014
maize	1 – 36%	18	0.03	Roßberg 2016
oilseed rape	0 – 4%	9	2.7	Roßberg 2016
onion	0 – 11%	11	0.7	Roßberg & Hommes 2014
potato	0 – 10%	14	0.8	Roßberg 2016
pumpkin	1 – 8%	18	0.5	Own data mean of 18 conv. fields
raphanus	0 – 4%	11	2.0	DLR, pers. comm.
rhubarb	0 – 2%	10	0.0	DLR, pers. comm.
salad	0 – 3%	10	2.7	Roßberg & Hommes 2014
strawberry	0 – 4%	7	2.4	Roßberg 2009
sugar beet	0 – 18%	17	0.14	Roßberg *et al.* 2010
vine	0 – 14%	9	0.4	Roßberg 2010
winter wheat	1 – 41%	18	0.7	Roßberg 2016

Table S6.2 Pearson rank correlation coefficients for all pairs of explanatory variables (lower panel) and asymptotic p-values (upper panel). Pearson correlations with r ≥ 0.40 (p ≤ 0.1) are marked in bold. Variables with r > 0.6 are not included in the same model. For variables with r < 0.4 covariances were fixed in the structure equation model.

	Adjacent SNH	Organic	% Agricultural land	% SNH	Insecticide intensity
Adjacent SNH		1.0	0.08	0.61	0.04
Organic	0		1.0	0.52	0.93
% Agricultural land	**-0.42**	0		0.004	0.10
% SNH	0.13	-0.16	**-0.65**		0.11
Insecticide intensity	**-0.48**	-0.02	0.40	-0.39	

Table S6.3 Direct effects of adjacent habitat (factor: crop or SNH), field management (factor: organic or conventional), proportion of seminatural habitats in 1 km radius (% SNH, continuous), and insecticide intensity in the landscape (continuous) on visits of honey and bumble bees and direct and indirect effects of them on pollen delivery. Indirect effects on pollen delivery are split in effects mediated by bumble bee visits or by honey bee visits. Results from the structure equation model (number of observations = 18, minimum generalised least-squares chi-square statistic = 12.5, df = 11) are displayed. For all predictors estimates, standard errors, z-values and p-values are given. R^2 is given per response.

response	**mediated by**	**predictor**	**estimate**	**Std.Err**	**z-value**	**p**	**R^2**
Honey bee visits		~					0.19
		Adjacent SNH	-1.4	20.2	-0.07	0.95	
		Organic	-18	11	-1.7	0.096	
		% SNH	0.4	0.6	0.7	0.51	
		Insecticide intensity	-1.7	5.2	-0.3	0.75	
Bumble bee visits		~					0.51
		Adjacent SNH	12	10	1.2	0.24	
		Organic	7.3	5.6	1.3	0.20	
		% SNH	0.6	0.3	1.9	0.050	
		Insecticide intensity	1.8	2.5	0.7	0.48	
Pollen delivery		~					0.82
		Honey bee visits	6	21	0.3	0.77	
		Bumble bee visits	255	51	5.0	< 0.001	
	Honey bee visits	Adjacent SNH	-8	125	-0.07	0.95	
		Organic	-112	394	-0.3	0.78	
		% SNH	2	9	0.3	0.80	
		Insecticide intensity	-10	46	-0.2	0.82	
	Bumble bee visits	Adjacent SNH	3052	2567	1.2	0.23	
		Organic	1859	1382	1.3	0.18	
		% SNH	152	74	2.1	0.040	
		Insecticide intensity	460	651	0.7	0.48	

Table S6.4 Number and mode of field operations (number of herb management operations (mechanical and herbicide applications), number of applications of insecticides and fungicides, and the amount of nitrogen in kg/ha) are based on farmer´s questionaires. The proportion of weed cover was measured in four 5m^2-plots per field at four samplings (28.-30.5., 25.-27.6., 15.-17.7. and 6.-9.8.2014). The diversity and abundance of flowering weeds was measured in twenty 1m^2- plots per field at four samplings (28.-30.5. and parallel to the three pollination samplings on 2-6, 15-17, 23-25 of July 2014). Superscript letters (A, B) mark significant different groups. The test statistic (F- or χ^2-value with degrees of freedom and p-value) are given.

variable	**organic**		**conventional**	**value**	**p**
	EU-Bio	Bio-association			
N fields	3	6	9		
N herb management	2.3^{A}	2.3^{A}	3.3^{B}	$F_{1,16} = 7.2$	0.016
Mode herb management	mechanical		Herbicides (1.4) + mechanical (1.9)		
% weed cover	2.3^{A}	4.8^{A}	8.5^{B}	$\chi^2_{1,16} = 3.9$	0.049
N flowering weeds (log)	1.8	1.7	2.5	$F^2_{1,16} = 2.5$	0.13
S flowering weeds	4.3	4.8	6.8	$\chi^2_{1,16} = 1.5$	0.22
N insecticides	3^{A}	0^{B}	0.3^{B}	$\chi^2_{2,14} = 19$	< 0.001
N fungicides	2.3^{A}	0^{B}	2^{A}	$\chi^2_{2,14} = 32$	< 0.001
Nitrogen [kg/ha]	142^{A}	76^{B}	103^{AB}	$F_{2,14} = 3.6$	0.054
Fertilizer mode	organic		synthetic		

Chapter 7 Potential of seminatural habitats to support wild bees

7.1 Methods

7.1.1 Study sites

Pollinators were sampled in 69 seminatural habitats (local scale) of four different types (HA = herbaceous areal, HL = herbaceous linear, WA = woody areal, and WL = woody linear) in 18 agricultural landscapes (landscape scale) in Germany. Detailed information on the German study sites is given in section 2.2.1 (p. 57, Fig. 2.1) and 3.2.1 (p. 83).

7.1.2 Sampling

Bees were recorded with standardized transect walks and pan traps to combine the strengths of both methods. Pan traps are a very effective, collector unbiased method to sample pollinators across different habitats and regions (Westphal *et al.* 2008). On the other hand standardized transect walks are collector biased, but they really measure abundances in a defined area, provide information on bee-flower interactions and cover large bees like honey and bumble bees, that might be undersampled by pan traps (Westphal *et al.* 2008). Detailed information on pan trap sampling is given in section 2.2.2 (p. 59) and section 3.2.2 (p. 84).

For the standardized transect walks two transects (50 m length x 1.5 m width) were sampled in each SNH. One transect was always located at the field edge (0.5 m distance). In WA and HA the second transect was located in the interior of the SNH (12.5 m from the edge), while in HL and WL the second transect was located at the other edge of the habitat (similar to the location of the pan traps). Transect walks were performed between 9:30 and 17:30 under suitable weather conditions (no rain, temperature above 13°C and at least 60% clear sky or temperature above 17°C, and wind velocity below 2.5 m/s). The timing of the transect walks in a certain SNH was varied between the four samplings to account for varying bee activity. During a 10-min walk per transect syrphid flies (Syrphidae), butterflies (Lepidoptera) and bees (Hymenoptera, Apoidea) - including *Apis mellifera*, bumble bees to species level, and other wild bees - were recorded (Westphal *et al.* 2008). Species, that could not be identified in the field (all wild bees except for bumble bees), were captured for later identification, whenever possible. Wild bees collected during the transect walks were frozen and insects collected in the pan traps were stored in 70% ethanol for preserving and identification in the laboratory. The bee identification followed Schmid-Egger et al. (1995), Amiet (1996) and Amiet & Krebs (2012). Wild bees were identified to the genus level.

Per SNH and sampling the flower abundance (total number of flowers) and flower richness was recorded simultaneously to the transect walks (see section 3.2.2, p. 84f).

7.1.3 Statistics

The data was analysed in R 3.3.1 (R Core Team 2015). Species richness (= number of different bee genera) and the abundances of bees and flowering plants were summarized per SNH and sampling. The species richness of flowering plants and the floral cover were log10(x+1)-transformed to reach normal distribution. Only the species richness of flowering plants was included in the models, because the richness and the cover of flowers were correlated (Pearson correlation r = 0.75). Across samplings the floral resources varied, therefore generalized linear mixed models (glmmPQL, package MASS, Venables & Ripley 2002) nesting the samples in the individual SNH were conducted. Further the 69 individual SNH were nested in the 18 landscapes, because the surrounding landscapes of the different local SNH types overlapped. For the abundance data the quasipoisson-distribution was used and for the species richness data the gaussian distribution. The effects of the local SNH type (factor with four levels: ha, hl, wa, wl), the species richness of flowering plants (continuous) and the proportion of SNH in 1 km radius (continuous) on the species richness and abundances of bees in pan traps and transects were tested.

7.2 Results

Overall 3070 bees of 24 genera were caught in the pan traps and 1243 bees of 15 genera were sampled in the standardized transect walks, thereof honey bees (25%), bumble bees (20%) and halictid bees (37%) were the most abundant (Table 7.1). Honey bees were three times more abundant in hedgerows and grass strips and even five times more abundant in grasslands than in forests (Fig. 7.1A). Further honey bees were three times more abundant in grasslands than in hedgerows. Hedgerows contained three times more bee genera than all other local SNH types (Fig. 7.1B). The abundances of wild bees (in total and per genus) and bumble bees were not influenced by local habitat type (Fig. 7.1C, D), but the species richness of flowering plants was three to five times lower in forests compared to all other habitat types (Fig. 7.1E, Table 7.1).

Flower richness in turn had a strong positive influence on the species richness and abundance of all bees sampled in the transect walks (Fig. 7.2 A-E), whereas it did not influence the bees caught in the pan traps, except for bumble bees (Table 7.1). Landscape complexity (= proportion of seminatural habitats in the surrounding of the focal habitat) had no significant effect neither on the bees nor on flowering plants (Table 7.1).

Table 7.1 Effects of the local seminatural habitat type, flower richness (S flowers, log-transformed) and landscape complexity (%SNH landscape) on the abundance and the species richness of bees (sampled with pan traps or in transect walks) in total and per genera. Given are t-values for numerical variables and Chi-square values for factors, both with degrees of freedom. (*) $p < 0.1$, '*' $p < 0.05$, '**' $p < 0.01$, '***' $p < 0.001$.

method	**response**	**SNH type**	**S flowers**	**%SNH landscape**	**sum**
Pan trap	Honey bees	$Chi^2_{3, 44} = 28.4$***	$t_{206} = 0.2$	$t_{47} = -0.2$	547
Transect	Honey bees	$Chi^2_{3, 44} = 8.0$*	$t_{206} = 5.5$***	$t_{47} = 1.0$	517
Pan trap	S bees	$Chi^2_{3, 44} = 7.6$ (*)	$t_{206} = 1.6$	$t_{47} = -0.3$	24 genera
Transect	S bees	$Chi^2_{3, 44} = 12.6$**	$t_{206} = 7.1$***	$t_{47} = -0.7$	15 genera
Pan trap	N wild bees	$Chi^2_{3, 44} = 4.3$	$t_{206} = 0.7$	$t_{47} = -1.3$	2523
Transect	N wild bees	$Chi^2_{3, 44} = 3.2$	$t_{206} = 8.6$***	$t_{47} = -1.5$	726
Pan trap	Bumble bees	$Chi^2_{3, 44} = 3.1$	$t_{206} = 4.3$***	$t_{47} = 0.2$	294
Transect	Bumble bees	$Chi^2_{3, 44} = 2.0$	$t_{206} = 5.2$***	$t_{47} = -1.6$	581
Pan trap	B. terrestris	$Chi^2_{3, 44} = 1.1$	$t_{206} = 0.9$	$t_{47} = -1.0$	276
Transect	B. terrestris	$Chi^2_{3, 44} = 0.2$	$t_{206} = 4.5$***	$t_{47} = -1.5$	171
Pan trap	Halictid bees	$Chi^2_{3, 44} = 5.0$	$t_{206} = 0.1$	$t_{47} = -1.5$	1499
Transect	Halictid bees	$Chi^2_{3, 44} = 4.9$	$t_{206} = 7.5$***	$t_{47} = -1.4$	87
Pan	Andrena	$Chi^2_{3, 44} = 4.1$	$t_{206} = 0.6$	$t_{47} = -0.2$	455
Count	S flowers	$Chi^2_{3, 44} = 10.3$*		$t_{47} = -1.4$	238 species

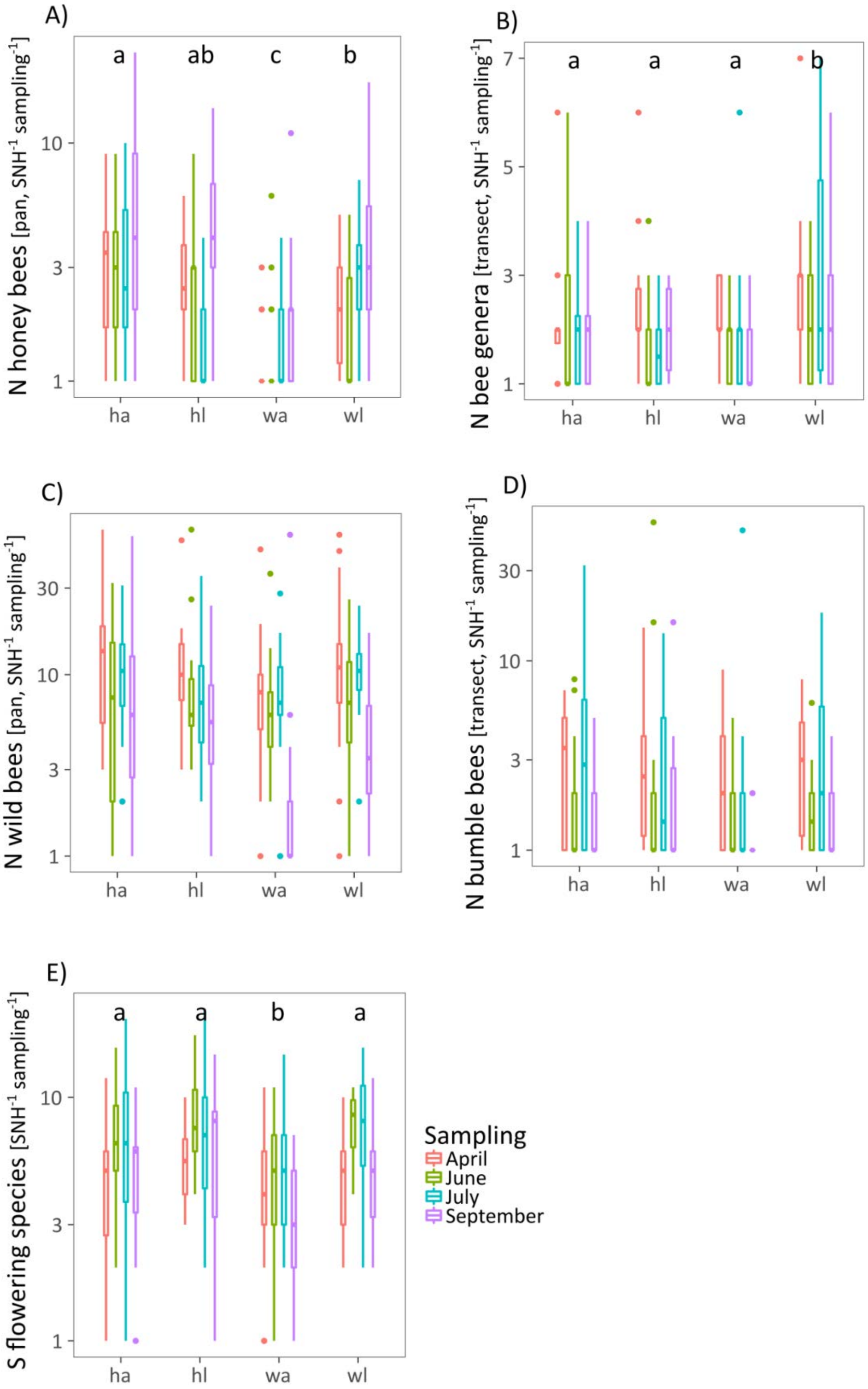

Figure 7.1 Effects of the seminatural habitat type (ha = 16 grasslands, hl = 18 herbaceous field margins, wa = 17 forests or shrublands, wl = 18 hedgerows) on A) the abundance of honey bees, B) the number of genera of wild bees (bee richness) C) the abundance of wild bees, D) the abundance of bumble bees and E) the species richness of flowering plants shown with boxplots. The values are the sums per seminatural habitat and sampling (red = April, green = June, blue = July, purple = September). Significant differences between seminatural habitat types are indicated with different letters. Statistics see Table 7.1.

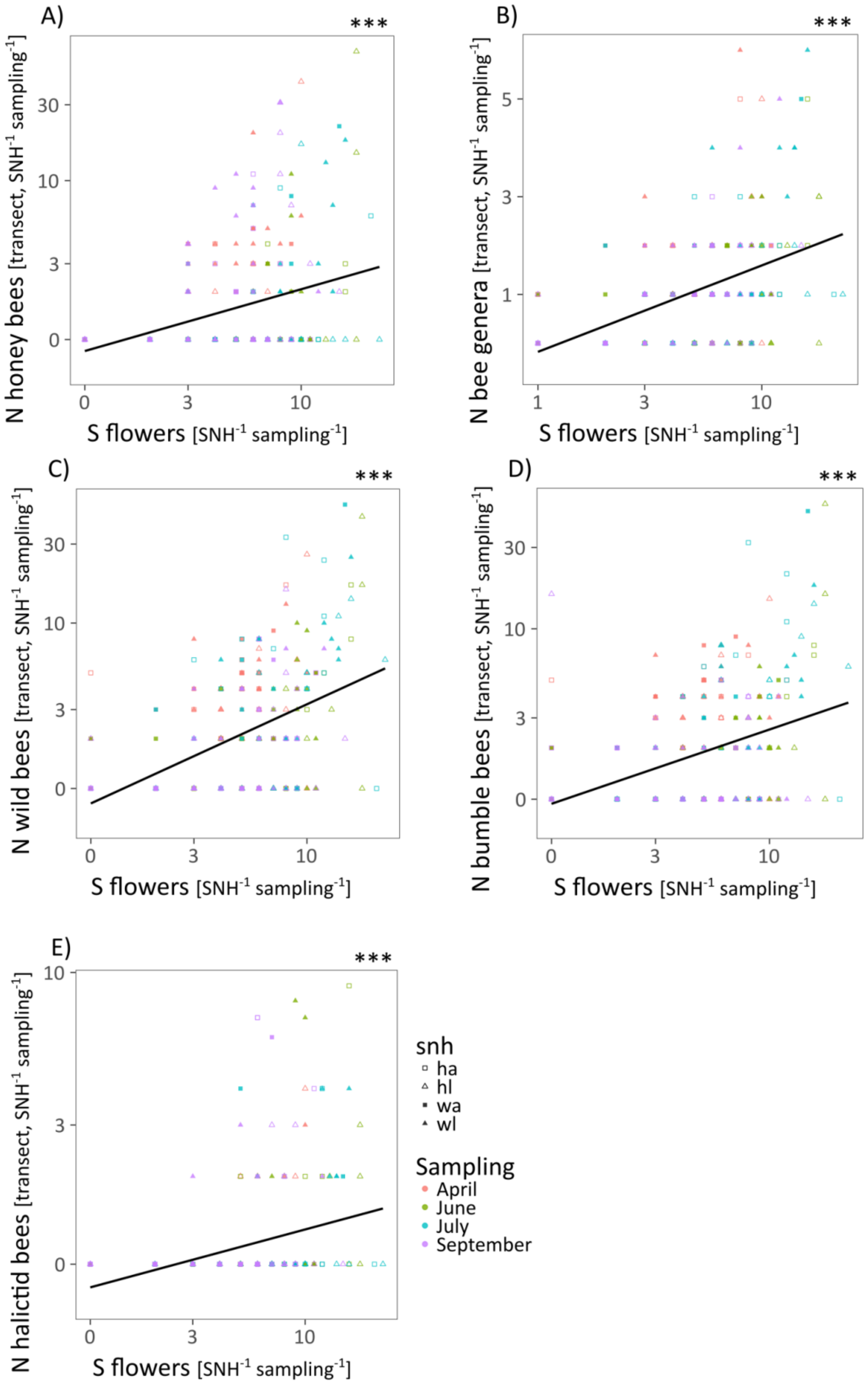

Figure 7.2 The species richness of flowering plants positively affected A) the abundance of honey bees, B) the species richness of bees (number of bee genera), C) the abundance of wild bees, D) the abundance of bumble bees and E) the abundance of halictid bees sampled in the transect walks. The values are the sums per seminatural habitat (shape) and sampling (colour). The significance value is displayed with stars `***´ p < 0.001. Statistics see Table 7.1.

7.3 Discussion

7.3.1 Local habitat type

The local SNH type only influenced the abundance of honey bees and the species richness of bees. Bee communities in hedgerows were more diverse than in all other habitat types. Honey bees avoided forests and were three times more abundant in hedgerows and grass strips and even five times more abundant in grasslands. Similarly, honey and wild bees were less abundant in the forest interior than in all other SNH types in the QuESSA pan trap data, which combines data from 217 SNH from four countries - Italy, Switzerland, Germany and the United Kingdom (Moonen *et al.* 2017). Thus, forests in our study region are no important habitat for bees, in contrast to forests in North America and China (Julier & Roulston 2009; Xie & An 2014).

Likely few bees were found in forests, because forests offered few floral resources (Moonen *et al.* 2017). Forests did not offer more floral resources in spring than other habitats, in contrast to forests in America (Hines & Hendrix 2005). Floral resources were much more important for the bees than the SNH type, in line with earlier studies (Ebeling *et al.* 2008; Potts *et al.* 2009; Roulston & Goodell 2011; Holland *et al.* 2015). The abundance and species richness of all bees sampled in the standardized transect walks was positively related to flower richness. Similarly, functional groups offering floral resources were more important than the SNH type for the bees in the combined QuESSA data set (Moonen *et al.* 2017). There, woody vegetation groups were characterized by early flowering and short flower duration (Moonen *et al.* 2017). However, most of these early flowering woody plants such as *Prunus* and *Crataegus* are typical for hedgerows and forest edges (Moonen *et al.* 2017). Early flowering resources are very important for pollinators, especially for bees with long flight seasons like bumble bees (Lye *et al.* 2009; Zurbuchen & Müller 2012), because these resources are often scarce in agricultural landscapes (Williams *et al.* 2012; Persson & Smith 2013). Further hedgerows also contained later flowering plants like *Rosa* and *Rubus* (Moonen *et al.* 2017). In addition, woody habitats are less disturbed than herbaceous habitats, for example by mowing (Shackelford *et al.* 2013). All this might be reasons why hedgerows contained the most diverse bee community.

Herbaceous habitats and plants therein also offer important, mainly intermediate and some late flowering floral resources like *Achillea*, *Taraxacum* and *Trifolium* (Orford *et al.* 2016; Moonen *et al.* 2017; Sutter *et al.* 2017). Different bee groups such as rare bees, wild crop pollinators (mainly bumble bees) and honey bees have different key plant species (Sutter *et al.* 2017). For example, *Achillea millefolium* and *Origanum vulgare* supported all three bee groups in Switzerland, whereas several key plant species only supported one group (e.g. *Lotus corniculatus* for wild crop pollinators) or two bee groups (e.g. *Trifolium pratense* for wild crop pollinators and rare bees) (Sutter *et al.* 2017). Legumes like *Onobrychis viciifolia*, *Melilotus* sp., *Trifolium* sp. are the main pollen resources for bumble bees and receive most bumble bee visits (Goulson & Darvill 2004; Goulson *et al.* 2005; Carvell *et al.* 2007). Further, bumble bees (especially *Bombus terrestris*) need perennial herbaceous habitats, that offer banks and withered tussocky grass and abandoned rodent nests, for nesting (Svensson *et al.* 2000; Kells & Goulson 2003; Osborne *et al.* 2008; Lye *et al.* 2009). Thus, herbaceous habitats and hedgerows and especially the floral resources offered by them are important for bees.

7.3.2 Landscape complexity

Landscape complexity had no influence on the diversity and the abundance of bees sampled in the SNH. However, bees are very mobile and therefore use different habitats during their life cycle (Mandelik *et al.* 2012). Diverse vegetation and SNH types can provide continuous, abundant and diverse floral resources and nesting sites for pollinators (Ebeling *et al.* 2008; Moonen *et al.* 2017). Further, different bee species and groups need different nesting sites and floral resources (Zurbuchen & Müller 2012; Sutter *et al.* 2017). Thus, landscapes with a diversity of SNH types with different vegetation characteristics and key plants are needed to support diverse bee communities (Moonen *et al.* 2017).

Acknowledgements

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Chapter 8 Effects on pumpkin yield

8.1 Methods

8.1.1 Effect of aphid densities on pumpkin yield

To determine the economic threshold we conducted an aphid-yield experiment with fixed aphid infestation levels at the beginning. We established five different levels of aphid infestation (0, 5, 20, 50, 100 individuals, each with eight replicates) on young pumpkin plants (one leave stage). Aphids used for this experiment were obtained from laboratory colonies of the Julius-Kühn Institute (JKI, Braunschweig). We used *Aphis fabae* Scopoli 1763, which was reared beforehand on faba bean (*Vicia faba* L.) at the JKI. Aphids were transferred to pumpkin plants (*Cucurbita maxima* Duchesne cv Hokkaido) and reared in a greenhouse for c. three weeks before we started the experiment (day: 15 hours, 24°C, 40%rh; night: 9 hours, 20°C, 45%rh). For the experiment we used organic pumpkin seedlings with one leaf (Rudolf Sinn GmbH & Co. KG, Lustadt). The plants were planted in an organic field (19.5.2015) in one row with a distance of 1 m between plants in a row and 2 m between rows. At the same day aphids were transferred with paintbrushes from infested pumpkin leaves from the greenhouse. Afterwards, the plants were caged with fine-mesh tomato-fleeces (nonwoven polypropylene fabric) to exclude natural enemies. After three weeks the fleeces were removed, because otherwise they would inhibit plant growth. Once per week from 19 May to 16 June we counted the number of occurring aphid individuals per leaf and the number of leaves infested by aphids. In cases where natural enemies or aphids in the control treatment (infestation = 0) were observed on the plants these were removed. The yield per plant was measured as the number and weight of the harvested pumpkins (18 September 2015).

Statistical Analyses

Aphid densities were calculated as the mean number per leaf and sampling. The effect of aphids on pumpkin yield was tested with a linear model using the maximum observed aphid density per leaf (continuous) as explanatory variable and the number of harvested pumpkins as the response variable (models using weight as response variable had similar results).

The economic threshold was calculated using the calculation of compound interest (Eq 1).

$$ET = \frac{\mathrm{EIL}}{(1+i)^t} \qquad \text{Eq 1}$$

The economic injury level EIL was derived from the yield-experiment. The lead time *t* was set to seven days, in which the farmers can react before the EIL is reached (Ragsdale *et al.* 2007; McCarville *et al.* 2011). The aphid growth rate *i* is the average growth rate per leaf from the yield experiments during the first three weeks, when unlimited growth was ensured by caging the plants. For the calculation of *i* Eq 2 was used.

The aphid growth *i* between two samplings was calculated using the calculation of compound interest as well (Eq 2). The aphid density A_y at the later sampling was divided by the aphid density of the previous sampling A_x. Then the root of *t* days between the two samplings of this term was calculated and 1 was deducted.

$$i = \sqrt[t]{\frac{Ay}{Ax}} - 1 \qquad \text{Eq 2}$$

8.1.2 Effect of field management, adjacent habitat and landscape complexity on pumpkin yield

In the 18 pumpkin fields, where we studied pest control (chapter 4) and pollination (chapter 6), pumpkin yields [in kg ha^{-1}] were recorded via farmer´s questionaires. A detailed description of the field design is given in chapter 4 (p. 106) and chapter 6 (p. 151). Further, herb management (number of mechanical and herbicide applications), fertilization [Nitrogen in kg ha^{-1}] and the number of insecticide and fungicide applications were recorded in the farmer’s questionaires (see Table S6.4, p. 165).

The effects of field management (factor: conventional vs. organic; or conventional vs. EU-organic vs. ‘strict’ organic), adjacent habitat type (factor: crop, herbaceous, woody) and proportion of agriculture in 1 km radius (continuous, 28-91%) on pumpkin yield [kg ha^{-1}] was determined with linear models. The significance of the effects of factors was tested with F-tests (package “car”, Fox & Weisberg 2010) and post-hoc Tukey tests (package “multcomp”, Hothorn *et al.* 2008). Data was analysed in R 3.3.1 (R Core Team, 2015).

8.2 Results

8.2.1 Effects of aphid densities on pumpkin yield

With an infestation level of 100 aphids maximum densities of up to 374 aphids per leaf (198 ± 115) were reached. However, aphid density had no effect on yield (number of harvested pumpkins per plant) in the aphid-yield experiments ($t_{38} = 0.30$, $p = 0.77$; Fig. 8.1A). Thus, no economic injury level could be defined, but it certainly lies above 200 aphids per leaf at peak infestation. When an assumed economic injury level of 200 aphids per leaf, a lead time for the farmers of 7 days and the mean growth rates per leaf from the experiment ($i = 0.06$) are used for the calculation, the economic threshold would be above 133 aphids per leaf.

8.2.2 Effects of field management, adjacent habitat and landscape complexity on pumpkin yield

For 15 of the 18 studied commercial pumpkin fields farmers provided the information on pumpkin yields. Pumpkin yields did not differ between conventional and organic farming ($F_{1,13} = 0.8$, p = 0.40), but were lower in fields under strict organic management according to the rules of organic farming associations than in fields managed organically according to the EU-Eco regulation 834/2007 ((EU-organic; European Commision 2007; t = -3.2, p = 0.02) or conventional fields (t = -2.5, p = 0.065; Fig. 8.1B). Adjacent seminatural habitats ($F_{2,12} = 0.5$, p =0.61) and proportion of agriculture in 1 km radius ($t_{13} = -0.2$, p = 0.81) had no effect on yield.

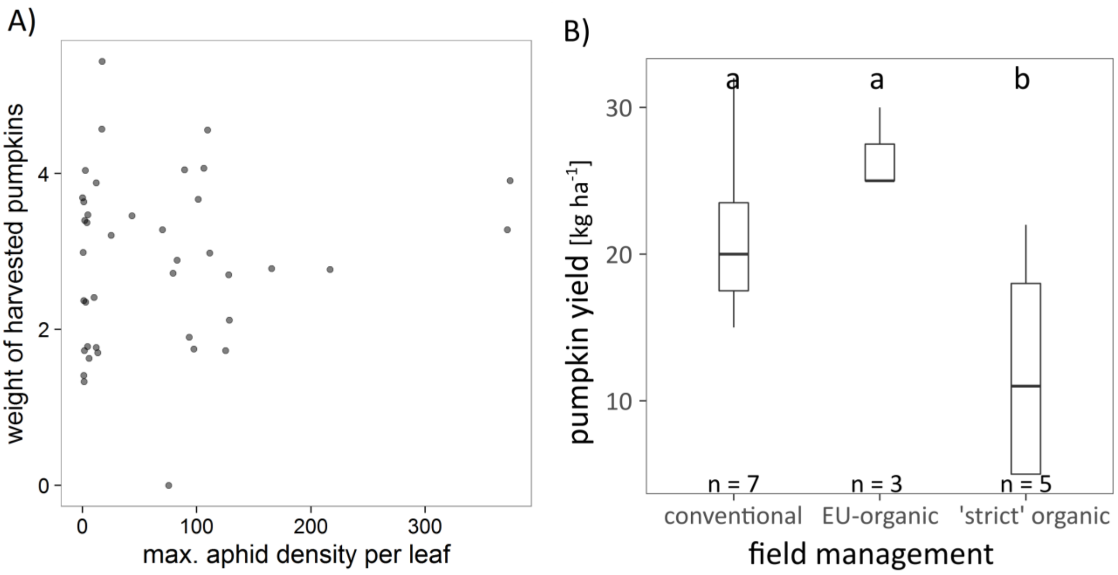

Figure 8.1 A) The maximum aphid density per leaf did not affect the weight of the harvested pumpkins [kg per plant] in our aphid-yield experiments.

B) Effect of field management (conventional vs. EU-organic vs. strict organic) on pumpkin yield [kg per ha] in 15 commercial pumpkin fields. Significant differences are indicated with different letters.

8.3 Discussion

The aphid-yield experiment illustrates that the economic injury level is above 200 aphids per leaf at peak infestation and therefore the economic threshold for pumpkin is certainly above 130 aphids per leaf. This is relatively high compared to the thresholds in other crops (e.g. Hansen 1991, Larsson 2005: 7 aphid per straw in cereals; Kerns *et al.* 2015: 50 aphids per leaf in cotton; Jeon *et al.* 2008: 20 aphids per plant in Chinese cabbage; or Ragsdale *et al.* 2007; McCarville *et al.* 2011: 250 aphids per plant in soybean). In the 18 commercial pumpkin fields, where pest control was investigated (chapter 4), aphid densities per leaf at peak infestation (mean of 20 leaves) exceeded 100 aphids only in one field. Thus, the aphid densities observed there were unlikely to affect yield.

Further, pumpkin yields in the 18 fields, where pest control and pollination were studied, were not limited by pollination (chapter 5). Therefore, it is not surprising that adjacent seminatural habitats and landscape complexity had no effect on yield. In contrast to most other yield comparisons between organic and conventional farming (Ponti *et al.* 2012; Seufert *et al.* 2012), pumpkin yields were similar in conventional and EU-organic farming. Field management affects yields in many ways, not only via effects on pest control and pollination, but also, for example, via the supply with nutrients and water. Thus, the higher yields in conventional and EU-organic fields compared to fields under strict organic farming are most likely not related to pest control or pollination, but caused by the more intensive management in those fields. For example, fertilization is positively related to pumpkin yield ($t_{13} = 2.3$, $p = 0.04$) and was higher in EU-organic and conventional farming than in strict organic farming (Table S6.4, p.165).

These results highlight, that

1) a more detailed consideration of farming practices is needed to disentangle their direct effects on yield via the supply of resources (such as nutrients and water) from their indirect effects on yield via pest control and pollination.
2) more studies on organic management according to the EU-Eco regulation 834/2007 are needed, because EU-organic farming might have the potential to provide similar high yields as conventional farming.

Acknowledgements

I am grateful to Julius Krebs for support in the field and laboratory.

Chapter 9 General Discussion and Outlook

9.1 Effects of organic farming on pest control and pollination

In contrast to former studies (Bengtsson *et al.* 2005; Batary *et al.* 2011; Krauss *et al.* 2011; Tuck *et al.* 2014; Lu *et al.* 2015) organic farming showed neither strong effects on the natural pest control of aphids (see chapter 4) nor on pollination (see chapter 6). There are three potential reasons why pest control and pollination services did not differ between organic and conventional farming in this thesis.

First, in those former studies pesticides were not applied in organic but in conventional farming (Bengtsson *et al.* 2005; Krauss *et al.* 2011; Lu *et al.* 2015). In this thesis six fields were managed organically according to the rules of organic farming associations and three fields were managed organically according to the EU-Eco regulation 834/2007 (EU-organic; European Commision 2007). EU-organic farming, which regulates the majority of the organic food production in Europe, allows the use of certain insecticides and fungicides (European Commision 2007), while in the organic fields managed by the rules of organic farming associations no pesticides were applied. Thus, the number of fungicide applications did not differ significantly between EU-organic and conventional management, and EU-organic farming had the highest number of insectide applications (Table S6.4, p. 165). However, the number of insecticide applications was overall low across all cultivation methods and did not show any effect on natural enemies of aphids or pollinators in pumpkin. One reason for this might be that farmers use less and beneficial friendly insecticides in pollinator-dependent crops. Nevertheless, the effects of these “organic” insecticides and fungicides should be studied in comparison to a management without any pesticides (“strict organic”) and in comparison to conventional management.

Second, positive effects of organic farming on pollinators (Holzschuh *et al.* 2007; Rundlöf *et al.* 2008; Hardman *et al.* 2016) and natural enemies (Krauss *et al.* 2011) are often mediated by positive effects on plants. Owing to the banning of herbicides, in former studies organic fields had a higher cover and diversity of weeds than conventional fields (Holzschuh *et al.* 2007; Batary *et al.* 2011; Krauss *et al.* 2011; Tuck *et al.* 2014). By contrast, conventional fields in this thesis had a higher weed cover and similar species richness than organic fields despite the use of herbicides (Table S6.4). The mechanical removal of weeds is much more effort and cost-intensive than the application of herbicides. Therefore, organic farmers try to keep weed pressures low at all times. Instead, conventional farmers can tolerate a higher weed cover, because pumpkin is able to outcompete the weed and the weed pressure in subsequent crops can be regulated by herbicides. Thus, if low weed covers in organic fields like in this thesis are more common than previous studies suggest, organic management might be less effective to attract pollinators (Batary *et al.* 2011; Kennedy *et al.* 2013; Tuck *et al.* 2014) and natural enemies (Krauss *et al.* 2011). On the other hand, organic farming might not have affected bumble bees, because pumpkin can attract bees from the wider landscape context independent of the local management (see section 6.4.2, p. 158). However, studies on effects of organic farming on pollination and pest control should always consider possible plant-mediated effects and report the cover and species richness of (flowering) weeds.

Third, some field management practices such as tillage could have adverse effects on natural enemies and pollinators (e.g. Williams *et al.* 2010; Tscharntke *et al.* 2016), but are not specifically related to organic or conventional farming. Thus, a more detailed consideration of farming practices and their effects can help to understand the responses of the beneficials (Puech *et al.* 2014).

Overall, the positive effects of organic farming on beneficial insects may have been overstimated owing to studies only including farms under very strict organic management (Bengtsson *et al.* 2005; Krauss *et al.* 2011; Lu *et al.* 2015). More studies on organic farming according to the EU-Eco regulation 834/2007 are needed. The more so, because EU-organic farming might provide similar yields to conventional farming (see chapter 8).

9.2 Effects of seminatural habitats at the local scale

9.2.1 Summarized effects of local seminatural habitats

As hypothesized local seminatural habitats support natural enemies (chapters 2, 3), pollinators (chapter 7) and tended to support pest control (chapter 4). Predatory flies responded to the local habitat type and were more abundant in woody habitats, especially in hedgerows, than in herbaceous habitats (chapters 2, 3). Bees were mainly related to floral resources (chapter 7). Especially, hedgerows, forest edges and herbaceous habitats provided important floral resources for bees (chapter 7; Moonen *et al.* 2017). Table 9.1 summarizes the effects of the local SNH type and of floral resources in the local SNH on predatory flies and on bees sampled in the SNH.

Seminatural habitats adjacent to pumpkin fields had no effect on pest control (chapter 4) or pollination (chapter 6). However, pest control in pumpkin was best supported by the flower density in the adjacent habitat. The flower density in the adjacent habitat positively affected the densities of natural enemies and tended to reduce aphid densities in pumpkin fields (chapter 4). Table 9.2 summarizes the effects of the adjacent habitat type and of the flower density in the adjacent habitat on pest control and pollination in pumpkin fields.

9.2.2 Discussion on effects of local seminatural habitats

A combination of different SNH types is best to support a diverse community of natural enemies and pollinators. Both natural enemies and pollinators, profit from the thereby provided diversity of (nesting) habitats and continuity of diverse floral resources, because different groups of pollinators and natural enemies use different resources (Table 9.3; Orford *et al.* 2016; Sutter *et al.* 2017). For example, bumble bees are specialized on legumes with hidden nectar (Goulson *et al.* 2005), whereas syrphid flies visit flowers with large inflorescences and unconcealed nectar (Branquart & Hemptinne 2000).

Woody, herbaceous and tailored herbaceous habitats can provide important resources for natural enemies and bees (Table 9.3 and references therein). Table 9.3 summarizes important plant species for natural enemies and bees according to the literature and dominant floral resources in the sampled habitats.

9.2.2.1 Woody habitats

Woody habitats, especially hedgerows, are important, because they provide 1) floral resources and aphids for natural enemies, 2) important early floral resources for bees, and 3) better conditions for predatory flies.

1) Woody habitats contain shrubs and trees such as *Prunus* sp., *Rubus* sp. and *Cornus sanguinea*, but also herbaceous plants such as *Heracleum sphondylium*, which provide floral resources and aphids for natural enemies such as syrphid flies, parasitoids and lady beetles (Branquart & Hemptinne 2000; van Rijn 2014; Orford *et al.* 2016).
2) Hedgerows and forest edges provide early floral resources, such as *Prunus* sp., and intermediate floral resourcesfor bees, such as *Rubus* sp. (Lye *et al.* 2009; Zurbuchen & Müller 2012; Moonen *et al.* 2017). Especially the supply with early flowering resources is important, because these are often scarce in agricultural landscapes (Williams *et al.* 2012; Persson & Smith 2013).
3) Woody habitats are important for predatory flies and parastic wasps (chapters 2 and 3; Moonen *et al.* 2017), because they offer moist conditions and shelter from harsh climate conditions and are less disturbed than herbaceous habitats (Röder 1990;

Cauwer *et al.* 2006; Rusch *et al.* 2010; detailed discussion in chapter 2, p. 67 and chapter 3, p. 93).

Thus, woody habitats, especially hedgerows, should be more included in environmental friendly farming, because they harbour predatory flies and a diverse bee community, and because so far environmental friendly farming focuses on herbaceous habitats (e.g. Pywell *et al.* 2015; European Commision 2016; MWVLW RLP 2016).

9.2.2.2 Herbaceous habitats

Herbaceous habitats mainly provide intermediate and some late flowering resources (Moonen *et al.* 2017). The studied herbaceous habitats contained *Achillea millefolium* and *Galium mollugo*, which are attractive for syprhid flies and parasitoids (Carrié *et al.* 2012; Dib *et al.* 2012; Wäckers 2004), and *Trifolium* sp. and other legumes, which are important pollen sources for bumble bees (Goulson & Darvill 2004). In addition, perennial herbaceous habitats offer nesting sites for bumble bees (Kells & Goulson 2003).

9.2.2.3 Tailored herbaceous habitats

Tailored out-of-production could be created to support pest control and pollination. For example, tailored flower strips containing *Anthemis arvensis*, *Centaurea cyanus*, *Coriandrum sativum* and *Fagopyrum esculentum* provide floral resources for lacewings, lady beetles, parasitoids and syrphid flies and consequently enhance the abundance and the reproduction of natural enemies (Ramsden *et al.* 2015; Tschumi *et al.* 2015; Tschumi *et al.* 2016b). As a result tailored flower strips reduce pest densities and plant damage and increase crop yield in adjacent fields (Tschumi *et al.* 2015; Tschumi *et al.* 2016a; Tschumi *et al.* 2016b). The results in this thesis indicate that such tailored flower strips should be located adjacent to the fields to provide pest control best.

Pywell et al. (2015) supported pest control and pollination and increased overall yield in the farms with a combination of different tailored annual, biennial and perennial out-of-production habitats (8% of the farm area). These habitats contained floral resources for natural enemies (e.g. *Fagopyrum esculentum, Centaurea*) and pollinators (e.g. *Onobrychis, Trifolium, Melilotus*) and thereby increased the richness and abundance of honey and bumble bees and pollination of field beans (Pywell *et al.* 2015). Thus, seminatural habitats can play an important role for pollination.

There are several reasons why pollinators and pollination of pumpkin were not affected by adjacent habitats in this thesis (chapter 6). First, honey and bumble bees have large foraging ranges and therefore are affected by landscape complexity (Greenleaf *et al.* 2007;

Kennedy *et al.* 2013). Second, floral resources are scarce in agricultural landscapes in late summer (Persson & Smith 2013). As a result, pumpkin, which offers high nectar and sugar amounts per flower in summer (Dmitruk 2008), may attract honey and bumble bee populations from the wider landscape context. However, pumpkin probably cannot really support the bee populations in contrast to late flowering legumes (Rundlöf *et al.* 2014), because honey and bumble bees do not use the pumpkin pollen (Michelbacher *et al.* 1964; own observations). In contrast to Holzschuh *et al.* (2016) no dilution effects of mass-flowering pumpkin were detected, but pumpkin only covered a small proportion of the surrounding landscape (on average 3% in 1 km radius).

Anyway, the presence and survival of bees in agricultural landscapes, especially those with long flight seasons such as bumble bees, depends on the provision of resources throughout the year (Carrie et al. 2017; Carvell et al. 2017). Therefore crop-pollinating bees can be supported by seminatural habitats, that provide nesting habitats and a continuity of floral resources (Zurbuchen & Müller 2012; Rundlöf *et al.* 2014).

In conclusion, a wide variety of seminatural habitat types can be used to support pest control and pollination. A combination of different habitats types is best to support a diverse community of natural enemies and pollinators, because depending on habitat type, management and vegetation different resources are provided and different beneficials are favoured. In simple landscapes larger SNH should be maintained and created to sustain populations of beneficial insects, because long-legged flies and non-aphidophagous Syrphidae were more susceptible to landscape simplification in linear habitats (chapters 2, 3).

Table 9.1 Effects of the local seminatural habitat type (four types: HA = grasslands, HL = grassy margins, WA = forests, WL = hedgerows) and of flower richness on aphids, natural enemies and pollinators in the seminatural habitats. Results are summarized from [1] = chapter 7; [2] = chapter 2; and [3] = chapter 3. ‘*’ $p < 0.05$, ‘***’ $p < 0.001$. Differences between local seminatural habitat types are only displayed in one direction “X is higher in habitat Y than in habitat Z”. Abbreviations: ‘x >’ = times higher in, ‘ns’ = not significant, ‘pos’ = positive, ‘N’ = abundance, ‘S’ = species richness, ‘DE’ = German case study, ‘CH’ = Swiss Case study, ‘AES’ = agri-environment scheme.

In SNH	**HA**	**HL**	**WA**	**WL**	**Flower richness**
Flower richness[1]	3x > WA	5x > WA		3x > WA	ns
Floral cover[3]	2x > WA	3x > WA		3x > WA	pos***
N Aphididae[3]	3x > WA	3x > WA		4x > WA	ns
Natural enemies					
N Dolichopodidae[2]	4x > WA	3x > WA		4x > WA	ns
N Empididae[2]			3x > HA,HL (DE)	3x > HA,HL (DE)	ns
S aphidophagous Syrphidae[3]	Higher in herbaceous habitats under AES in CH than unmanged ones in DE		3x > HA,HL (DE)	3x > HA,HL (DE)	ns
N aphidophagous Syrphidae (excluding *E. balteatus*)[3]			ns		ns
N *E. balteatus*[3]			4-5x > HA,HL (DE)	4-6x > HA,HL (DE)	ns
S non-aphidophagous Syrphidae[3]			ns		ns
N non-aphidophagous Syrphidae[3]			ns		pos*
Pollinators					
N honey bees[1]	5x > WA 3x > WL	4x > WA		3x > WA	pos***
N bee genera[1]				3x > HA,HL,WA	pos***
N wild bees[1]			ns		pos***
N bumble bees[1]			ns		pos***
N halictid bees[1]			ns		pos***

Table 9.2 Summarized effects of the adjacent habitat type (herbaceous, woody, crop) and of the flower density in the adjacent habitat on pest control (chapter 4) and pollination in pumpkin (chapter 6). (*) p < 0.1, '*' p < 0.05, '**' p < 0.01, '***' p < 0.001. Differences between local habitat types are only displayed in one direction "X is higher in habitat Y than in habitat Z". Abbreviations: 'x >' = 'times higher in'.

In-field	**herbaceous**	**woody**	**crop**	**Flower density in adjacent habitat**
flower density in adjacent habitat	2x > crop (*)			
Pest control				
density of aphids				Negative (*)
density of natural enemies				Positive**
density of aphid gall midges				Positive (*)
density of lacewings				Positive (*)
density of lady beetles				Positive***
density of parasitized aphids				Positive*
density of spiders			3x > woody* (end of May)	
density of syrphid flies				
Pollination				
Honey bee visits				
Bumble bee visits				
Pollen delivery				

Table 9.3 Summary of important plant species for natural enemies and bees according to the literature. References displayed with numbers, see below. Further the presence of these plants in the local seminatural habitat types (HA = grasslands, HL = grassy margins, WA = forests, WL = hedgerows; chapters 2, 3, 7) and the habitat types adjacent to pumpkin fields (herbaceous or woody; chapters 4 and 6) is indicated.

Plant species	Natural enemies	Bees	In SNH	In adjacent habitat
Achillea millefolium	syrphid flies [1], parasitoids [2]	wild bees [3]	HA, HL	herbaceous
Acer sp.	syrphid flies, lady beetles [4]		Mainly WA	Few in woody
Alnus glutinosa			Mainly WL	Few in woody
Chaerophyllum temulum	syrphid flies [5]		1 WA	woody
Cornus sanguinea	syrphid flies [4]		WL, WA	woody
Crataegus	syrphid flies [5]		WL, WA	Few woody
Daucus carota			HA	herbaceous
Euonymus europaeus	syrphid flies, lady beetles [4]		4 WL, 2 WA	Few woody
Galium mollugo	parasitoids [6]		Mainly HA	herbaceous
Heracleum sphondylium	syrphid flies [5], parasitoids [7]		3 WL	woody
Lamium album		bumble bees [8]	WL, HL	Few herb
Onobrychis viciifolia		wild bees [8], bumble bees [9,10]	1 HA, 1 HL	no
Prunus sp.	syrphid flies [5], lady beetles[4]	bumble bees [11]	Mainly WL	woody
Ranunculus repens	syrphid flies, lady beetles [7]	bumble and halictid bees [7]	Mainly HA	no
Rosa sp.			WL	few
Rubus sp.	syrphid flies [5]	bumble bees [10]	WL, WA	woody
Salix sp.	syrphid flies [5], lady beetles[4]		Mainly WL	few
Sambucus nigra			Mainly WL	woody
Taraxacum officinale	syrphid flies, lady beetles [7]	bumble and halictid bees [7]	Mainly HL	no
Trifolium (pratense)		bumble bees [3,9]	Mainly HA	herbaceous
Urtica dioica	Empididae, Dolichopodidae[12]		WL, WA	woody
Annual flower strips				
Anthemis arvensis	lacewings, lady beetles, parasitoids and syrphid flies [13–15]		no	no
Centaurea cyanus			1 HL	no
Coriandrum sativum			no	no
Fagopyrum esculentum			no	no

[1] Carrié *et al.* 2012, [2] Dib *et al.* 2012, [3] Sutter *et al.* 2017, [4] van Rijn 2014, [5] Branquart & Hemptinne 2000, [6] Wäckers 2004, [7] Orford *et al.* 2016, [8] Zurbuchen & Müller 2012, [9] Goulson & Darvill 2004, [10] Kleijn & Raemakers 2008, [11] Lye *et al.* 2009, [12] James *et al.* 2015, [13] Ramsden *et al.* 2015, [14] Tschumi *et al.* 2015, [15] Tschumi *et al.* 2016b.

9.3 Effects of seminatural habitats at the landscape scale

9.3.1 Summarized effects of landscape complexity

Landscape complexity supported natural enemies in seminatural habitats (chapters 2, 3) and pollination of pumpkin (chapter 6), but had no significant effect on pollinators in seminatural habitats (chapter 7) or pest control in pumpkin (chapter 4). As hypothesized, landscape complexity enhanced the abundance and species richness of predatory flies - long-legged flies, dance flies and syrphid flies - in local seminatural habitats (chapters 2, 3). Further, proximity to watercourses had positive effects on long-legged flies and dance flies (chapter 2). Nevertheless, landscape complexity had no effect on syrphid flies or on natural enemies in total in pumpkin fields. Bees in seminatural habitats were not affected by landscape complexity (chapter 7), but in the pumpkin fields bumble bee visits and consequently pollen delivery was lower in landscapes dominated by agriculture (chapter 6). The effects of landscape complexity on natural enemies and pollinators in SNH and on pest control and pollination in pumpkin fields are summarized in Table 9.4.

9.3.2 Effects of landscape complexity on pest control

The results show that most natural enemies - long-legged flies, dance flies, syrphid flies, lady beetles, aphid gall midges and lacewings - respond at the landscape scale (Table 9.4) and are consequently very mobile. However, landscape complexity had no clear effect on pest control in pumpkin. There are several reasons for this: 1) landscape complexity had contrasting effects on different natural enemy groups, and 2) crops can be important habitats for aphids and natural enemies at certain times of the year (detailed discussion in chapter 4, p. 118).

1) In-field densities of aphid gall midges and lacewings were negatively affected by the proportion of agriculture as expected. In contrast, in-field densities of lady beetles in mid summer were positively related to agriculture in the surrounding. Syrphid flies were not affected by landscape complexity, which might be a result of contrasting responses of different syrphid fly species or owing to the pattern of the dominant syrphid fly *Episyrphus balteatus*. *E. balteatus* did not respond to landscape complexity in 1 km radius (reasons see 2) and in detail in chapter 2), whereas most syrphid fly species clearly benefited from landscape complexity in seminatural habitats (chapter 2).

2) Crops can be important habitats for aphids and their natural enemies at certain times of the year (Tscharntke *et al.* 2016). Thus, lady beetles might have built up their populations in other crops (Bianchi & van der Werf 2004; Caballero-López *et al.* 2012)

and then migrated into the pumpkin fields. However, lady beetles and syrphid flies use different habitats throughout the year (Alignier *et al.* 2014) and overwinter in seminatural habitats (Sarthou *et al.* 2014). Thus, seminatural habitats are also important for them.

In conclusion, complex landscape with a high proportion of different SNH types support natural enemies, but this might not be evident when only in-field densities in mid summer are measured.

9.3.3 Effects of landscape complexity on pollination

Landscape complexity had no influence on species richness and the abundance of bees in seminatural habitats. Nevertheless, local seminatural habitats, especially those offering floral resources, supported pollinators (chapter 7). Thus, there is a potential to support pollinators with complex landscapes, because pollinators respond at the landscape scale (chapter 6; Greenleaf *et al.* 2007).

Bumble bee visits and pollination of pumpkin were negatively related to agriculture and positively, but more weakly, to the proportion of seminatural habitats in 1 km radius (chapter 6). The hostility of agricultural landscapes seems to be mainly related to the lack of nesting sites and floral resources, because insecticide intensity in the surrounding landscape had no significant effect (chapter 6). Thus, reducing farming intensity or adding small surfaces of ecological compensation areas may offer little prospects of sustaining this ecosystem service in landscapes dominated by agriculture. Sufficient areas of non-crop habitats like seminatural and urban habitats need to be maintained for pollinators in agricultural landscapes. Urban habitats can enhance bumble bee visits in nearby crops (Carré *et al.* 2009) and pollination of sentinel plants in landscapes dominated by urban habitats (Theodorou *et al.* 2016). Especially gardens offer nesting sites (Osborne *et al.* 2008; Lye *et al.* 2012) and floral resources for (bumble) bees (Goulson *et al.* 2008).

However, while urban habitats seem to enhance the abundance of common species with long flight seasons, seminatural habitats are needed to secure diverse bee communities (Palma *et al.* 2015). Biodiversity conservation requires the management targeted towards threatened species and their habitats, because management targeted to crop pollination only supports common species (Kleijn *et al.* 2015). Thus, to support wild bees and thereby ensure the pollination of pollinator-dependent crops we need a mixture of different non-crop habitats that provide nesting sites and continuous, abundant and diverse floral resources.

Table 9.4 Effects of landscape complexity in SNH (proportion of SNH in 1 km radius, 1-64%) and in pumpkin fields (proportion of agriculture in 1 km radius around pumpkin fields, 28-91%) on natural enemies and pollinators. Summary from [1] = chapter 2; [2] = chapter 3; [3] = chapter 4, [4] = chapter 7 (bee abundance), and [5] = chapter 6 (bee visits). 'N' = abundance/ density, 'NA' = not measured, 'no' = no effect, 'pos' = positive effect, 'neg' = negative effect. (*) p < 0.1, '*' p < 0.05, '**' p < 0.01, '***' p < 0.001. Significant effects are highlighted in bold.

organism	In SNH, % SNH	In pumpkin fields, % agriculture
Pest control		
N aphids[2,3]	**neg***	**neg***
N Dolichopodidae[1]	**pos (in HL* and WL***)**	NA
N Empididae[1]	(% WA) **pos (*)**	NA
S aphidophagous Syrphidae[2]	**pos*****	NA
N aphidophagous Syrphidae[2, 3]	**pos***	no
N *Episyrphus balteatus*[2]	no	
S non-aphidophagous Syrphidae[2]	**pos*****	NA
N non-aphidophagous Syrphidae[2]	**pos*****	NA
N aphid gall midges[3]	NA	**neg (*)**
N lacewings[3]	NA	**neg (*)**
N lady beetles[3]	NA	**pos***
N parasitized aphids[3]	NA	no
N spiders[3]	NA	no
N natural enemies	NA	no
Pollinators		
Honey bees (N[4]/ visits[5])	no	no
Bumble bees (N[4]/ visits[5])	no	**neg*****
Halictid bees (N[4]/ visits[5])	no	no
Number of genera of wild bees[4]	no	NA
Pollen delivery[5]	NA	**neg****

9.4 Effects on yield

Pumpkin yields were not affected by aphid density (chapter 8) or limited by pollination (chapter 5). Consequently adjacent seminatural habitats and landscape complexity had no effect on yield as well (chapter 8). On the other hand, field management had an effect on pumpkin yield. Pumpkin yields were similar in conventional and EU-organic farming, but lower in fields under strict organic management, because conventional and EU-organical field were managed more intensively (chapter 8). For example, higher yields were related to higher fertilization (chapter 8). Thus, a more detailed consideration of farming practices is needed to disentangle their direct effects on yield via the supply of resources such as nutrients and water from their indirect effects on yield via pest control and pollination. Further, more studies on organic management according to the EU-Eco regulation

834/2007 are needed, because EU-organic farming might have the potential to provide similar high yields as conventional farming.

9.5 Future research

9.5.1 Future research on pest control

Pest control studies should consider the whole natural enemy community, taking the different responses and interactions among different enemy groups into account, to identify the overall effects on pests (Rusch *et al.* 2016). Thus, future studies should address the importance of long-legged flies and dance flies as pest control agents and sample also night-active species such as lacewing adults, syrphid larvae and spiders (Ximenez-Embun *et al.* 2014; Petersen & Woltz 2015). To measure the whole natural enemy community new methods could be used: for example infrared video sampling (Sutter et al, pers. comm.) or odor footprints (Ninkovic *et al.* 2013).

Moreover, pest control studies should always measure the impact on pest populations and on yield (Rusch *et al.* 2016). As the indirect damage of aphids by virus transmission is often more severe than the direct feeding damage, more pest control studies are needed that include virus transmission (Dedryver *et al.* 2010). However, this is very complicated, because often several viruses play a role for one crop and most viruses transmitted by aphids are non-persistent (Dedryver *et al.* 2010). Non-persistent viruses cannot be controlled by pesticides, because they are often not related to aphid abundance and transferred in a very short period by several non-colonizing aphid species (Dedryver *et al.* 2010; Angelella *et al.* 2015).

9.5.2 Future research on pollination

Pumpkin yield in this thesis was not pollination-limited owing to the high levels of bee visits and is fairly resilient against pollinator decline. However, other crops might suffer from yield losses owing to 1) lower visitation rates, 2) lower single visit deposition or 3) higher pollination demand compared to pumpkin.

1) Visitation rates might be lower owing to several reasons: First, early flowering crops like cherry and apple are mainly pollinated by solitary mining bees (*Andrena*), because few pollinators are active early in the season (e.g. Holzschuh *et al.* 2012; Mallinger & Gratton 2015). Second, pollinators can be diluted, when there are many simultaneously flowering resources (e.g. oilseed rape; Holzschuh *et al.* 2016). Third, the visitation might be low, when the crop flowers are not very attractive for

pollinators (e.g. kiwi; Tsirakoglou *et al.* 1997). Low visitation rates can be measured with little temporal expenditure using a new method, chemical footprints (Kämper *et al.* 2017)

2) In addition, lower single visit deposition reduces the pollination efficiency. Single visit deposition of conspecific pollen depends on 1) the pollinator species, 2) the supply of pollen in the flowers and 3) heterospecific pollen loads, when the pollinators also visit other plants (chapter 5; Ne'eman *et al.* 2010). In addition to bees also other pollinators such as flies have to be considered in many crops (Rader *et al.* 2016). For many partially pollinator-dependent crops such as strawberry also wind- and self-pollination must be considered (Klein *et al.* 2007).
3) Especially further studies should quantify the relationship that links pollen receipt to seed/fruit set to precisely evaluate the impact of lower pollinator abundances on yield. Up to now the relationship of pollen receipt to seed/fruit set is only known for three crops: pumpkin, cranberry (Cane & Schiffhauer 2003) and oilseed rape (Hoyle & Cresswell 2007).

Combining all this quantitative information the resilience of other pollinator-dependent crops to potential pollinator decline can be determined in different regions.

To identify if environmental friendly farming really supports pollinators, nest densities and population sizes must be measured, for example via genetic methods (Darvill *et al.* 2004; Holzschuh *et al.* 2016; Carvell *et al.* 2017).

9.5.3 Future research on ecosystem services and seminatural habitats in general

Resources, especially floral resources, in seminatural habitats are important for pollinators and natural enemies. Thus, future research is required to determine

a) which resources are provided by agricultural landscapes,
b) the plants which provide the best resources,
c) the times at which these resources are mainly needed,
d) the spatial scale at which they are important,
and e) how they can be enhanced by habitat management.

Especially more research is needed on the management and upgrading of hedgerows and other perennial habitats to favour pest control and pollination.

Moreover, future studies should also include other ecosystem services and the trade-offs and synergies between them, because different stakeholders that influence the landscape design, are interested in different ecosystem services (Geertsema *et al.* 2016). For example farmers are very much interested in soil fertility.

9.6 Recommendations for environmental friendly farming

9.6.1 Recommendations for farmers

Farmers and policy makers should promote natural pest control via field-bordering habitats that offer numerous floral resources for natural enemies. Pesticide use should be reduced, because, at least in pumpkin, it is rarely needed and can have adverse effects on natural enemies and pollinators.

Farmers should preferably support wild (bumble) bees over commercial bumble bees and honey bees, because bumble bees are the key pollinators of pumpkin and commercial bees can transfer diseases to local honey bees, bumble bees and other wild bees (Goulson *et al.* 2015).

Farmers, policy makers and communities should promote the connectivity and mixture of different non-crop habitats that offer nesting sites and continuous, abundant and diverse floral resources. To secure and enhance bumble bee visits sufficient seminatural habitats and other non-crop habitats in agricultural landscapes are needed. Especially hedgerows and perennial herbaceous elements favour wild bees, because combined they offer flowers throughout the vegetation period and provide undisturbed nesting sites.

9.6.2 Caveats of the agricultural policy of the European Union

The present agricultural policy of the European Union, the so called “Greening”, is likely not enough to promote pest control and pollination, because

1) Ecological focus areas only need to cover 5% of the agricultural area.
2) Most of the ecological focus areas are only available for a short-term period: In Rhineland-Palatinate 98% of the ecological focus areas implemented in 2015 were annual habitats, mainly catch crops (55%, need to be available from October till mid February), fallows (33%, annual) and nitrogen fixing crops (10%, need to be available from mid May till mid August) and only very few buffer strips (0.9%, need to be available from mid May till October).
3) The “Greening” do not have to contain a mix of different habitats (LWK Niedersachsen 2015; European Commision 2016; LEL Schwäbisch Gmünd 2016; MWVLW RLP 2016; Pe'er *et al.* 2016).

9.6.3 Need for perennial habitats

Annual habitats can support natural enemies (Ramsden *et al.* 2015; Tschumi *et al.* 2015; Tschumi *et al.* 2016b) and pollinators (Carreck *et al.* 2002; Carvell *et al.* 2007) to some extent. For example, legumes provide late flowering resources in July and August for bumble bees (Carvell *et al.* 2007). However, there are several disadvantages of these annual habitats.

1) Annual habitats are per se herbaceous habitats, but woody habitats are important for predatory flies and bees (see 9.2).
2) Current annual ecological focus areas often cannot be used for overwintering.
3) Annual habitats sown in April or May do not offer early flowers.

Thus, annual flower strips could be improved to provide early flowering resources and a better overwintering habitat, if they were sown in autumn

4) Annual flower strips are constrained by the available seed mixtures and therefore often contain non-native and cultivated species such as buckwheat, flax, sunflower and *Phacelia tanacetifolia* (MWVLW RLP 2016), which are not necessarily the best plants to support a diverse community of natural enemies and pollinators. The species selection is constrained further, because it should be possible to convert the annual flower strips back into cropland without facing severe weed problems. This is especially important for organic farmers.

Therefore, perennial seminatural habitats are needed. Better incentives and financial support are needed 1) to create new perennial habitats and 2) to maintain and improve existing ones (Pe'er *et al.* 2016). Depending on the regeneration capacity of the vegetation, it can be advisable to upgrade habitats with seed mixtures (Goulson *et al.* 2008; Holland *et al.* 2016), because the vegetation and seed banks in agricultural landscapes are impoverished (Roschewitz *et al.* 2005; Buhk *et al.* 2017). Nevertheless, natural regeneration often results in high floral diversity (Goulson *et al.* 2008; Holland *et al.* 2016).

Overall, the Greening should be improved in order to provide a mixture of different - annual and perennial, woody and herbaceous, in- and out-of-production - habitat types for various purposes.

9.6.4 Engaging with stakeholders

With a good tailored management seminatural habitats deliver pest control and pollination to agriculture and can provide other ecosystem services such as biodiversity conservation and aesthetic value.

To improve the current practice we need

1) a knowledge transfer to raise the awareness of consumers,
2) coordination and cooperation between stakeholders for the design of agricultural landscapes,
3) and a good political framework to support seminatural habitats and environmental friendly agricultural landscapes.

1) Information about environmental friendly farming can raise the consumer acceptance of fruits and vegetables with some "faults", which is needed to reduce pesticide use (Dedryver *et al.* 2010). Providing transparency on the food production further gives consumers a choice and could let them contribute to the financial support of environmental friendly farming. The EU-certification of organic farming is a good example for such a transparency, knowledge transfer and financial support. However, for out-of-production schemes no certification or label exist, although they are often more important for pest control and pollination than in-production schemes such as organic farming (Batary *et al.* 2015). Agricultural landscapes at the landscape scale cannot be changed by single farmers (Landis 2017). As a result, certification of environmental farming at the landscape scale cannot directly be related to single farmers. A possible solution could be the marketing of regions.

2) Different local stakeholders shape and profit from agricultural landscapes. Therefore, communities including farmers, residents, researchers, local administration and owners from seminatural habitats need to be involved in the maintenance and creation of environmental friendly agricultural landscapes (Pe'er *et al.* 2016). A dialogue between all stakeholders can raise the awareness of benefits and result in context-specific designs of landscapes, which provide certain ecosystem services desired by the local community (Geertsema *et al.* 2016). For these social processes a coordination is needed (Landis 2017). Researchers should engage in these processes to provide the scientifical background and research to put the context-specific landscapes design into practice (Geertsema *et al.* 2016; Landis 2017).

3) A good political framework is needed to support this knowledge transfer, cooperation and financial support for environmental friendly farming. Thereby environmental friendly

farming can be designed to deliver not only pest control and pollination to agriculture, but also support other ecosystem services such as biodiversity and aesthetic value.

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Curriculum vitae

Sonja C. Pfister

Education

Apr 2013 – present	**Ph.D. Environmental Sciences**, *University of Koblenz-Landau, Landau.* Thesis: Potential of SemiNatural Habitats to support pest control and pollination – including a case study on pumpkin.
Oct 2007 – Mar 2013	**Dipl. Umweltwissenschaften**, *University of Koblenz-Landau, Landau* Thesis: Influence of landscape context and cultivation (organic/ conventional) on the pollination and seed set of *Cucurbita maxima.*

Work Experience

Apr 2013 – Jan 2017	**Research Assistant**, *University of Koblenz-Landau, Landau* Project: “Quantification of Ecological Services for Sustainable Agriculture (QuESSA)”.
Apr 2008 – Mar 2013	**Zoo educator**, Zooschule Landau, *Landau.*
Jan 2012	**Internship**, environmental planning office Institut für Umweltstudien Weibel & Ness GmbH, *Kandel.*
Sep – Dec 2011	**Internship**, nature conservation association Gesellschaft für Ornthologie und Naturschutz Rheinland-Pfalz e.V. (GNOR), *Neustadt a. d. Weinstraße.*
Mar 2011	**Internship**, Verbraucherzentrale Rheinland-Pfalz e.V., *Mainz*.
Aug 2006 – Jul 2007	**Internship**, Naturerlebniszentrum Wappenschmiede, *Fischbach/ Dahn* Voluntary Ecological Year.

Skills

Languages	German (native) English (business fluent) Spanish (good working knowledge) Latin (qualification in Latin)
Computer skills	Microsoft Office (Word, Excel, PowerPoint, Access) geographical information system software (ArcGIS, QuantumGIS) statistical data analysis (R) reference management program (Citavi)
Drivers licence	class B

Voluntary work

Umweltgruppe d. Uni Landau	Shopping guide for sustainable consumption in Landau, movies with discussion on sustainable topics, tours to globalization and sustainable consumption, greening of the university
o since Oct 2007	
Tag zur Nachhaltigkeit (TzN)	ecotaining day on the subject sustainability
o TzN 2012	project leader
o TzN 2014, 2015, 2017	management team
Nature conservation (GNOR)	voluntary assistant at the society for nature conservation and ornithology in Rhineland-Palatinate e.V. (GNOR)
o since Sep 2007	
Collegiate representation	
o Mai 2011 – Mai 2014	student representative at the “Studierendenwerk Vorderpfalz“
o Jul 2011 – Jun 2012	member of the student representation of the Institute of Environmental Sciences
o Jun 2009 – Mai 2011	student parliament
Social engagement	care of handicapped children at the „Referat Menschen mit Behinderung“, *Mainz*.
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Publications and Conference contributions

Articles

[1] Fusser, Moritz S.; **Pfister, Sonja C.**; Holland, John M., Entling, M.H.; Schirmel, J. (2017) Effects of field margin type and landscape composition on predatory carabids and slugs in wheat fields. *Agric. Ecosyst. Environ.* 247, 182-188.

[2] **Pfister, Sonja C.**, P. W. Eckerter, J. Schirmel, J.E. Cresswell, M.H. Entling (2017) Sensitivity of commercial pumpkin yield to potential decline among different groups of pollinating bees. *Royal Society Open Science*, 4, 170102.

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[5] **Pfister, Sonja C.**; Schäfer, Ralf B.; Schirmel, J.; Entling, M.H. (2015). Effects of hedgerows and riparian margins on aerial web-building spiders in cereal fields. *J. Arachnology* 43, 400-405.

Conference presentations

[1] **Pfister, Sonja C.**; Schirmel, J.; Entling, M.H. (2017). Pollination and biological control of aphids on pumpkin in Germany. QuESSA International Conference Quantification of Ecological Services for Sustainable Agriculture, Rome.

[2] **Pfister, Sonja C.**; Schirmel, J.; Entling, M.H. (2016). Aphids and aphidophaga in pumpkin fields respond differently to management, local and landscape features. Ecology of Aphidophaga 13, Freising.

[3] **Pfister, Sonja C.**; Eckerter, P.W.; Krebs, J.; Schirmel, J.; Entling, M.H. (2015). Seminatural habitats enhance pollination of pumpkin. 45th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (GFÖ), Göttingen.

Conference posters

[1] **Pfister, Sonja C.**; Sutter, L.; Albrecht; M., Marini, S.; Schirmel, J.; Entling, M.H. (2016). Forgotten fies: Effects of local and landscape factors on predatory Diptera. Poster. 46th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (GFÖ), Marburg.

[2] **Pfister, Sonja C.**; Kahles, K.; Droste, I.; Heuring, A.; Schirmel, J.; Entling, M.H. (2014). Effects of local and landscape factors on pollinators in different types of field margins. Pollinators in Agriculture, Brussels.

As a service to the scientific community I performed a total of 3 reviews for the journals Biological Control and Insect Science.