

Master's thesis for achievement of the academic degree "Master of Science" (M.Sc.)
at the Faculty of Environment and Natural Resources
University Freiburg im Breisgau

Ecosystem services and agri-environment schemes: how effective are flower strips versus organic farming in controlling crop pests?

prepared at the
Georg-August University Göttingen
Faculty of Agricultural Sciences,
department for Crop Sciences, section: Agroecology

submitted by



First supervisor: Prof. Dr. Alexandra-Maria Klein (Uni. Freiburg)
Second supervisor: PD Dr. Péter Batáry (Uni. Göttingen)

Göttingen, March 2017



Crop field close to Göttingen, summer 2016

Intensive agriculture is one of the main causes for the loss of biodiversity and associated ecosystem services. Therefore, European agricultural aid has to be changed. It has to be aligned to the principle that public funds are only given to public services, such as ecological services provided by farmers.

Beate Jessel (2016)

Federal Agency for Nature Conservation, Germany

Table of contents

1	Abstract	1
2	Introduction	2
2.1	Agri-environment schemes	2
2.2	Land sharing versus land sparing strategies of AES.....	3
2.2.1	Organic farming in Lower Saxony - a land sharing strategy	4
2.2.2	Flower strips in Lower Saxony – a land sparing strategy	5
2.3	Effects of landscape structure	6
2.4	Edge effect	7
2.5	Study organisms	8
2.5.1	Aphids and their natural enemies.....	8
2.5.2	Cereal leaf beetles and their natural enemies.....	10
2.6	Research questions and hypotheses	11
3	Material and Methods.....	13
3.1	Study area and experimental design	13
3.2	Field surveys.....	15
3.2.1	Survey of cereal leaf beetle larvae.....	15
3.2.2	Survey of aphids and their natural enemies.....	15
3.2.3	Survey of natural enemies via sweepnetting	16
3.2.4	Aphid predation experiment	17
3.3	Data analysis.....	18
4	Results	20
4.1	Cereal leaf beetle larvae	20
4.2	Aphids and their natural enemies	21
4.2.1	Aphid density	21
4.2.2	Aphid parasitism	22
4.2.3	Predator-prey ratio for aphids.....	23
4.3	Aphid predation experiment	24
4.4	Natural enemies caught via sweepnetting.....	25
4.5	Summary of all models	26

5	Discussion	27
5.1	Organic farming vs. flower strips (land sharing vs. land sparing).....	27
5.1.1	Cereal leaf beetle larvae.....	27
5.1.2	Aphids.....	28
5.1.3	Aphid parasitism	29
5.1.4	Predator-prey ratio for aphids.....	30
5.1.5	Aphid predation experiment	30
5.2	Edge effect	31
5.3	Effect of landscape configuration heterogeneity	31
5.4	Assessment of hypotheses	32
5.5	Limitations of the experiment	33
6	Conclusion and Outlook	34
7	Acknowledgements.....	36
	References.....	37
	Statement of Authentication.....	I
	Appendix	II

1 Abstract

Agricultural intensification has led to a dramatic loss of species and associated ecosystem services over the past centuries. In the European Union, agri-environment schemes (AES) have been developed to react to the challenges caused by agricultural intensification, to promote biodiversity and ecosystem services. Several schemes follow either a land sparing (production and conservation goals on separate areas) or a land sharing strategy (production and conservation goals on the same area). Organic farming can be seen as land sharing practice, since whole fields are managed in an environment friendly way to achieve a high level of biodiversity on the fields. Other schemes, such as sowing of flower strips along field margins, separate land for conservation from land for production. Natural biological control of agricultural pest insects is an important, but often still unrecognized agroecosystem service that can be mediated by species-rich communities of natural enemies. In my thesis I aim to test, which of the two AES strategies is more effective in controlling crop pests via natural enemies. In the state of Southern Lower Saxony (Germany), I selected 10 agricultural landscapes that contained three winter wheat fields each (one organic field, one conventional field with adjacent flower strip and one conventional control field). The landscapes represent a gradient from small to large fields to take the landscape structure into account. I used two transects per field (one transect in the field edge and one in the interior, 10 m from the edge). There I surveyed the crop pests, cereal leaf beetles (CLB) and cereal aphids as well as their natural enemies. My results indicate that control of CLB was best under organic farming, and there were less CLB larvae at field edges than in the interior of fields independent of management type. Flower strips had ambiguous effects on the abundance of aphids. On the one hand, they supported infestation of aphids in the fields, suggesting a disservice of this scheme. On the other hand, they also increased parasitism rates of aphids by hymenopteran wasps, potentially outweighing this previous negative effect. Natural enemies were supported by landscapes with small mean field sizes. However, a higher abundance of enemies in those landscapes did not reduce crop pest densities substantially. This study demonstrates that the two currently most popular AES in Lower Saxony, that represent either a land sharing (organic farming) or a land sparing (flower strips) strategy, are both not yet optimized for natural pest control. In order to meet the objectives they are targeted for, they have to be designed more carefully and managed for the specific production system and region. I suggest several alterations in the design of flower strips, such as longer flowering times (also before crop blooming and after harvest), perennial application and the use of native plant species. Furthermore, regular monitoring and evaluation of the success of AES are crucial for the optimization process.

2 Introduction

Natural biological control of pest insects in arable fields is an important agro-ecosystem service, but its value is still not well recognized (Östman, Ekbohm & Bengtsson 2003; Landis *et al.* 2008; Power 2010). Tscharrntke *et al.* (2007) suggested complex landscapes with species-rich natural enemy communities to be important for long-term conservation of natural biological control. However, agricultural expansion and intensification has led to a dramatic species loss during the past centuries (Henle *et al.* 2008; Foley *et al.* 2011), also threatening abundance and species richness of natural enemies of crop pests (Sunderland & Samu 2000; Thies *et al.* 2011; Zhao *et al.* 2015). Inputs of mineral fertilizers or antibiotics in manure and pesticides have led to a degradation of habitat quality at local-field scales, while transformations of extensive grasslands to arable fields and destructions of field boundaries and hedges resulted in a loss of semi-natural habitats and homogenization at landscape scales (Robinson & Sutherland 2002; Tscharrntke *et al.* 2005). This includes changes in the distribution and supply of resources for many species and thereby affects community compositions and food web structures (Thies *et al.* 2011). For future sustainable and cost-effective agricultural production, it is inevitable to take ecosystem services such as natural biological control into account and promote them with appropriate management strategies (Foley *et al.* 2011). Biological control can reduce the need for pesticide application, and thus not only save money for the farmers, but also contribute to biodiversity conservation in agricultural landscapes (Bianchi, Booij & Tscharrntke 2006; Landis *et al.* 2008; but see Ekroos *et al.* 2014; Kleijn *et al.* 2015).

2.1 Agri-environment schemes

Agri-environment schemes (AES) have been developed to react to the challenges caused by increased agricultural intensification. In the European Union, AES were initially designed to protect environmentally sensitive areas by compensating farmers for income losses associated with less intensive management (Batáry *et al.* 2015). Over time, the emphasis shifted to prevention of species loss and to improve and conserve ecosystem services, such as natural biocontrol and pollination (Ekroos *et al.* 2014). Today, AES are the main tool for conservation of farmland biodiversity in Europe (Batáry *et al.* 2015), with payments worth over 2.7 billion \$ each year to EU farmers (European Environment Agency 2002).

The effectiveness of agri-environment schemes in promoting farmland biodiversity has been relatively well studied (Tscharntke *et al.* 2012). Most studies found mixed effects of AES and showed that they benefited common species more than threatened ones (e. g. Kleijn *et al.* 2006). In contrast, the effect of AES on biodiversity-mediated ecosystem services, such as natural pest control remain largely unexplored (Tschumi *et al.* 2016). However, demonstrating benefits of agri-environmental measures for pest control and crop yield can improve the reputation of AES and increase the likelihood of land owners to participate in such schemes (Cardinale *et al.* 2012).

2.2 Land sharing versus land sparing strategies of AES

One of the largest controversies in nature conservation is the land sharing versus land sparing debate (e.g. Green *et al.* 2005, Phalan *et al.* 2011, Fischer *et al.* 2011). It distinguishes between two contrasting strategies of how to meet the demand for food production and conservation of biodiversity on the same land – the integration (“land sharing”) and the separation (“land sparing”) of conservation and production (Fischer *et al.* 2014). The land sharing strategy includes wildlife-friendly farming methods that aim at increasing biodiversity on farmland. Unfortunately, a likely side effect of this strategy is that lower yields increase the need for more agricultural land in order to meet the demands for food, feed, fibre and fuel. Researchers who favour the land sparing strategy, however, argue that a high percentage of wild species cannot survive in farming systems, even if managed wildlife-friendly. Therefore, they support high-yield farming to save wild land outside of farmed areas that can be set aside to host these species (Phalan *et al.* 2011).

In Europe, in a similar sense as the debate in the tropics above, different AES follow either the land sparing or the land sharing strategy. Organic farming aims at managing land in an environmentally friendly way to achieve a high level of biodiversity within the fields and to preserve natural resources (Council of the European Union 2007). This can be seen as on-field or land sharing strategy (Hodgson *et al.* 2010). Other schemes, such as the implementation of hedgerows, flower strips or fallow land, set aside land within the agricultural landscape for the explicit goal of benefitting biodiversity. The surrounding fields serve the main purpose of producing food and other agricultural products, achieving high quality yields. This means that actions taken for biodiversity conservation are spatially separated from productive areas. Therefore, these latter schemes can be seen as land sparing within the agricultural landscape (Balmford, Green & Phalan 2012; Quinn, Brandle & Johnson 2012; Gabriel *et al.* 2013).

In Lower Saxony, annual flower strips and organic farming are two of the most popular AES, both in terms of area where they are applied and the amount of subsidies payed to farmers (AES Lower Saxony 2012). Therefore, I selected these two AES as typical examples for land sparing and land sharing for testing their effectiveness against the background of European agricultural policy.

2.2.1 Organic farming in Lower Saxony - a land sharing strategy



Figure 1: Organic winter wheat field in Bodensee

The Council Regulation (EC) No. 834/2007 of 28 June 2007 defined the framework requirements for organic farming and labelling of organic products within the European Union. For instance, it is prohibited to use agrochemicals, such as mineral fertilizer and synthetic pesticides (Council of the European Union 2007). Instead fields are fertilized through the use of organic manure and nitrogen-fixing legumes, whereas weed control is achieved through wider crop rotations, intercropping and mechanical weeding (Gabriel *et al.* 2010). Many studies have shown that plant diversity and cover of non-crop plant species is higher on extensively managed, organic than on conventional fields (e.g. Fuller *et al.* 2005; Gabriel *et al.* 2006). There is some evidence that biological pest control is more effective on organic farms than on farms managed using conventional methods (Östman, Ekbom & Bengtsson 2001; Puech *et al.* 2014). According to the niche theory and intermediate-disturbance theory, extensively managed farmland is generally characterized by high within-field heterogeneity and low rates of disturbances caused by soil cultivation or pesticide applications (Case & Gilpin 1974; Tscharrntke *et al.* 2012). This provides habitat to species with different ecological niches and thereby increases the potential for natural biological control due to higher functional diversity (Tscharrntke *et al.* 2007; Kleijn *et al.* 2011).

Within Germany, each federal state has its own regulations concerning design of and compensation for AES. In Lower Saxony, organic farming is an AES that is applied to the whole farm and farmers can apply for subsidies under the scheme farm commitment (Betriebliche Verpflichtungen - BV1) (AES Lower Saxony 2016). One commitment period lasts five years and farmers can get up to 1,275 € per ha and year, depending on the crop type. For cropland they get subsidised with 234 € per ha and year. Between 2011 and 2014, 32 % of expenditures for AES have been spend on this scheme and around 75,000 ha have been managed organically in Lower Saxony (Statistisches Bundesamt 2015). This corresponds to 1.5 % of its surface area and to 2.8% of its farmed land.

2.2.2 Flower strips in Lower Saxony – a land sparing strategy



Figure 2: Winter wheat field with adjacent flower strip in Opperhausen

There are several schemes that subsidise flower strips in Lower Saxony, but the scheme for annual flower strips (BS11 – einjährige Blühstreifen) is the most popular one. Since organic farming is not compatible with other AES, flower strips are typically used by conventional farmers. Between 2011 and 2014 flower strips have been applied on 7,500 ha and 13 % of expenditures for AES have been spent on them (AES Lower Saxony 2012). Farmers are subsidised with 700 € per ha flower strip per year. If beekeepers are involved into the selection of the seed mixture, farmers get an additional 100 € per ha. Seed mixtures have to contain at least five species out of a list of 28 defined plant species (Table S 2, Appendix) and must be designed for providing flowers between June and October. Flower strips are 6 - 30 m wide and the area is restricted to 10 ha per farm. They have to be sown until the 15th April of each year and 30 % of the total flower strip area per farm has to be left untouched until the 15th February of the following year.

The rest of the flower strips can be removed starting from the 15th October (ML 2016). The application of fertilizer and pesticides is not allowed. According to the Lower Saxony Ministry of Food, Agriculture, and Consumer Protection, flower strips shall provide food and shelter to natural enemies of crop pests, pollinators and other wild animals (AES Lower Saxony 2016). As they maintain common species generally, it is a scheme that supports agro-ecosystem services rather than serving biodiversity conservation (Ekroos *et al.* 2014).

The positive effect of sown flower strips on natural enemies has been underpinned by several studies (e.g. Haaland, Naisbit & Bersier 2011; Ramsden *et al.* 2015). A possible reason is that many parasitoids as well as predators – both playing an important role in the regulation of herbivore populations – require nectar or other sugar sources to cover their energetic needs once they are adult (Wäckers & van Rijn 2012). Larvae of parasitic wasps, hoverflies or lacewings for example are carnivorous predators of many pest insects, whereas their adult stages are melliphagous, meaning they feed on floral nectar and pollen (Sutherland, Sullivan & Poppy 2001; Bianchi & Wäckers 2008). Furthermore, flower strips can provide shelter for natural enemies or moderate microclimate in which they may overwinter or seek refuge from factors such as environmental extremes or pesticides (Landis, Wratten & Gurr 2000). Thus, flower strips provide additional food sources and habitat, also in times when the crop plants are harvested, and may therefore be important to stabilize the populations of natural enemies.

2.3 Effects of landscape structure

Landscape structure of agricultural regions is often described in one of two ways: either as *compositional* or *configurational* heterogeneity (Plecas *et al.* 2014). According to Fahrig *et al.* 2011, compositional heterogeneity refers to the number and proportions of different crop types in a landscape sector. A higher total proportion of non-crop habitats usually implies a higher proportion of intrinsically complex and more-natural habitat types (Roschewitz *et al.* 2005; Fahrig *et al.* 2011). Configurational heterogeneity on the other hand refers to a more complex spatial arrangement of cover types in a landscape, often resulting from smaller mean field sizes (Bianchi, Booij & Tscharrntke 2006). This implies more frequent alteration of crop types and management regimes per unit area. It may also include higher compositional heterogeneity and usually an increased proportion of non-crop habitats due to a higher density of field margins. Effects of landscape composition on biocontrol have been tested in different studies, whereas the effect of landscape configuration is less studied (Plecas *et al.* 2014).

Regarding the effectiveness of AES and landscape complexity towards biological control, there is contradictory evidence from available studies. As many species associated with farmland require different food resources and habitat conditions through their life cycles, they can only thrive in fine-grained landscapes (Benton, Vickery & Wilson 2003). Generally, more heterogeneous landscapes are

expected to positively affect populations of both crop pests and their natural enemies (Al Hassan *et al.* 2012). This is because semi-natural habitats such as field margins (similar to flower strips) are areas free of insecticide use that provide additional food sources, refuges after harvest and overwintering sites for both (Bianchi & van der Werf 2003; Thies, Roschewitz & Tschardtke 2005; Plecas *et al.* 2014). However, various aspects of landscape composition and configuration might have different effects on crop pests and their enemies due to the complexity and dynamics of their interactions (Gagic *et al.* 2011). Roschewitz *et al.* (2005) and Thies *et al.* (2005) found that complex landscapes increased aphid parasitism rate but also aphid abundances, hence counterbalancing possible positive effects on biological control. Conversely, a study by Vollhardt *et al.* (2008) could not show an effect of landscape complexity on parasitism rate, whereas Bianchi *et al.* (2006) found that complex landscapes frequently support a greater abundance of natural enemies and lower pest populations than large-scale, monoculture landscapes. These contradictory findings highlight the importance for further research about the effects of landscape complexity on the effectiveness of AES regarding natural biological control.

2.4 Edge effect

The effect of landscape complexity on within-field species richness is limited by edge effects (Zhao *et al.* 2013). Many natural enemy species in fields depend on source populations from field margins to colonize the fields after anthropogenic disturbances such as tillage, insecticide treatments or harvesting (Wissinger 1997; Landis, Wratten & Gurr 2000; Tschardtke, Rand & Bianchi 2005). As their mobility varies between taxonomic groups, not all of them are able to enter the centre of large fields (Krauss, Gallenberger & Steffan-Dewenter 2011; Batáry *et al.* 2012). For instance, Duelli *et al.* (1990) showed ground-dwelling predators to be generally less mobile than flying predators. However, Tschardtke, Rand & Bianchi (2005) suggested that also densities of flying insects such as parasitoid wasps decrease at greater distance from field edges. Parasitoids depend on both non-crop habitats such as field edges that provide them with floral nectar sources and favourable microclimate and on crops that provide them with hosts (Dyer & Landis 1996). Thus, parasitism levels generally decrease at further distance from field edges, reflecting distribution patterns of ecotone species (Tschardtke, Rand & Bianchi 2005). When quantifying the effect of locally applied measures such as field margins and flower strips on insect species, the decline of their effect with distance has therefore to be taken into account. This can be done by analysing field edges separately from field centres (Krauss, Gallenberger & Steffan-Dewenter 2011).

2.5 Study organisms

Aphids and cereal leaf beetles are two major invertebrate pests of small grains in Central Europe (Meindl *et al.* 2001; Schmidt *et al.* 2003). Both have been reported to cause economically important yield losses, which are expected to become even more severe with warming climates in the future (Olfert & Weiss 2006). I studied their abundance on winter wheat fields (*Triticum aestivum* L.) in Southern Lower Saxony. Winter wheat is the most-planted crop across Germany, covering more than 20 % of all arable land (Statistisches Bundesamt 2015). In order to better understand the dynamics of pest infestations in wheat fields, I will describe the ecology of the two crop pests and their natural enemies in the following sections.

2.5.1 Aphids and their natural enemies

The three most common aphid species (Hemiptera: Aphididae) in winter wheat in Germany are *Sitobion avenae* (Fabricius), *Metopolophium dirhodum* (Walker) and *Rhopalosiphum padi* (L.) (Alignier *et al.* 2014). *S. avenae* is the dominant species in wheat fields, making up for 70 – 90% of aphid individuals (Schmidt *et al.* 2003; Roschewitz *et al.* 2005).

Aphids have a complex lifecycle, involving bisexual and parthenogenetic generations, winged and wingless individuals and usually an alternation of host plants over the year (Borrer & White 1970). The three above mentioned species overwinter as eggs on different primary hosts. *S. avenae* overwinter on plants of the *Rubus* genus, *M. dirhodum* on rose (*Rosa*) species and *R. padi* on *Prunus padus* trees (Chinery 1987). In spring, wingless females (fundatrices) hatch and reproduce parthenogenetically, giving live birth to one to five young per day. With an average life expectancy of 18 days this results in around 70 offspring per aphid. After two or more generations of such females have been produced, a generation of winged females (alates) appears, that migrates to new host plants in early June (Borrer & White 1970). Secondary host plants of *S. avenae*, *M. dirhodum* and *R. padi* belong to the *Poaceae* family and are mostly wheat and barley. There, winged and wingless generations alternate; with wingless generations increasing local infestations and winged generations extending populations to new habitats (Chinery 1984). In early growth stages of the crop, aphids colonize flag leaves. Later they change to the inflorescence. Mass infestations usually appear after wheat flowering with temperatures over 20 °C and dry, sunny weather. At the end of milk ripening populations on wheat and barley suddenly collapse, as aphids move to other, still green host plants, such as maize (Heitefuss *et al.* 1993). Late in the season, winged forms return to the primary host. A generation of males and females appears, reproduces sexually and females lay eggs that overwinter (Borrer & White 1970). During mild winters, however, aphids may abandon the development on primary hosts and viviparous parthenogenetic females overwinter (anholocyclic life cycle) on autumn grown cereals and are already present in the crop by spring. In Western Europe,

S. avenae is already considered to be autoecious, spending all stages of their life cycle on grasses and cereals (Collins *et al.* 2002).



Figure 3: Wheat spike colonized by aphids

Damages of crops are caused on the one hand, when aphids occur in large colonies and weaken the host plants by sucking on phloem sap. On the other hand, aphids can transmit virus infections such as Barley yellow dwarf, when damaging plant cells with their stylet. Furthermore the excretion of honeydew facilitates the colonization of fungi on the leaf surface, which also harm the plants (George 1974). All three factors may result in considerable losses of grain, both in quantity and quality (Dixon 1977). The threshold level of economic damage for which an insecticide application is recommended, is three to five aphids per shoot (Giller *et al.* 1995). Economically important damages caused by cereal aphids in Europe have been recorded since the early 1970s. They have been related among others to the intensification of agriculture, including increased applications of nitrogen fertilizers in combination with growth regulators and pesticides (Thies *et al.* 2011). This is because the use of insecticides not only reduces crop pests, but also their natural enemies and consequently inhibits natural pest control. Similarly, nitrogen fertilization has been found to increase density, body size and fecundity of aphids (Duffield *et al.* 1997; Gash 2012).

Outside of manmade monocultures, mass infestations of aphids are rare. On the one hand, the survival of aphid populations in grain fields depends on semi-natural habitats: as aphids cannot survive on ploughed fields, young crops get re-colonized by aphid populations from neighbouring field borders and grasslands (Gilbert *et al.* 2009). On the other hand, natural and semi-natural habitats also host species-rich enemy communities and stable food web structures prevent aphid population outbreaks naturally (Robinson & Sutherland 2002; Zhao *et al.* 2015).

Biological control of cereal aphids is of considerable economic value in Europe (Östman, Ekblom & Bengtsson 2003). Aphids are attacked by various arthropod natural enemies, including generalist ground-dwelling predators, more specialized vegetation-dwelling predators and highly specialized parasitoids (Jonsson *et al.* 2014). Ground-dwelling predators include carabids, staphylinid beetles and

spiders. They feed on aphids fallen to the ground due strong wind and rain (Winder *et al.* 2013). Vegetation-dwelling predators such as lady beetles (Coleoptera: Coccinellidae), lacewing larvae (Neuroptera: Chrysopidae), hoverfly larvae (Diptera: Syrphidae), predatory bugs (Hemiptera: Heteroptera), spiders (Araneae) and parasitoid wasps (Hymenoptera: mainly Aphidiidae) contribute to biological control mainly in the later population growth phase of aphids when they multiply in the crop (Schmidt *et al.* 2003). Recent findings indicate that ground-dwelling predators respond relatively slowly to aphid infestations and control them less effectively than flying natural enemies such as lady birds, hoverflies and parasitoids (Holland *et al.* 2008). Some studies even showed that parasitoids are the most important group of all natural enemies (Schmidt *et al.* 2003). Females of parasitoid wasps lay their eggs into aphids, where the larva feeds on their body substance. After undergoing several larval stages, the larva pupates within the dead aphid body, which is then called mummy (Vollhardt *et al.* 2008). Mummies are easily distinguishable from alive aphids in the field and the ratio of mummies to total aphids can be used as a measure for aphid parasitism (Schmidt *et al.* 2003). All groups of natural enemies are assumed to be enhanced by semi-natural habitats providing food resources and overwintering sites (Thies, Roschewitz & Tscharncke 2005). The use of insecticides, however, not only reduces the number of pest insects, but also the potential for natural biological control (Geiger *et al.* 2010).

2.5.2 Cereal leaf beetles and their natural enemies



Figure 4: Adult cereal leaf beetle

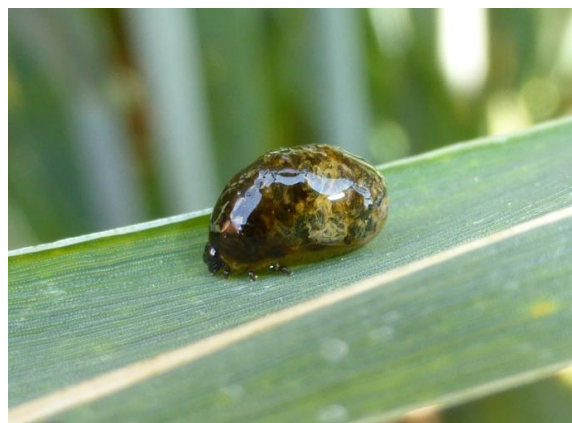


Figure 5: CLB larvae with typical feeding damage on wheat

Cereal leaf beetles (CLB) (Coleoptera: Chrysomelidae; *Oulema* spp.) are another important group of crop pests in Europe, Asia and North America (Ihrig *et al.* 2001). In central Germany, three *Oulema* species occur: *O. melanopus* (L.), *O. duftschmidi* (Redtenbacher) and *O. lichenis* (Voet.) (Zahradnik 1985, Dr. Lehnhus (Julius Kühn-Institut), pers. comment 24th January 2017). As their larvae are not distinguishable visually in the field, I did not analyse them separately.

CLB are univoltine, meaning that they produce one generation per year. Adults overwinter in protected areas such as forest edges, hedgerows and woodlots (Häni *et al.* 2008). At the end of April, they leave their overwintering sites and do maturation feeding on grasses. At the beginning of May,

adults disperse into cereal crops (preferably oat and wheat), mate and females deposit eggs singly or in pairs on crop leaves. The oviposition period can last until June and one female CLB produces between 50 and 200 eggs (Schmitt 1988). After 7-15 days, the larvae (Figure 5) hatch and start the most damaging period of their lifecycle. During their maturation, which lasts 3-4 weeks, they feed on the superficial layer of leaves, hindering the leaves' photosynthetic potential (Haynes & Gage 1981; Nentwig, Poehling & Schärer 1994). Besides that, the physical injury of the leaf surface leads to an increase in plant transpiration and a higher risk of fungi infections. One larva per flag leaf can lead to a total yield loss of 10 % (Jossi & Bigler 1996). Therefore a density of 0.4 larvae per tiller has been suggested as a threshold to justify the need for insecticide application (Buntin *et al.* 2004).

Larvae appear white or yellow. However, most of them have a shiny black appearance, as they cover themselves with their own excrements. This is probably a defence mechanism against predators and prevents desiccation (Jossi & Bigler 1996). After the fourth instar, larvae pupate in the soil at a depth of 2-5 cm (*O. melanopus* and *O. duftschmidt*) or inside a hardened foam cocoon on the host plant (*O. lichenis*). Adults emerge a few weeks later and after feeding on corn and other grasses, they disperse to overwintering sites from August onwards (Cooter 1991). Natural enemies of CLB are generalist predators such as rove beetles, carabids, spiders, ladybirds, predatory bugs and lacewing larvae, and also specialized parasitic hymenoptera (Meindl *et al.* 2001).

2.6 Research questions and hypotheses

To date, the effectiveness of agri-environment schemes in enhancing biodiversity has been mixed, whereas their effect on ecosystem services such as natural biological control remain largely unexplored (Kleijn & Sutherland 2003; Kleijn *et al.* 2006; Batáry *et al.* 2015). In my study, I aim to answer the question, whether a land sharing (organic farming) or a land sparing design (flower strips) of AES is suited better to increase biological control by natural enemies on fields. Therefore, I compared the abundance of crop pests and their natural enemies, levels of parasitism and the predation rate of crop pests by natural enemies between management types. Conventionally managed fields served as control group. I took into account the edge effect by taking samples, both at the edge and in the interior of the fields. Additionally, I tested the influence of landscape structure on natural pest control. This was done by selecting fields along a gradient from small to large fields.

I tested the following hypotheses:

- (1) Flower strips offer more food and shelter to natural enemies than organic fields due to a higher density of flowers and more complex vegetation structures. Therefore, at the field edges, flower strips are more effective than organic farming concerning natural pest control. Both management types perform better than conventional farming (Figure 6).

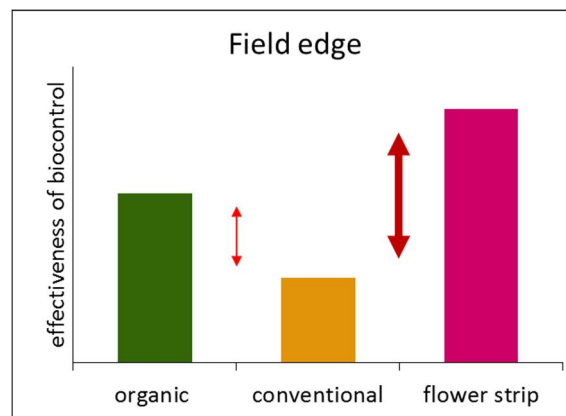


Figure 6: First hypothesis

- (2) In the field interior, organic farming is more effective in natural pest control than flower strips, as the positive effect of flower strips declines with distance. The difference in performance between flower strip fields and conventional fields is much smaller (Figure 7).

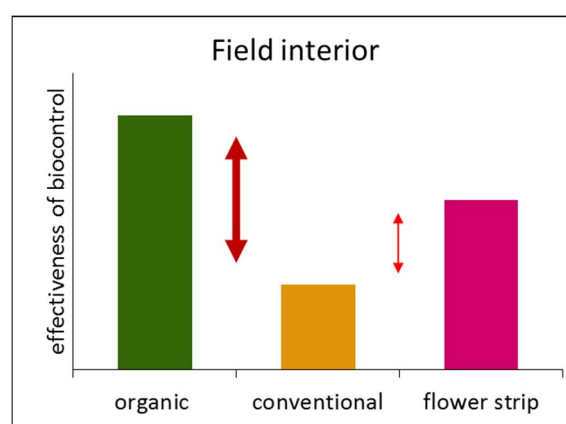


Figure 7: Second hypothesis

- (3) Due to higher densities of natural enemies at field edges (edge effect), the effectiveness of biocontrol is better in edge than in interior transects, independent of management type.
- (4) Landscapes with smaller field sizes support populations of natural enemies better than landscapes with large fields, as they have a higher proportion of field margins and thus provide more habitat and food resources. Therefore, also natural pest control is influenced positively by smaller fields.

The present study is embedded into the “Land sparing – Land sharing project” (2LS Project) and part of the larger project “Biodiversity and associated ecosystem services in small vs. large scale agriculture”, which is funded by DFG (Deutsche Forschungsgemeinschaft). The project is conducted by Dr. Péter Batáry from the Agroecology working group at Göttingen University. The 2016 2LS field work team consisted of two master students (Jacob Rosenthal and Carolina Steffen), a doctoral student (Marian Mendoza García), a postdoctoral researcher (Rita Földesi) and me.

3 Material and Methods

3.1 Study area and experimental design

The study sites were located in Southern Lower Saxony, as a typical example of an intensive agricultural region in Western Europe. In the counties Göttingen, Northeim and Osterode (Harz) (Figure 8) Jacob Rosenthal and I selected 10 villages with pairs of organic and conventional farms ($N = 10$ villages \times 2 farms = 20 farms in total). Maps showing the arrangement of crop fields were obtained from "Servicezentrum Landentwicklung und Agrarförderung" (Lower Saxony). Information on location and managers of flower strips was provided by "Niedersächsisches Ministerium für Umwelt, Energie und Klimaschutz".



Figure 8: Location of the counties Göttingen, Northeim and Osterode (Harz) within Germany

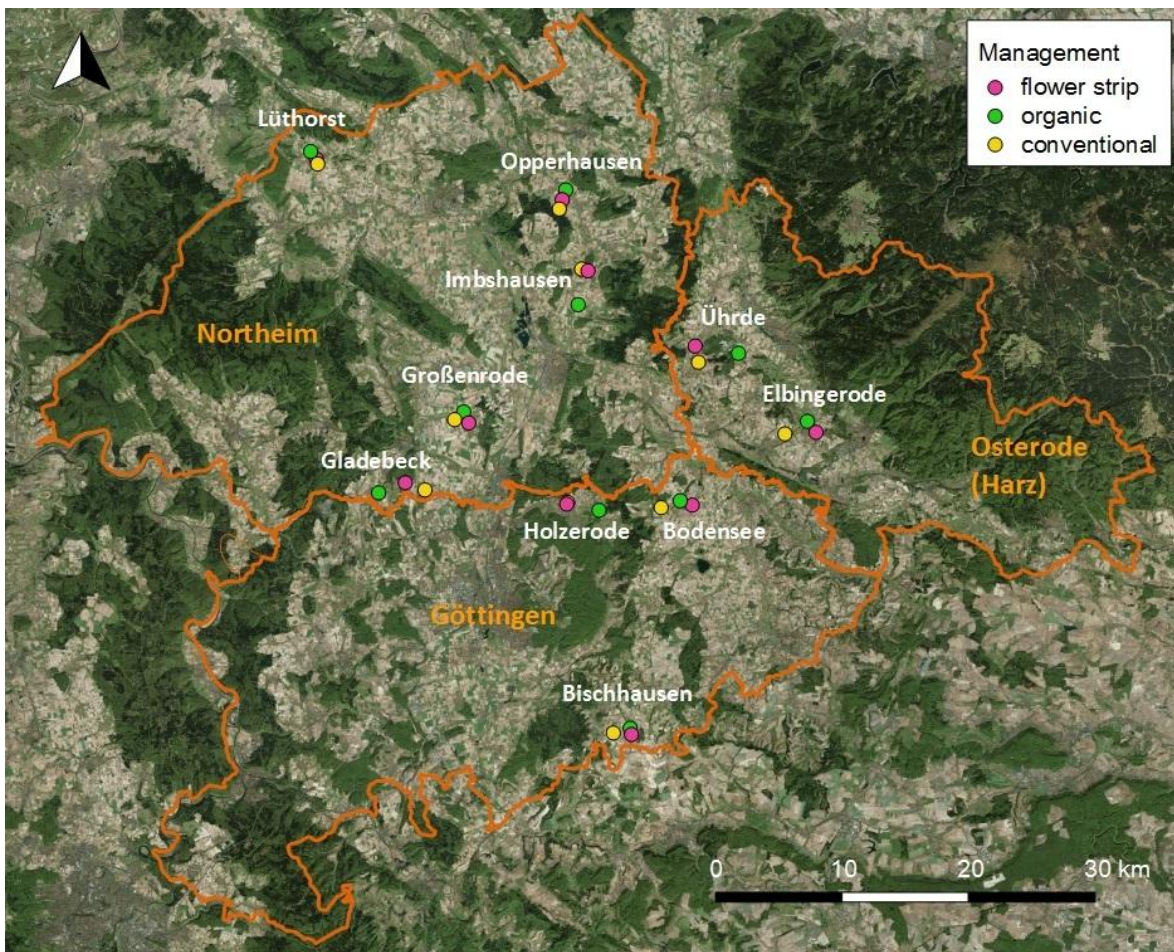


Figure 9: Position of villages (in white) and study fields within the counties Göttingen, Northeim and Osterode (Harz)

Contact details of organic farmers were derived from the online portal BioC (Directory of Certified Organic Operators 2016). With this information, a preselection of possible fields was performed in QGIS (QGIS Development Team 2009). "Bing" areal maps from the "OpenLayers" plugin in QGIS were used to check for landscape parameters such as forests and built-up areas. The final selection of villages and fields was done during farmer interviews and site visits in April and May 2016.

From each village, we selected three winter wheat fields: one of the organic farm and two of the conventional farm (one field with adjacent flower strip, hereafter called flower strip field, and one control field without flower strip). This way we obtained 30 study fields (Figure 9) with a mean size of 10.2 ± 0.36 ha (range 0.87 - 19.2 ha). The fields of one village had a maximum distance of 2 km to each other in order to minimize edaphic and climatological differences amongst them (see Gabriel et al. 2010). The landscapes around the fields represented a gradient of configurational heterogeneity (measured as mean field size), thus we studied a gradient of small to large-scale agricultural systems. Mean field size of the landscape was calculated within a 500 m radius around each study field. This radius is considered adequate to study responses of specialist pests and natural enemies to the landscape context (Chaplin-Kramer *et al.* 2011). The calculation was performed using ArcGIS for Desktop 10.2 (ESRI 2016). Landscape composition measured as percentage of arable land was kept constant by selecting fields in the agricultural matrix away from forests and built-up areas (Figure 9).

All study edges of the selected fields were bordered by grassy field margins and a dirt road adjacent to it (Figure 10). In each field we set up 2 transects, each 50 m long. One transect was located directly at the edge (hereafter edge transect) and the other transect parallel to it, 10 m inside the field (hereafter interior transect). This way we had $3 \times 2 = 6$ transects per landscape.

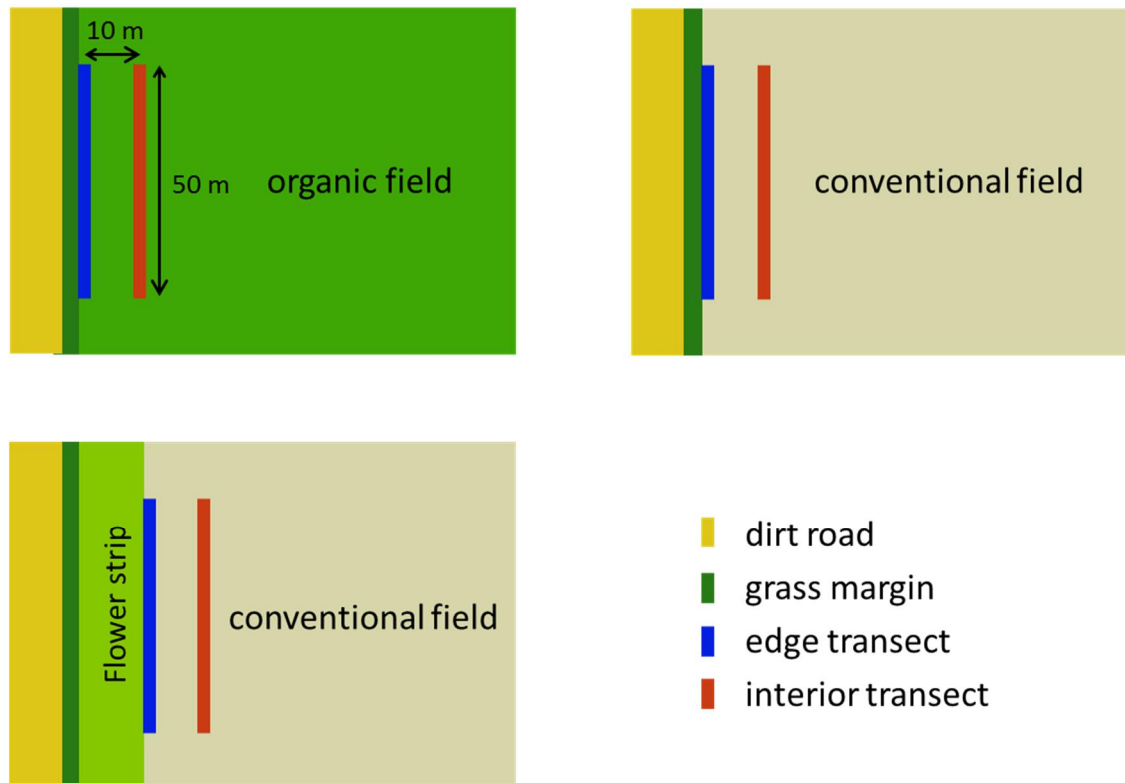


Figure 10: Experimental design of fields and transects belonging to one village

3.2 Field surveys

3.2.1 Survey of cereal leaf beetle larvae

I quantified the infestation of wheat by larvae of the CLB, as this development stage causes most damage to crops. The number of CLB larvae was counted in transect walks from 6th to 9th June 2016, during the peak of larval appearance (early June) according to Ihrig et al. (2001). I walked each transect for 10 minutes and recorded the number of CLB larvae I spotted within 1m to either side. A direct counting of CLB larvae per wheat tiller was not feasible as the total infestation was low and distribution of CLB larvae was scattered.

3.2.2 Survey of aphids and their natural enemies

For counting the number of aphids and their natural enemies, I randomly selected 10 tillers at five sites per transect (10 tillers x 5 spots = 50 tillers per transect). I screened the tillers from base to spike and counted the number of aphid and natural enemy individuals present. The organisms recorded as natural enemies were ladybirds (adults and larvae), hoverflies (pupae and larvae), lacewing larvae and spiders. I did not include heteroptera in the analysis, as it was not possible to identify in the field whether individuals belonged to predatory or herbivorous species. Nevertheless their frequency on the surveyed tillers was negligible.



Figure 11: Mummified (brown) and non-mummified (green) aphids

Furthermore, I registered whether aphids were parasitized by hymenopteran wasps (mummified aphids; Figure 11). With this data I later determined the parasitism rate (ratio of mummies to total number of aphids).

The survey was carried out twice, i.e. during wheat flowering (second half of June) and milk ripening stage (beginning of July). I pooled the data from both rounds, and therefore results are given as the sum of aphids and natural enemies on 100 tillers per transect and aphid parasitism rate as average of the two rounds.

3.2.3 Survey of natural enemies via sweepnetting

Additionally to the survey of natural enemies directly on the wheat tillers, I carried out a sweep net sampling to collect natural enemies along the transects. Sweep netting was standardized with 60 sweeps per transect (one sweep per footstep). I used a heavy duty sweep net with 38 cm in diameter from the supplier BioQuip Products (www.bioquip.com). The sampling was carried out at the beginning of July. All insects in the net were collected and later identified in the laboratory. I counted the number of ladybirds (larvae and adults; Figure 12), hoverflies (larvae and adults; Figure 13), lacewing larvae (Figure 14), spiders, parasitoids wasps and predatory bugs. Bugs were identified to species level by an expert (Gyula Szabó). For my analyses I selected the species that are predators of aphids according to the book "Wanzen beobachten und kennen lernen" by Wachmann, Melber & Deckert 2008 (Table S 1, Appendix).



Figure 12: Ladybird larva



Figure 13: Hoverfly larva



Figure 14: Lacewing larva

3.2.4 Aphid predation experiment

In order to study the biological pest control potential, I performed an experiment in which I determined the predation pressure exerted by natural enemies of aphids in the fields. I prepared 5 x 6 cm cards of sandpaper with three pea aphids (*Acyrtosiphon pisum*) attached to it as artificial prey (Geiger *et al.* 2010; Bertrand, Baudry & Burel 2016). The aphids were supplied alive from KatzBiotech (www.katzbiotech.de). Before attaching them to the cards, the aphids were deep-frozen for approximately two hours to make them immobile. Then only big, adult aphids were selected and glued onto the rough side of the cards (Figure 15). The glue used for fixation was "Aurum Insekten Leim" from W. Neudorff GmbH KG (www.neudorff.de). Until the cards were brought to the fields, they were stored in a deep freezer at - 18 °C.



Figure 15: Aphid card with three pea aphids



Figure 16: Aphid card installed in the field

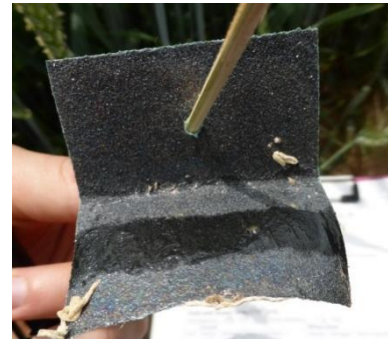


Figure 17: Aphid card predated by slugs

On each transect, I installed five cards at a distance of approximately 10 m. Hence, there was a total of 15 decoy aphids per transect. The cards were attached to the wheat stem directly underneath the spike with a foldover clip (Figure 16). They were folded like a tent with the rough side pointing downwards to protect the aphids against rain. I placed the cards into the upper part of the vegetation to make them approachable for insects that usually prey on aphids directly on the wheat tillers. After one week, the cards were collected and the number of missing aphids was recorded. If aphids were unequivocally predated by slugs (slime traces on the card; Figure 17), those cards were treated as missing data, as I did not want to include the effect of slugs into the analysis. The experiment was performed between 27th June and 7th July.

3.3 Data analysis

Statistical analyses were conducted using the software R version 3.3.1 (R Core Team 2016). I either used linear mixed-effects models (LMEs) or generalized linear mixed-effects models (GLMMs) to analyse the data. All full models contained the fixed effects *management* (factor with three levels: conventional, flower strip and organic), *transect* (factor with two levels: edge and interior), *mean field size* within 500 m radius around the focal field (continuous explanatory variable) and their two-way interaction terms. Random factors were *farmer* nested within *village*, as the conventional and the flower strip field always belonged to the same farmer. In all models the response variables were pooled within transect and accordingly the number of observations was 60 (10 villages x 3 management types x 2 transects).

Linear mixed-effects models (LMEs) were created using the `lme` function from the 'nlme' package (Pinheiro *et al.* 2016). Model-formula in R-syntax: "`lme (y ~ (management + transect + mean_field_size) ^2, random = ~ 1|village/farmer)`". I used LMEs to model the effects on CLB density (response variable: total number of CLB larvae per transect), aphid density (response variable: total number of individuals per transect pooled from both sampling rounds) and natural enemy density (response variable: number of predatory insect individuals caught via sweepnetting per transect). In order to achieve normally distributed residuals and avoid heteroscedasticity, I square-root-transformed the number of CLB larvae and log-transformed the number of natural enemies. Model selection was done with stepwise backward selection based on the Akaike information criterion (AIC). For this I used the `stepAIC` function of the 'MASS' package (Venables & Ripley 2002). The model with the lowest AIC was selected as the final model. Restricted maximum likelihood (REML) estimations were then used to fit this model. Model assumptions were checked visually by investigating normal quantile-quantile plots and residuals against fitted values, as recommended by Zuur *et al.* (2009).

To analyse proportional data, generalized linear mixed-effects models (GLMMs) with binomial distribution were applied. For that purpose I used the `glmer` function of the 'lme4' package (Bates *et al.* 2015) with binomial error distribution (`logit-link` function). Model-formula in R-syntax: "`glmer (cbind (successes, failures) ~ (management + transect + mean_field_size) ^2 + (1|village/farmer), control = glmerControl (optimizer = "bobyqa"), family = binomial)`". In this model, the dependent variables were data frames consisting of two columns: the numbers of "successes" versus the number of "failures". For the parasitism rate, this was the total number of parasitized versus the number of non-parasitized aphids per transect (pooled from both sampling rounds); for the proportion of natural enemies to aphids, it was the total number of natural enemies versus the total number of aphids per transect; and for the predation experiment I contrasted the number of predated aphids (x) versus the number of non-predated aphids per transect (number total decoy aphids – x). As some of the aphid cards were missing on the day of collection or predated by slugs, the number of total decoy aphids (maximum 3 aphids x 5 cards = 15 aphids) was reduced accordingly

for those transects. Of the total 300 aphid cards, 26 were dealt as missing data. In the GLMMs, fixed and random effect terms were the same as in LMEs. However, the fixed effect mean field size had to be rescaled because the model cannot deal with variables on very different scales. I did the rescaling with the formula: $\frac{\emptyset \text{ field size} - \min(\emptyset \text{ field size})}{\max(\emptyset \text{ field size}) - \min(\emptyset \text{ field size})}$. That way the rescaled values for the mean field size ranged on a scale from 0 to 1. For the model simplification I used the drop1 function, which is also based on the Akaike information criterion. In stepwise backward selection non-significant fixed effects and interaction terms were removed manually until the minimal adequate model with the lowest AIC value was obtained. Again, I checked model assumptions according to graphical validation procedures (Zuur *et al.* 2009). If needed, model fit was improved with the control parameter optimizer = "bobyqa" which is part of the 'minqa' package (Bates *et al.* 2015).

The values in the summary table (Table 7), that gives an overview of all main fixed effects, were obtained from type II Wald chi-squared tests. These originated from the Anova function of the 'car' package (Fox & Weisberg 2011).

4 Results

4.1 Cereal leaf beetle larvae

The number of CLB larvae counted per transect ranged from 3 (interior of organic field in Gladebeck) to 134 larvae per transect (edge of conventional field in Opperhausen). Abundances differed significantly between management types and transect positions. Most CLB larvae occurred in the interior transects of conventional fields, whereas least CLB larvae were found in the edge transects of organic fields (Figure 18). In general, the number of CLB larvae in conventional and flower strip fields was significantly higher than in organic fields, and interior transects hosted significantly more CLB larvae than edge transects (Table 1). Mean field size did not have an effect on CLB abundances.

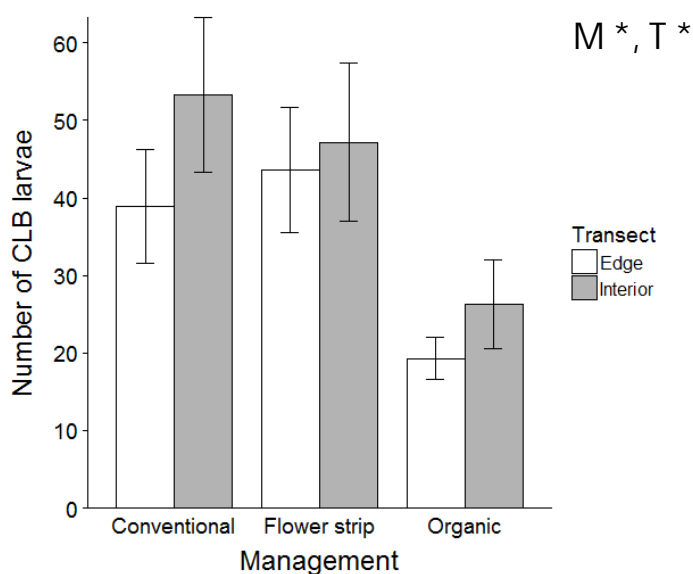


Figure 18: Mean number of CLB larvae per transect in relation to transect position (edge vs. interior) and management type (conventional, flower strip or organic). Error bars represent standard error means (SEM). Results are based on type II Wald chi-squared tests (Table 7) with *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$ (M: effect of management; T: effect of transect position).

Table 1: Effects of management and transect position on the number of CLB larvae. The table shows parameter estimates from a LME fitted using treatment contrasts (i.e. flower strip was the reference level for all comparisons). The contrast among conventional and organic management was derived by re-fitting the model using conventional as the baseline level. Bold font indicates significant effects ($p < 0.05$).

Parameter	Estimate \pm CI	t	p
Management			
flower strip - conventional	0.13 \pm 0.66	0.38	0.709
flower strip - organic	-1.86 \pm 1.38	-2.65	0.027 *
conventional - organic	-1.99 \pm 1.38	-2.83	0.020 *
Transect (edge - interior)	0.55 \pm 0.54	2.12	0.04 *

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, (*) $p < 0.1$

4.2 Aphids and their natural enemies

4.2.1 Aphid density

I counted a total of 2457 aphids on 6000 tillers during two survey rounds, resulting in 0.4 aphids per tiller on average. The number includes parasitized and non-parasitized aphids from all three species that usually occur in central European cereal fields. *Sitobion avenae* was the most abundant species (90 % of all individuals). As the impact of all three species is similar, I analysed the effect of management, transect position and mean field size on the three species jointly. The only predictor having a significant effect on aphid abundance was management: flower strips had a strong effect on aphids, increasing their number by 81 % compared to organic fields and by 103 % compared to conventional fields (Figure 18 and Table 2). However, the mean number of aphids per tiller never exceeded the threshold level of economic damage (3-5 aphids per tiller (Giller *et al.* 1995)). The highest number of aphids per tiller was 1.55, which I counted in the first survey round in the edge transect of the organic field in Gladebeck.

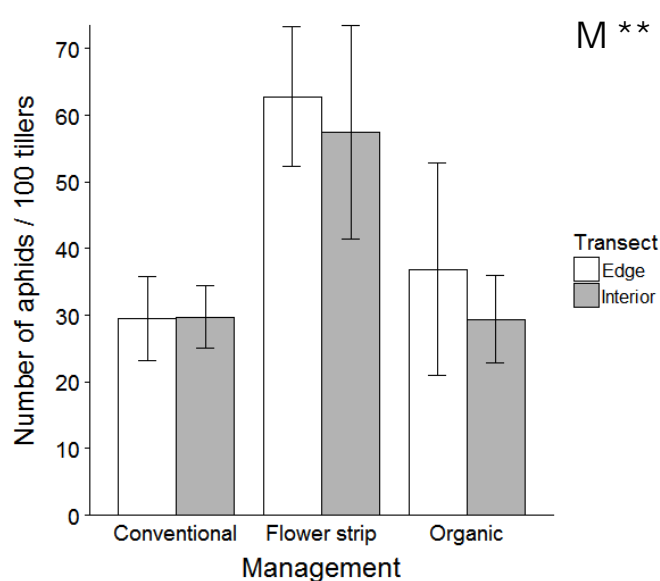


Figure 19: Mean number of aphids per transect (data pooled from both rounds) in relation to transect position (edge vs. interior) and management type (conventional, flower strip or organic). Error bars represent SEM. Results are based on type II Wald chi-squared tests (see Table 7) with *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$ (M: effect of management).

Table 2: Effects of management on aphid density. The table shows parameter estimates from a LME fitted using treatment contrasts (i.e. flower strip was the reference level for all comparisons). The contrast among conventional and organic management was derived by re-fitting the model using conventional as the baseline level. Bold font indicates significant effects ($p < 0.05$).

Parameter	Estimate \pm CI	<i>t</i>	<i>p</i>
Management			
flower strip - conventional	-30.50 \pm 17.23	-3.47	0.001 **
flower strip - organic	-26.95 \pm 23.26	-2.27	0.049 *
conventional - organic	3.55 \pm 23.26	0.30	0.772

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, (*) $p < 0.1$

4.2.2 Aphid parasitism

Parasitism rates ranged between $8.24 \pm 3.40\%$ in the organic edge transects and $27.07 \pm 3.89\%$ in the flower strip edge transects. Mean field size (removed from final model) and transect ($\chi^2 = 0.58$, d.f. = 1, $p = 0.448$) did not significantly influence aphid parasitism rate (Figure 20 and Table 3). However, management and the interaction of management \times transect showed significant effects. In the interior transects, parasitism rates did not differ between management types, but in the edge transects, parasitism rates in flower strip fields was much higher than for organic or conventional fields, respectively.

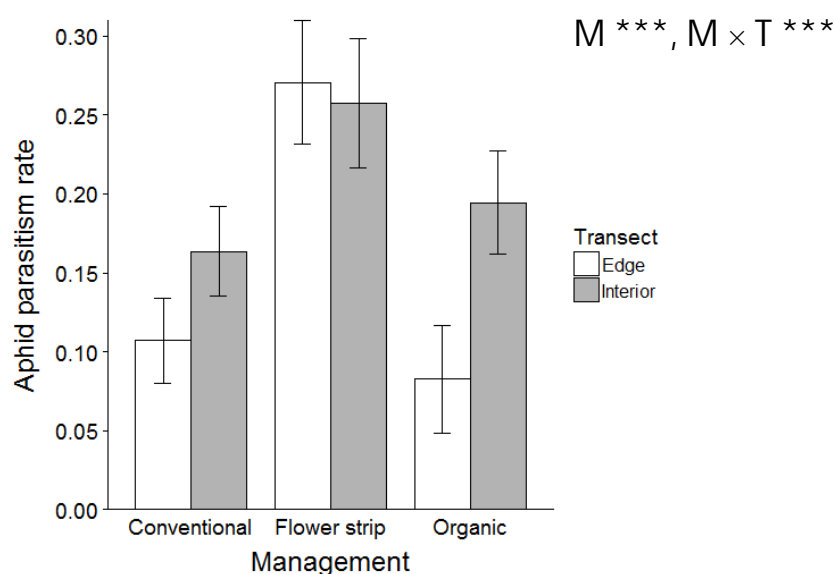


Figure 20: Proportion of parasitized aphids on the total number of aphids per transect (data pooled from both rounds) in relation to transect position (edge vs. interior) and management type (conventional, flower strip or organic). Error bars represent SEM. Results are based on type II Wald chi-squared tests (see Table 7) with *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$ (M: effect of management; M \times T: interaction between effects of management and transect).

Table 3: Effects of the interaction between management and transect position on aphid parasitism rate. The table shows parameter estimates from a GLMM fitted using treatment contrasts (i.e. flower strip was the reference level for all comparisons). The contrast among conventional and organic management was derived by re-fitting the model using conventional as the baseline level. Bold font indicates significant effects ($p < 0.05$).

Parameter	Estimate \pm CI	<i>z</i>	<i>p</i>	
Interior transect				
flower strip - conventional	-0.30 \pm 0.39	-1.53	0.126	
flower strip - organic	-0.08 \pm 0.46	-0.34	0.736	
conventional - organic	0.22 \pm 0.51	0.86	0.388	
Edge transect				
flower strip - conventional	-1.12 \pm 0.43	-5.13	<0.001	***
flower strip - organic	-1.51 \pm 0.54	-5.50	<0.001	***
conventional - organic	-0.39 \pm 0.63	-1.23	0.221	

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, (*) $p < 0.1$

4.2.3 Predator-prey ratio for aphids

The numbers of natural enemies counted per tiller did not differ significantly between management types, transects or along the gradient of field size. For the ratio of natural enemies to aphids per tiller however, I found significant effects. The ratio ranged from 0.06 ± 0.02 in the conventional edge transects to 0.28 ± 0.12 in the organic edge transects (Figure 21). In general, the proportion of natural enemies was significantly higher both in organic and conventional fields than in the flower strip fields (Table 4). Transect did not have a significant effect ($\chi^2 = 1.95$, d.f. = 1, $p = 0.163$), but there were proportionately more natural enemies per aphid on smaller fields, i. e. natural enemy proportion increased with decreasing mean field size .

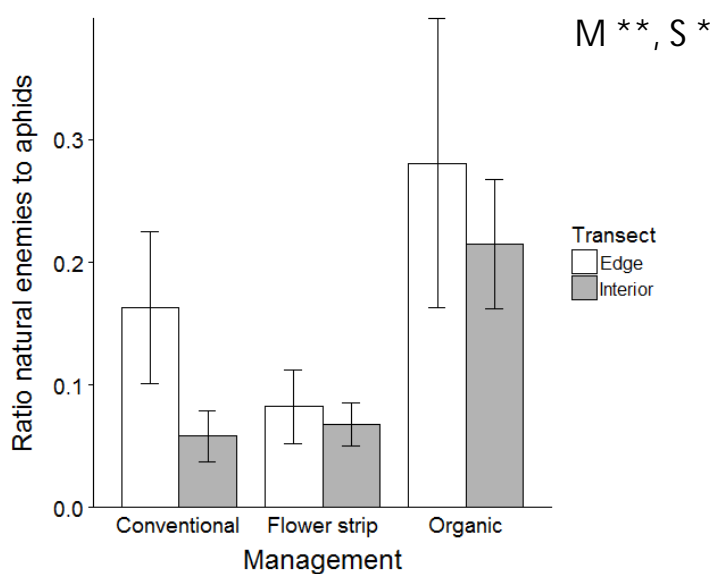


Figure 21: Ratio of natural enemies to aphids (data pooled from both rounds) in relation to transect position (edge vs. interior) and management type (conventional, flower strip or organic). Error bars represent SEM. Results are based on type II Wald chi-squared tests (see Table 7) with *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$ (M: effect of management; S: effect of mean field size).

Table 4: Effects of management, transect position and mean field size on the ratio of natural enemies to aphids. The table shows parameter estimates from a GLMM fitted using treatment contrasts (i.e. flower strip was the reference level for all comparisons). The contrast among conventional and organic management was derived by re-fitting the model using conventional as the baseline level. Bold font indicates significant effects ($p < 0.05$).

Parameter	Estimate \pm CI	z	p	
Management				
flower strip - conventional	0.49 ± 0.39	2.42	0.016	*
flower strip - organic	0.96 ± 0.69	2.73	0.006	**
conventional - organic	0.47 ± 0.70	1.31	0.190	
Transect (edge - interior)	-0.23 ± 0.32	-1.40	0.163	
Mean field size	-2.02 ± 1.76	-2.25	0.025	*

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, (*) $p < 0.1$

4.3 Aphid predation experiment

Mean predation rate across all aphid cards was 38.44 ± 3.42 %. Predation rate on flower strip fields (31.25 ± 5.11 %) was significantly lower compared to organic (43.05 ± 4.91 %) and conventional fields (41.16 ± 7.52 %) (Figure 22 and Table 5). Transect (removed from final model) and mean field size ($\chi^2 = 2.25$, d.f. = 1, $p = 0.134$) did not have a significant effect on predation rate.

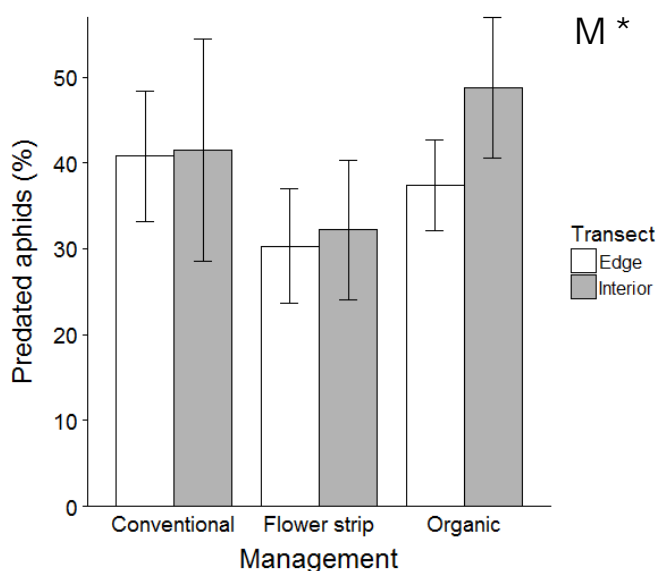


Figure 22: Percentage of predated aphids in relation to transect position (edge vs. interior) and management type (conventional, flower strip or organic). Error bars represent SEM. Results are based on type II Wald chi-squared tests (see Table 7) with *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$ (M: effect of management).

Table 5: Effects of management and mean field size on the percentage of predated aphids. The table shows parameter estimates from a GLMM fitted using treatment contrasts (i.e. flower strip was the reference level for all comparisons). The contrast among conventional and organic management was derived by re-fitting the model using conventional as the baseline level. Bold font indicates significant effects ($p < 0.05$).

Parameter	Estimate \pm CI	<i>z</i>	<i>p</i>
Management			
flower strip - conventional	0.46 ± 0.40	2.27	0.024 *
flower strip - organic	0.58 ± 0.38	2.38	0.013 *
conventional - organic	0.12 ± 0.74	0.31	0.753
Mean field size	1.43 ± 1.87	1.50	1.336

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, (*) $p < 0.1$

4.4 Natural enemies caught via sweepnetting

Of the hymenoptera I caught, only individuals from the family Nabidae were classified as predatory bugs, resulting in 17 individuals of predatory bugs out of 681 (Table S 1, Appendix). The total number of natural enemies I caught with the sweepnet was not influenced by management type or transect position, but there was a marginal significant effect of mean field size (Table 6). The number of natural enemies was lower in areas with larger fields (Figure 23).

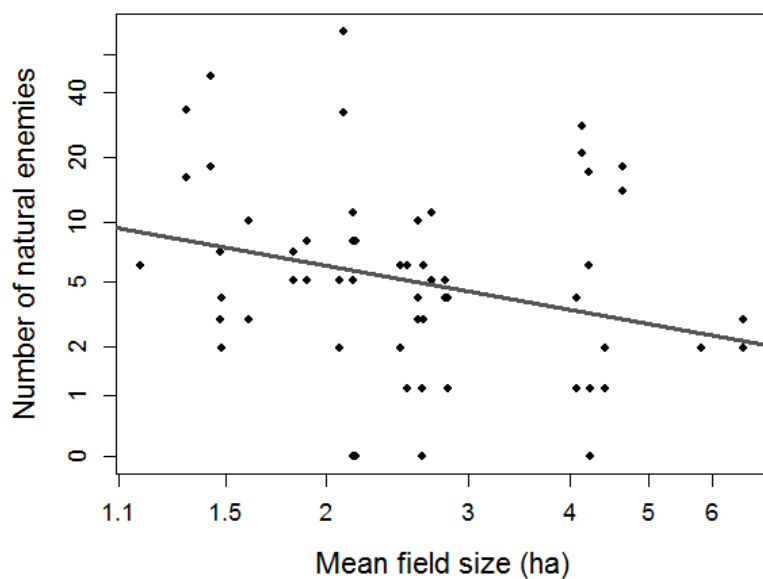


Figure 23: Abundance of natural enemy individuals obtained from sweepnetting in relation to mean field size, presented on logarithmic scales.

Table 6: Effect of mean field size on the abundance of natural enemies. The table shows the parameter estimate from a LME. Bold font indicates significant effects ($p < 0.05$).

Parameter	Estimate \pm CI	<i>t</i>	<i>p</i>
Mean field size	-0.65 \pm 0.64	-1.97	0.056 (*)

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, (*) $p < 0.1$

4.5 Summary of all models

Table 7: Summary of main fixed effects management (factor with three levels: conventional, flower strip and organic), transect (factor with two levels: edge and interior), their interaction and mean field size within 500m radius around focal field (continuous explanatory variable) on all response variables. χ^2 -values, degrees of freedom (d.f.), and p-values from type II Wald chi-squared tests (see 3.4 Data analysis) are shown. Significant p-values of explanatory variables are indicated in bold ($p < 0.05$).

	Management	Transect	M × T	Ø field size
CLB larvae density	$\chi^2 = 8.11$, d.f.=2, $p=0.017$ *	$\chi^2 = 4.49$, d.f.=1, $p=0.034$ *	-	-
Aphid density	$\chi^2 = 13.17$, d.f.=2, $p=0.001$ **	-	-	-
Aphid parasitism rate	$\chi^2 = 26.02$, d.f.=2, $p<0.001$ ***	$\chi^2 = 0.58$, d.f.=1, $p = 0.448$	$\chi^2 = 27.86$, d.f.=2, $p<0.001$ ***	-
Enemies/aphids ratio	$\chi^2 = 10.58$, d.f.=2, $p=0.005$ **	$\chi^2 = 1.95$, d.f.=1, $p=0.163$	-	$\chi^2 = 5.05$, d.f.=1, $p=0.024$ *
Natural enemy density	-	-	-	$\chi^2 = 4.03$, d.f.=1, $p=0.048$ *
Predation experiment	$\chi^2 = 6.03$, d.f.=2, $p=0.049$ *	-	-	$\chi^2 = 2.25$, d.f.=1, $p=0.134$

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Table 7 shows a summary for the main fixed effects of all analyses performed in this study. Management type significantly affected all studied organisms, with exception of natural enemies caught via sweepnetting. Transect position however only influenced the number of CLB larvae. Aphid parasitism rate on the other hand was not influenced by transect position directly, but by the interaction of management type and transect position. The third fixed effect, mean field size, did not have an effect on the abundance of any crop pest organism, but it affected the abundance of natural enemies both in relation to the number of aphids on wheat tillers and absolutely when caught via sweepnetting.

5 Discussion

The results of my study showed that the biological pest control potential of flower strips and organic farming was different depending on the type of crop pest and the location within the field. Control of CLB was best under organic farming and there were less CLB larvae at field edges than in the interior of fields, independent of management type. Control of aphids was not different between organic and conventional management, but flower strips had ambiguous effects. On the one hand, they supported infestation of aphids in the fields, but on the other hand they also increased parasitism rates of aphids by hymenopteran wasps. Thus I cannot give a general recommendation, whether flower strips or organic farming are better to promote pest control services.

5.1 Organic farming vs. flower strips (land sharing vs. land sparing)

5.1.1 Cereal leaf beetle larvae

Organic farming seems to influence pest control of CLB positively, as there were significantly less CLB larvae in organic than in conventional fields, irrespective of whether they were bordered by flower strips or not. Several studies have shown a higher abundance of natural enemies in organic compared to conventional fields (e.g. Kromp 1989; Östman, Ekblom & Bengtsson 2001; Crowder *et al.* 2010; Geiger *et al.* 2010). This is probably related to the absence of insecticides, which appeared to influence biological pest control negatively. Krauss, Gallenberger & Steffan-Dewenter (2011) found insecticide treatment to have only a short-term effect on pest densities (here: aphids), while later in the season, pest densities were even higher and natural enemy populations lower in treated compared to untreated fields. This indicates that insecticide treatment keeps predator abundances low throughout the season and thereby significantly reduces top-down control of pest populations.

Apart from that, organic fields are characterized by more weeds in comparison to conventional fields as the application of herbicides is banned (Fuller *et al.* 2005; Gabriel *et al.* 2006; Rader *et al.* 2014). A higher number and diversity of non-crop plants results in higher micro-climatic heterogeneity within the fields (Kromp 1989). Therefore, structurally more complex organic fields are likely to provide an elevated number of ecological niches, and thus may support a higher variety of natural enemies (Batáry *et al.* 2012).

As the use of synthetic fertilizers is not allowed in organic farming, mean nitrogen inputs are typically lower in organic than in conventional fields (Schneider *et al.* 2014). Improved nitrogen nutrition changes many plant characteristics and can therefore indirectly influence herbivore density. For example leaf area, the number of shoots per plant and nitrogen content of the plant sap tend to increase (Honěk 1991). Also, plants supplied with optimum nitrogen levels are able to retain photosynthetically active leaves for longer due to delayed senescence (Gash 2012). These are all characteristics that make plant leaves more attractive to herbivores. Accordingly, positive effects of

nitrogen fertilization have been found for aphids (Duffield *et al.* 1997) and other herbivorous insects (Awmack & Leather 2002). Zhao *et al.* (2015) showed increasing nitrogen input to influence natural enemies asymmetrically and species-specific, leading to disturbances in arthropod food webs and declining predator-prey ratios. They pose two hypotheses accountable for this: the nitrogen limitation hypothesis and the plant vigour hypothesis. The hypotheses argue that plant nitrogen content is an important limiting factor, which determines the development rate, breeding behaviour and fecundity of insect herbivores. In contrast to their natural enemies, these pest insects could benefit more from increasing nitrogen input due to the direct improvement of both food quantity and quality. Consequently, higher densities of CLB larvae in conventional fields could be a result of higher nitrogen contents, making wheat more attractive to CLB, whereas altering food webs of natural enemies disadvantageously.

Another factor influencing abundance of CLB and their natural enemies could be differing microclimatic conditions inside the fields between management types. The 2016 plant survey accompanying my study showed wheat shoot density to be lower in organic than in conventional fields. This resulted in more light reaching the ground and a generally warmer and drier microclimate within organic fields. According to Dr. Thies (pers. comment 31st January 2017), dry conditions could be detrimental to CLB larvae since they are susceptible to dehydration. On the other hand, parasitoids of CLB have been shown to be positively influenced by warmer temperatures. For example, Weber (1992) found the larval development period of *Necremnus leucarthos* (Nees) (Hymenoptera: Eulophidae), a parasitoid of CLB, to be reduced by over 70 % with a temperature increase of 10 °C (from 17 to 27 °C). This indicates that generation times of parasitoids shorten significantly in warmer climates, leading to potentially higher rates parasitism and thus better biocontrol of CLB in organic fields.

There was no difference between conventional fields with and without flower strip, so the flower strip apparently did not influence natural pest control of CLB. In conclusion, my results showed that organic farming is better for controlling CLB than conventional farming, regardless of fields being bordered by flower strips or not. This resulted probably from a combination of different advantages of organic farming for natural enemies and a lower attractiveness of organic wheat to CLB.

5.1.2 Aphids

In contrast to CLB, aphid density did not differ between organic and conventional fields, but flower strip fields contained significantly more aphids than the other two management types. This was surprising, as several studies have found flower strips to increase natural enemy abundance, suggesting positive effects of flower strips on biological pest control (e. g. Haaland, Naisbit & Bersier 2011; Ramsden *et al.* 2015). However, there are other studies indicating that semi-natural habitats and

field margins promote aphid abundances within fields (see Tscharrntke *et al.* 2016). Al Hassan *et al.* (2013) suggested that aphid populations depend on undisturbed habitats for overwintering. As fields are ploughed every year, aphids cannot live there permanently and populations are sustained by recolonization from neighbouring, less disturbed habitats. Thus semi-natural habitats can be sources and crop fields sinks in aphid population dynamics, as argued by Dunning *et al.* (2016). Even though the flower strips investigated in this study are managed under the scheme “annual flower strips”, at least 30 % of the area has to be left untouched until the next year (ML 2016). Therefore, flower strips might serve as overwintering sites for aphids, leading to higher aphid populations in their vicinity. According to Zhang *et al.* (2007), ecological processes that reduce productivity or increase production costs in agricultural systems, such as herbivory, are regarded as ecosystem disservices. Thus, my results indicate that flower strips are providers of disservices concerning aphid infestation levels.

Regardless of the apparently negative effect of flower strips concerning aphids, infestations in my study fields averaged 0.4 individuals per shoot, which is well below the threshold level of economic damage of 3 - 5 per shoot (Giller *et al.* 1995). Therefore, the higher aphid abundances in flower strip fields are surprising, but with current levels not alarming. In an aphid outbreak year, however, damages could be critical without the use of insecticides. To sum up, the effects of neither of the two agri-environment schemes (organic farming and flower strips) manifested themselves in reduced total numbers of aphids compared to conventional fields.

5.1.3 Aphid parasitism

Regarding aphid parasitism rates however, I found positive effects of flower strips. In the interior transects, parasitism rates did not differ between the three management types, but at the edges, parasitism rates were significantly higher in flower strip fields than in organic or conventional fields. These findings go alongside with a study by Ramsden *et al.* (2015), who also observed higher rates of mummified aphids adjacent to floral resources. My results support the parasitoid nectar provision hypothesis, brought up by Heimpel & Jervis (2005). The hypothesis suggests that the presence of nectar-providing plants can improve biological control of pests by supplying parasitoids with sugar. The hypothesis has been underpinned by different studies so far. For example, Lee & Heimpel (2008) found floral resources to increase longevity and oviposition rate of parasitoids in the field. Another study carried out in the laboratory found that typical lifespans ranged between 1 – 5 days for starved parasitoids, whereas sugar-fed parasitoids lived between 2 – 8 weeks (Thompson 1999). Thus, parasitoids provided with sufficient nectar can attack more hosts during longer lifetimes.

Large monoculture fields are thought to be relatively devoid of sugar resources (Heimpel & Jervis 2005). The presence of flower strips can therefore add valuable food sources that are vital to support the performance of parasitoids. Ramsden *et al.* (2015) even claimed that providing suitable nectar and pollen sources represents the greatest opportunity for enhancing naturally occurring

parasitoids in agro-ecosystems. Model simulations suggest that flower strips also attract parasitoids from the surrounding area (Bianchi, Goedhart & Baveco 2008). These are all reasons that might explain the higher level of aphid parasitism close to flower strips in my study.

Hence, although total numbers of aphids were highest in flower strip fields, these aphids also exhibited highest rates of parasitism, potentially outweighing the negative effect of flowers strips on aphid infestation. The parasitism rates of $27.07 \pm 3.89\%$ along the flower strips were close to the value of 32 – 36 % that Hawkins & Cornell (1994) have found to be the threshold for successful biological control. As parasitoids respond numerically to aphid abundances (host density effect) (Schmidt *et al.* 2003), it is possible that levels of parasitism further increased after the date of the survey, leading to a subsequent decrease in aphid populations. From my results I conclude that flower strips are a suitable scheme to support melliphagous parasitoids of crop pests.

5.1.4 Predator-prey ratio for aphids

The ratio of natural enemies to aphids counted per tiller was lowest in flower strip fields and did not differ significantly between organic and conventional fields. Since the total number of enemies was not different between management types, this was most likely an effect of aphid density. The total number of aphids was highest in flower strip fields, thus these fields exhibited the lowest predator-prey ratio. In organic and conventional fields I counted fewer aphids and as a result, the predator-prey ratio was higher there. Hence, management type did not affect the number of natural enemies observed on the tillers directly, but it influenced the ratio of natural enemies to aphids. My results indicate that in organic fields, due to higher predator-prey ratios, predation by natural enemies might be a more important biocontrol-factor than in flower strip fields.

5.1.5 Aphid predation experiment

Similar to the previous results, predation rate of aphids was lowest in flower strip fields and there was no difference between organic and conventional fields. Equally to the predator-prey ratio, this relationship is inversely proportional to aphid density. Accordingly, this result might also have been a negative aphid density effect. As aphid density was highest in flower strip fields, there was abundant food supply for natural enemies. Therefore, in flower strip fields, there was no need for predators to feed on aphids from the aphid cards. Consequently, fewer aphids were missing on the cards within flower strip fields.

5.2 Edge effect

The only group of organisms for which an edge effect was found, were CLB. I counted significantly more CLB larvae in the interior than in the edge transects across all three management types. One reason might be, that biological control of CLB is higher at the edges than in the interior of fields, as many natural enemy populations are associated with field margins and have limited dispersal distances into fields (Tscharrntke *et al.* 2007). Field margins are known to increase populations of polyphagous predators, because they provide additional food sources, shelter from pesticide use and favourable microclimatic conditions (Thies, Roschewitz & Tscharrntke 2005). Several studies have shown higher abundances of predatory insects close to field edges compared to field centres (Landis, Wratten & Gurr 2000; Krauss, Gallenberger & Steffan-Dewenter 2011). Also rates of parasitism of crop pests have found to be higher close to field edges (e. g. Landis & Haas 1992; Thies & Tscharrntke 1999). For example, Thies and Tscharrntke (1999) found that parasitism of a herbivorous beetle in oil seed rape was higher in parts of wheat fields with adjacent ruderal field edge than in the interior of large wheat fields. This finding is in accordance with Weber (1992) who showed that a parasitoid of CLB (*Necremnus leucarthros*) needs constant food supply during its oviposition period. This means that parasitoids need an environment rich in different flowering plant species. Field edges may provide parasitoids with their food demands and therefore biocontrol of CLB might be more efficient close to field edges, as more CLB larvae get parasitized.

Another reason for higher CLB larvae density in the interior transects might be that CLB adults, during their maturation feeding, are attracted by the interior of wheat fields. The plant survey accompanying my study showed that the density of wheat tillers was lower and that leaves were drier at the field edges than inside the fields. According to the plant vigour hypothesis, this could have made wheat plants in the field interior more attractive to CLB adults (see Price 1991) so that they colonized the field interiors rather than the edges. As they lay eggs after a short period of maturation feeding (Haynes & Gage 1981), this may lead to a higher density of eggs and thus a higher density of larvae inside the fields.

5.3 Effect of landscape configuration heterogeneity

An effect of landscape configuration heterogeneity was found for the predator-prey ratio of aphids and their natural enemies on wheat tillers and for the number of natural enemies caught via sweep-netting. Both numbers increased with decreasing mean field sizes. This result suggests that a higher proportion of field margins in a landscape has a positive effect on natural enemy abundances. These findings are in line with several other studies. For example, Alignier *et al.* (2014) found higher abundances of natural enemies of aphids in complex landscapes with a higher proportion of semi-natural habitats. Thies & Tscharrntke (1999) showed that also levels of parasitism increased and crop damage decreased in structurally complex landscapes.

Populations of crop pest, however, were not affected by mean field sizes in my study, indicating that higher numbers of natural enemies do not necessarily translate into better pest control. This conclusion is in accordance with a meta-analysis conducted by Chaplin-Kramer *et al.* (2011). They assessed 46 landscape-level studies and found that natural enemies show consistent positive responses to landscape complexity, whereas responses of pest abundances do not differ significantly. This is because increased parasitism or predation can be offset by greater pest colonization in complex landscapes, resulting in no net change in pest populations over a landscape gradient (Thies, Roschewitz & Tschardtke 2005).

5.4 Assessment of hypotheses

My first two hypotheses were based on the assumption that there was an interaction between the effects of management and transect position. I hypothesized that at field edges, flower strips performed better than organic farming regarding biocontrol (1), whereas in the field interior, organic farming was more effective (2). I furthermore predicted that in both cases conventional farming was least effective. As I did not find interactions, except for aphid parasitism rates, these two hypotheses can only partly be confirmed. In the interior transects, parasitism rates did not differ between management types, but in the edge transects, parasitism rate was highest in flower strip fields and there was no significant difference between organic and conventional fields. This result confirms my first hypothesis and suggests that flower strips are suitable schemes for promoting melliphagous parasitoids, which are an important – if not the most important (Schmidt *et al.* 2003) - group of natural enemies for aphid control. The high numbers of aphids in flower strip fields, however, demonstrated that an increase in numbers of natural enemies does not necessarily translate into better pest control. For aphid density, predator-prey ratio and the aphid predation experiment, organic farming performed better in biocontrol than flower strips, but there was no difference between organic and conventional farming. This indicates potential disservices of flower strips regarding natural pest control, resulting from habitat improvements that favour aphids more than their natural enemies. With respect to the control of CLB, organic fields performed best. This suggests that organic fields are less attractive to CLB or that natural enemies of CLB are better supported by organic than by conventional farming. Flower strips cannot provide similar benefits and therefore could not show an improvement in biocontrol of CLB. I conclude, that the two schemes, organic farming and flower strips, have different effects regarding biocontrol, depending on the group of organisms. Therefore, none of the two could be shown to perform generally better than the other.

My third hypothesis was that biocontrol is better at field edges than in the field interior. This hypothesis could be confirmed for CLB. For the other surveys I did not find significant differences between edge and interior transects.

My last hypothesis, that natural pest control is influenced positively by smaller field sizes, could also partly be confirmed. Predator-prey ratios of aphids and their natural enemies and abundances of natural enemies caught via sweepnetting increased for decreasing field sizes. However, higher numbers of natural enemies did not affect pest densities. Therefore, field size did not have a direct impact on pest control.

5.5 Limitations of the experiment

The method used for determining CLB densities (transect walks) did not allow for determining infestation rates as number of larvae per tiller. Because wheat shoot density in organic fields was lower than in conventional fields, the ratio of larvae per tiller might have been relatively higher than the numbers I obtained from transect walks. However, I chose the transect walk method because total infestation of CLB was low and counting larvae per tiller would have resulted into many zero counts. Therefore, numbers of CLB larvae should be corrected for wheat shoot density in following analyses of my data, when results from the plant survey are evaluated.

Furthermore, the sampling of aphids was probably carried out too late. According to Dr. Krüssel (office for crop protection of the Lower Saxon Chamber of Agriculture, pers. comment 17th January 2017), the peak of aphid appearance had been at the end of May / beginning of June 2016 and aphid densities had reached up to 30 individuals per tiller. With the beginning of wheat flowering, the activity of natural enemies had led to a breakdown of aphid populations below the damage threshold. I surveyed aphids for the first time during wheat flowering, therefore I missed the peak of aphid infestation.

Apart from that, I suggest to carry out sweepnetting of natural enemies simultaneously or slightly before the survey of pest insects. This allows drawing direct conclusions about the effect of natural enemies on pest densities. In our field work period, limited time and labour resources did not allow for simultaneous surveys and I did the sweepnetting after the survey of crop pests.

Finally, I had to deal with some constraints regarding the aphid predation experiment. In a first trial experiment, where aphid cards were exposed for 24 h, the majority of cards did not show any signs of predation. Therefore I extended the exposure time to one week. After this time, predation rates were in general high enough so differences between treatments could be analysed statistically. However, aphid cards were exposed to wind and rain for one week, and I cannot exclude that some aphids might have been removed mechanically.

6 Conclusion and Outlook

Flower strips might be suitable to support populations of pollinators and melliphagous predators (Haaland, Naisbit & Bersier 2011; Ramsden *et al.* 2015), but my study could not show better biocontrol resulting from flower strips than from other management types. In contrary, especially regarding aphid infestation, flower strips provided a disservice, as aphid densities were higher and predator-prey ratios and predation rates were lower in flower strip fields compared to organic or conventional fields. The only survey, in which flower strips performed best, was aphid parasitism. In the edge transects, most aphids were parasitized close to flower strip fields compared to organic or conventional fields. However, this did not result in lower aphid densities. Therefore, I suggest schemes to be designed more carefully, considering the individual needs of the species that shall be promoted. From my observation in the fields and farmer interviews, I derived the following recommendations for the design of future flower strips:

- 1) Sowing times of seed mixtures should be more flexible. Under the current scheme, flower strips have to be sown until the 15th of April of each year (ML 2016). However, many farmers told me that this was often not feasible, as weather conditions were still too wet or there was frost after the sowing date, which destroyed the young seedlings. This posed a dilemma to the farmers: either they complied with the formalities, risking the establishment of flower strips to fail, or they sowed the seed mixtures later, risking losing the subsidies.
- 2) More attention should be directed towards diversified flowering times. According to the regulations for annual flower strips, seed mixtures shall be suited to provide insects with floral resources over the whole period between June and October (ML 2017). However, I observed some flower strips not to come into bloom until the end of June and often strips were dominated by one or two flowering species that might not have been able to be used by all natural enemies. Floral resources adjacent to crop fields might be most beneficial to insects at times when farmers do not apply insecticides, since sprayed pesticides may drift into the flower strips. Therefore, there should also be flowers before crop blooming and after harvest.
- 3) Perennial flower strips should be preferred to annual flower strips. The current AES scheme for perennial flower strips in Lower Saxony is relatively demanding, while not compensating farmers adequately. This makes perennial flower strips less attractive to farmers with the result that most farmers chose the scheme for annual flower strips. However, several studies have found schemes that include perennial vegetation to be more efficient in natural pest control (e. g. Thies & Tschardtke 1999).

- 4) Native plant species should be given preference over exotic and crop species in seed mixtures. Of the 28 species that are included in the list for potential seed mixtures, only five species are native to Germany according to BfN 2016 (Table S 2, Appendix). The other 23 species are either archaeophytic crop species or neophytes. Several authors have noted that to selectively enhance natural enemies, their special needs should be considered, rather than encouraging plant diversity per se (Van Emden 1990; Isaacs *et al.* 2009). For example, not all flowers are suited for all hymenopteran parasitoids. There are significant differences in the accessibility of nectaries as a result of floral architecture (Landis, Wratten & Gurr 2000). Therefore, flower species have to be chosen carefully and requirements of natural enemies have to be taken into account. As many insects are especially adapted to some plant species, the use of native plants might be suited best to support local natural enemy populations (Wäckers & van Rijn 2012).

This study demonstrates that the two currently most popular AES in Lower Saxony, that represent either a land sharing (organic farming) or a land sparing (flower strips) strategy, are both not yet optimized in their performance regarding natural pest control. Whether they provided services or disservices to farmers depended very much on the type of crop pest. Regarding control of CLB, organic farming was most effective, whereas flower strips increased parasitism of aphids. From my results I can therefore not draw a general conclusion on whether the implementation of flower strips in the current form or organic farming is a better strategy for enhancing biocontrol. Appropriate modifications could improve the performance of flower strips. But due to edge effects, their scope will be always limited. Alternatively, flower strips could be installed in the middle of large fields, in order to increase the proportion of field edges within fields (Blaauw & Isaacs 2014). Having said this, the general division of AES into either land sharing or land sparing seems very strict and the optimal solution lies probably somewhere in between. I appeal that farmers should be allowed to apply schemes more flexible in order to respond to local differences and unpredictable natural events. This could also include a combination of organic farming and locally applied AES, such as flower strips. More research is needed in order to design schemes so they meet the objectives they are targeted for. Therefore, regular monitoring and evaluation of the success of AES are crucial (Donald & Evans 2006; Batáry *et al.* 2015).

7 Acknowledgements

I would like to express gratitude to my first supervisor Prof. Dr. Alexandra Klein for her confidence and for allowing me to prepare this thesis externally at Göttingen University. Likewise I am thankful to Prof. Dr. Teja Tscharntke for hosting me in his wonderful working group Agroecology in Göttingen and PD Dr. Péter Batáry for giving me the opportunity to participate in this exciting project. I learned so much during the last year, not only about scientific work, but also about agricultural practice and the handling of more than 20 project partners (the farmers), that all have their own ideas and timetables. Without their cooperation, this project could not have been realized. I want to thank them for answering my plentiful questions, that might be obvious for experienced practitioners, but not for novices in this broad field of agriculture.

I am deeply grateful for the good spirit and mutual support of the field work team. In their company, the long hours of field survey under the hot German sun did almost not feel like work. I owe special thanks to Carolina Steffen and Jacob Rosenthal for lifting the mood; even after 12 hours of work and unpredictable changes of plans. Furthermore, I want to thank the whole Agroecology group for adopting me so quickly and making me feel welcome in this new environment. Coming here every day felt more like seeing friends than working colleagues. Thank you for your support and new ideas in situations when I was stuck. Last but not least I am much obliged to Tom Oesterreich and Siegfried Opolka from the IT-team of our department for solving any software struggles, to Gyula Szabó (Hortobágy National Park, Hungary) for determining hundreds of bugs and to the DFG for funding this whole project.



Thank you very much!

References

- AES Lower Saxony. (2012) *Programm Zur Förderung Im Ländlichen Raum Niedersachsen Und Bremen 2007 Bis 2013, Zwischenbericht 2011 [Program to Promote Rural Development in Lower Saxony and Bremen 2007 to 2013, Interim Report 2011]*. Niedersächsisches Ministerium für Ernährung, Landwirtschaft, Verbraucherschutz und Landesentwicklung, Hannover.
- AES Lower Saxony. (2016) Richtlinie über die Gewährung von Zuwendungen für Niedersächsische und Bremer Agrarumweltmaßnahmen [Directive on subsidy granting of agri-environmental measures in Lower Saxony and Bremen], http://www.ml.niedersachsen.de/download/85298/Richtlinie_AUM_2016.pdf
- Alignier, A., Raymond, L., Deconchat, M., Menozzi, P., Monteil, C., Sarthou, J.P., Vialatte, A. & Ouin, A. (2014) The effect of semi-natural habitats on aphids and their natural enemies across spatial and temporal scales. *Biological Control*, 77, 76–82.
- Awmack, C.S. & Leather, S.R. (2002) Host Plant Quality and Fecundity in Herbivorous Insects. *Annual Review of Entomology*, 47, 817–844.
- Balmford, A., Green, R. & Phalan, B. (2012) What conservationists need to know about farming. *Proceedings of the Royal Society B: Biological Sciences*, 279, 2714–2724.
- Batáry, P., Dicks, L. V., Kleijn, D. & Sutherland, W.J. (2015) The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, 29, 1006–1016.
- Batáry, P., Holzschuh, A., Orci, K.M., Samu, F. & Tscharntke, T. (2012) Responses of plant, insect and spider biodiversity to local and landscape scale management intensity in cereal crops and grasslands. *Agriculture, Ecosystems and Environment*, 146, 130–136.
- Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, 18, 182–188.
- Bertrand, C., Baudry, J. & Burel, F. (2016) Seasonal variation in the effect of landscape structure on ground-dwelling arthropods and biological control potential. *Basic and Applied Ecology*, 17, 678–687.
- BfN - Bundesamt für Naturschutz. (2016) FloraWeb, <http://www.floraweb.de>
- Bianchi, F.J.J.A., Booij, C.J.H. & Tscharntke, T. (2006) Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B: Biological Sciences*, 273, 1715–1727.

- Bianchi, F.J.J.A., Goedhart, P.W. & Baveco, J.M. (2008) Enhanced pest control in cabbage crops near forest in the Netherlands. *Landscape Ecology*, 23, 595–602.
- Bianchi, F.J.J.A. & Wäckers, F.L. (2008) Effects of flower attractiveness and nectar availability in field margins on biological control by parasitoids. *Biological Control*, 46, 400–408.
- Bianchi, F.J.J.A. & van der Werf, W. (2003) The effect of the area and configuration of hibernation sites on the control of aphids by *Coccinella septempunctata* (Coleoptera: Coccinellidae) in agricultural landscapes: A simulation study. *Environmental Entomology*, 32, 1290–1304.
- Blaauw, B.R. & Isaacs, R. (2014) Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *Journal of Applied Ecology*, 51, 890–898.
- Borror, D.J. & White, R.E. (1970) *Peterson Field Guides - Insects*. Houghton-Mifflin Company, New York.
- Buntin, G.D., Flanders, K.L., Slaughter, R.W., Zandra, D., Buntin, G.D., Flanders, K.L. & Slaughter, R.W. (2004) Damage loss assessment and control of the cereal leaf beetle (Coleoptera: Chrysomelidae) in winter wheat. *Journal of Economic Entomology*, 97, 374–382.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., A.Wardle, D., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012) Biodiversity loss and its impact on humanity. *Nature*, 489, 326–326.
- Case, T.J. & Gilpin, M.E. (1974) Interference competition and niche theory. *Proceedings of the National Academy of Sciences*, 71, 3073–3077.
- Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J. & Kremen, C. (2011) A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters*, 14, 922–932.
- Chinery, M. (1984) *Insekten Mitteleuropas*, 3rd ed. Paul Parey, Hamburg and Berlin.
- Chinery, M. (1987) *Pareys Buch Der Insekten*, 2nd ed. Paul Parey, Hamburg and Berlin.
- Collins, K.L., Boatman, N.D., Wilcox, A., Holland, J.M. & Chaney, K. (2002) Influence of beetle banks on cereal aphid predation in winter wheat. *Agriculture, Ecosystems and Environment*, 93, 337–350.
- Cooter, J. (1991) *A Coleopterist's Handbook*. The Amateur Entomologist's Society, Middlesex.
- Council of the European Union. (2007) Verordnung (EG) Nr. 834/2007 des Rates vom 28. Juni 2007 über die ökologische/biologische Produktion und die Kennzeichnung von ökologischen/biologischen Erzeugnissen und zur Aufhebung der Verordnung (EWG) Nr. 2092/91
- Crowder, D.W., Northfield, T.D., Strand, M.R. & Snyder, W.E. (2010) Organic agriculture promotes evenness and natural pest control. *Nature*, 466, 109–112.
- Directory of Certified Organic Operators. (2016) BioC, <https://www.bioc.info>.

- Dixon, A.F.G. (1977) Aphid ecology: life cycles, polymorphism, and population regulation. *Annual Review of Ecology, Evolution, and Systematics*, 8, 329–353.
- Donald, P.F. & Evans, A.D. (2006) Habitat connectivity and matrix restoration: The wider implications of agri-environment schemes. *Journal of Applied Ecology*, 43, 209–218.
- Duffield, S.J., Bryson, R.J., Young, J.E.B., Sylvester-Bradley, R. & Scott, R.K. (1997) The influence of nitrogen fertiliser on the population development of the cereal aphids *Sitobion avenae* (F.) and *Metopolophium dirhodum* (Wik.) on field grown winter wheat. *Annals of Applied Biology*, 130, 13–26.
- Dunning, J.B., Danielson, B.J. & Pulliam, H.R. (2016) Ecological processes that affect populations in complex landscapes. *Oikos*, 65, 169–175.
- Dyer, L.E. & Landis, D.A. (1996) Effects of habitat, temperature, and sugar availability on longevity of *Eriborus terebrans* (Hymenoptera: Ichneumonidae). *Environmental Entomology*, 25, 1192–1201.
- Ekroos, J., Olsson, O., Rundlöf, M., Wätzold, F. & Smith, H.G. (2014) Optimizing agri-environment schemes for biodiversity, ecosystem services or both? *Biological Conservation*, 172, 65–71.
- Van Emden, H.F. (1990) Plant diversity and natural enemy efficiency in agroecosystems. *Critical Issues in Biological Control* (eds M. Mackauer, L. Ehler, & J. Roland), pp. 63–80. Intercept Ltd, Andover.
- ESRI. (2016) *ArcGIS for Desktop*. Environmental Systems Research Institute Inc., Redlands, CA, USA.
- European Environment Agency. (2002) *Environmental Signals 2002, Benchmarking the Millennium*. Office for Official Publications of the European Communities, Copenhagen.
- Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. & Martin, J.L. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, 14, 101–112.
- Fischer, J., Abson, D.J., Butsic, V., Chappell, M.J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H.G. & von Wehrden, H. (2014) Land sparing versus land sharing: Moving forward. *Conservation Letters*, 7, 149–157.
- Fischer, J., Batáry, P., Bawa, K.S., Brussaard, L., Chappell, M.J., Clough, Y., Daily, G.C., Dorrrough, J., Hartel, T., Jackson, L.E., Klein, A.M., Kremen, C. & Von Wehrden, H. (2011) Conservation : limits of land sparing. *Science*, 334, 593.
- Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., Mueller, N.D., O'Connell, C., Ray, D.K., West, P.C., Balzer, C., Bennett, E.M., Carpenter, S.R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., Tilman, D., Zaks, D.P.M. & O'Connell, C. (2011) Solutions for a cultivated planet. *Nature*, 478, 337–342.

- Fox, J. & Weisberg, S. (2011) *An R Companion to Applied Regression*. Sage Publications, Thousand Oaks (CA).
- Fuller, R.J., Norton, L.R., Feber, R.E., Johnson, P.J., Chamberlain, D.E., Joys, a C., Mathews, F., Stuart, R.C., Townsend, M.C., Manley, W.J., Wolfe, M.S., Macdonald, D.W. & Firbank, L.G. (2005) Benefits of organic farming to biodiversity vary among taxa. *Biology Letters*, 1, 431–434.
- Gabriel, D., Roschewitz, I., Tschardtke, T. & Thies, C. (2006) Beta diversity at different spatial scales: Plant communities in organic and conventional agriculture. *Ecological Applications*, 16, 2011–2021.
- Gabriel, D., Sait, S.M., Hodgson, J.A., Schmutz, U., Kunin, W.E. & Benton, T.G. (2010) Scale matters: the impact of organic farming on biodiversity at different spatial scales. *Ecology Letters*, 13, 858–869.
- Gabriel, D., Sait, S., Kunin, W. & Benton, T. (2013) Food production vs. biodiversity: Comparing organic and conventional agriculture. *Journal of Applied Ecology*, 50, 355–364.
- Gagic, V., Tschardtke, T., Dormann, C.F., Gruber, B., Wilstermann, A. & Thies, C. (2011) Food web structure and biocontrol in a four-trophic level system across a landscape complexity gradient. *Proceedings of the Royal Society B: Biological Sciences*, 278, 2946–2953.
- Gash, A.F.J. (2012) Wheat nitrogen fertilisation effects on the performance of the cereal aphid *Metopolophium dirhodum*. *Agronomy*, 2, 1–13.
- Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tschardtke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Onate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W. & Inchausti, P. (2010) Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied Ecology*, 11, 97–105.
- George, K.S. (1974) Damage assessment aspects of cereal aphid attack in autumn-and spring-sown cereals. *Annals of Applied Biology*, 77, 67–74.
- Gilabert, A., Simon, J.C., Mieuze, L., Halkett, F., Stoeckel, S., Plantegenest, M. & Dedryver, C.A. (2009) Climate and agricultural context shape reproductive mode variation in an aphid crop pest. *Molecular Ecology*, 18, 3050–3061.
- Giller, P.S., Ryan, B., Kennedy, T. & Connery, J. (1995) Aphid-parasitoid interactions in a winter cereal crop: field trials involving insecticide application. *Journal of Applied Entomology*, 119, 233–239.
- Green, R.E., Cornell, S.J., Scharlemann, J.P.W. & Balmford, A. (2005) Farming and the fate of wild nature. *Science*, 307, 550–555.
- Haaland, C., Naisbit, R.E. & Bersier, L.F. (2011) Sown wildflower strips for insect conservation: A review. *Insect Conservation and Diversity*, 4, 60–80.

- Häni, F.J., Popow, G., Reinhard, H., Schwarz, A. & Voegeli, U. (2008) *Pflanzenschutz Im Nachhaltigen Ackerbau*. Edition-Imz, Zollikofen.
- Al Hassan, D., Burel, F., Plantegenest, M., Kindlmann, P., Butet, A. & Parisey, N. (2012) Relationship between landscape composition and the abundance of aphids and their natural enemies in crop fields. *Journal of Environmental Sciences*, 2, 89–101.
- Al Hassan, D., Georgelin, E., Delattre, T., Burel, F., Plantegenest, M., Kindlmann, P. & Butet, A. (2013) Does the presence of grassy strips and landscape grain affect the spatial distribution of aphids and their carabid predators? *Agricultural and Forest Entomology*, 15, 24–33.
- Hawkins, B.A. & Cornell, H. V. (1994) Maximum parasitism rates and successful biological control. *Science*, 266, 1886–1887.
- Haynes, D.L. & Gage, S.H. (1981) The cereal leaf beetle in North America. *Annual Review of Entomology*, 26, 259–287.
- Heimpel, G.E. & Jervis, M.A. (2005) Does floral nectar improve biological control by parasitoids? *Plant-provided food for carnivorous insects: a protective mutualism and its applications* (eds F.L. Wäckers, P.C. van Rijn, & J. Bruin), pp. 267–304. Cambridge University Press, Cambridge.
- Heitefuss, R., König, K., Obst, A. & Reschke, M. (1993) *Pflanzenkrankheiten Und Schädlinge Im Ackerbau*. Verlagsunion Agrar, Frankfurt am Main.
- Henle, K., Alarbd, D., Clitherowc, J., Cobb, P., Firbank, L., Kull, T., McCracken, D., Moritz, R., Niemeläi, J., Rebane, M., Wascherk, D., Watt, A. & Young, J. (2008) Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe – A review. *Agriculture, Ecosystems and Environment*, 124, 60–71.
- Hodgson, J.A., Kunin, W.E., Thomas, C.D., Benton, T.G. & Gabriel, D. (2010) Comparing organic farming and land sparing: Optimizing yield and butterfly populations at a landscape scale. *Ecology Letters*, 13, 1358–1367.
- Holland, J.M., Bianchi, F.J.J.A., Entling, M.H., Moonen, A.-C., Smith, B.M. & Jeanneret, P. (2016) Structure, function and management of semi-natural habitats for conservation biological control: A review of European studies. *Pest Management Science*, 72, 1638–1651.
- Holland, J.M., Oaten, H., Southway, S. & Moreby, S. (2008) The effectiveness of field margin enhancement for cereal aphid control by different natural enemy guilds. *Biological Control*, 47, 71–76.
- Honěk, A. (1991) Nitrogen fertilization and abundance of the cereal aphids *Metopolophium dirhodum* and *Sitobion avenae* (Homoptera, Aphididae). *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz*, 98, 655–660.

- Ihrig, R.A., Herbert, D.A., Van Duyn, J.W. & Bradley, J.R. (2001) Relationship between cereal leaf beetle (Coleoptera: Chrysomelidae) egg and fourth-instar populations and impact of fourth-instar defoliation of winter wheat yields in North Carolina and Virginia. *Journal of Economic Entomology*, 94, 634–639.
- Isaacs, R., Tuell, J., Fiedler, A., Gardiner, M. & Landis, D. (2009) Maximizing arthropod-mediated ecosystem services in agricultural landscapes: The role of native plants. *Frontiers in Ecology and the Environment*, 7, 196–203.
- Jonsson, M., Bommarco, R., Ekbom, B., Smith, H.G., Bengtsson, J., Caballero-Lopez, B., Winqvist, C. & Olsson, O. (2014) Ecological production functions for biological control services in agricultural landscapes. *Methods in Ecology and Evolution*, 5, 243–252.
- Jossi, W. & Bigler, F. (1996) Getreidehähnchen: Befall und Resistenz bei Winterweizen (Schweiz). *Agrarforschung*, 3, 117–119.
- Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tschardtke, T., Verhulst, J., West, T.M. & Yela, J.L. (2006) Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, 9, 243–254.
- Kleijn, D., Rundlöf, M., Scheper, J., Smith, H.G. & Tschardtke, T. (2011) Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology and Evolution*, 26, 474–481.
- Kleijn, D. & Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, 40, 947–969.
- Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., Klein, A.-M., Kremen, C., M'Gonigle, L.K., Rader, R., Ricketts, T.H., Williams, N.M., Lee Adamson, N., Ascher, J.S., Báldi, A., Batáry, P., Benjamin, F., Biesmeijer, J.C., Blitzer, E.J., Bommarco, R., Brand, M.R., Bretagnolle, V., Button, L., Cariveau, D.P., Chifflet, R., Colville, J.F., Danforth, B.N., Elle, E., Garratt, M.P.D., Herzog, F., Holzschuh, A., Howlett, B.G., Jauker, F., Jha, S., Knop, E., Krewenka, K.M., Le Féon, V., Mandelik, Y., May, E.A., Park, M.G., Pisanty, G., Reemer, M., Riedinger, V., Rollin, O., Rundlöf, M., Sardiñas, H.S., Scheper, J., Sciligo, A.R., Smith, H.G., Steffan-Dewenter, I., Thorp, R., Tschardtke, T., Verhulst, J., Viana, B.F., Vaissière, B.E., Veldtman, R., Westphal, C. & Potts, S.G. (2015) Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications*, 6.
- Krauss, J., Gallenberger, I. & Steffan-Dewenter, I. (2011) Decreased functional diversity and biological pest control in conventional compared to organic crop fields. *PLoS ONE*, 6, 1–9.
- Kromp, B. (1989) Carabid beetle communities (Carabidae, Coleoptera) in biologically and conventionally farmed agroecosystems. *Agriculture, Ecosystems and Environment*, 27, 241–251.

- Landis, D.A., Gardiner, M.M., van der Werf, W. & Swinton, S.M. (2008) Increasing corn for biofuel production reduces biocontrol services in agricultural landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 20552–20557.
- Landis, D.A. & Haas, M.J. (1992) Influence of landscape structure on abundance and within-field distribution of European corn borer (Lepidoptera: Pyralidae) larval parasitoids in Michigan. *Environmental Entomology*, 21, 409–416.
- Landis, D.A., Wratten, S.D. & Gurr, G.M. (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, 45, 175–201.
- Lee, J.C. & Heimpel, G.E. (2008) Floral resources impact longevity and oviposition rate of a parasitoid in the field. *Journal of Animal Ecology*, 77, 565–572.
- Leitao, A.B., Miller, J., Ahern, J. & McGarigal, K. (2006) *Measuring Landscapes: A Planner*. Island Press, Washington.
- Meindl, P., Kromp, B., Bartl, B. & Ioannidou, E. (2001) Arthropod natural enemies of the cereal leaf beetle (*Oulema melanopus* L.) in organic winter wheat fields in Vienna, Eastern Austria. *IOBC WPRS Bulletin*, 24, 79–86.
- Nentwig, W., Poehling, H.M. & Schärer, P. (1994) *Analyse Dichtebeeinflussender Faktoren Beim Getreidehaehnenchen (Oulema Sp., Chrysomelidae, Coleoptera)*. Haupt, Bern.
- Niedersächsisches Ministerium für Ernährung Landwirtschaft und Verbraucherschutz (ML). (2016) Übersicht Agrarumweltmaßnahmen [Overview of agri-environment schemes in Lower Saxony], http://www.ml.niedersachsen.de/themen/landwirtschaft/agraarfoerderung/agraarumweltmassnahmen_aum/aum_alle_massnahmen_auf_einen_blick/aum---alle-manahmen-auf-einen-blick-121592.html
- Niedersächsisches Ministerium für Ernährung Landwirtschaft und Verbraucherschutz (ML). (2017) Merkblatt zu den Besonderen Förderbestimmungen. BS 1 - Anlage von einjährigen Blühstreifen auf Ackerland. BS 11 - Grundförderung, http://www.ml.niedersachsen.de/themen/landwirtschaft/agraarfoerderung/agraarumweltmassnahmen_aum/aum_details_zu_den_massnahmen/bs1_einjaehrige_bluehstreifen_bs11_bs12/bs-1---anlage-von-einjaehrigen-bluehstreifen-auf-ackerland-122369.html
- Olfert, O. & Weiss, R.M. (2006) Impact of climate change on potential distributions and relative abundances of *Oulema melanopus*, *Meligethes viridescens* and *Ceutorhynchus obstrictus* in Canada.
- Östman, Ö., Ekbom, B. & Bengtsson, J. (2001) Landscape heterogeneity and farming practice influence biological control. *Basic and Applied Ecology*, 2, 365–371.

- Östman, Ö., Ekbom, B. & Bengtsson, J. (2003) Yield increase attributable to aphid predation by ground-living polyphagous natural enemies in spring barley in Sweden. *Ecological Economics*, 45, 149–158.
- Papadimitriou, F. (2002) Modelling indicators and indices of landscape complexity: an approach using G.I.S. *Ecological Indicators*, 2, 17–25.
- Phalan, B., Onial, M., Balmford, A. & Green, R.E. (2011) Reconciling Food Production and Biodiversity Conservation: Land Sharing and Land Sparing Compared. *Science*, 333, 1289–1291.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2016) Linear and Nonlinear Mixed Effects Models. R package version 3.1-128, <http://cran.r-project.org/package=nlme>
- Plecas, M., Gagic, V., Jankovic, M., Petrovic-Obradovic, O., Kavallieratos, N.G., Tomanovic, Z., Thies, C., Tschardtke, T. & Cetkovic, A. (2014) Landscape composition and configuration influence cereal aphid-parasitoid-hyperparasitoid interactions and biological control differentially across years. *Agriculture, Ecosystems and Environment*, 183, 1–10.
- Power, A.G. (2010) Ecosystem services and agriculture: tradeoffs and synergies. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 365, 2959–2971.
- Price, P.W. (1991) The plant vigor hypothesis and herbivore attack. *Oikos*, 62, 244–251.
- Puech, C., Baudry, J., Joannon, A., Poggi, S. & Aviron, S. (2014) Organic vs. conventional farming dichotomy: Does it make sense for natural enemies? *Agriculture, Ecosystems and Environment*, 194, 48–57.
- QGIS Development Team. (2009) QGIS Geographic Information System. Open Source Geospatial Foundation, <http://www.qgis.org>
- Quinn, J.E., Brandle, J.R. & Johnson, R.J. (2012) The effects of land sparing and wildlife-friendly practices on grassland bird abundance within organic farmlands. *Agriculture, Ecosystems and Environment*, 161, 10–16.
- R Core Team. (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, <https://www.r-project.org>
- Rader, R., Birkhofer, K., Schmucki, R., Smith, H.G., Stjernman, M. & Lindborg, R. (2014) Organic farming and heterogeneous landscapes positively affect different measures of plant diversity. *Journal of Applied Ecology*, 51, 1544–1553.
- Ramsden, M.W., Menéndez, R., Leather, S.R. & Wäckers, F. (2015) Optimizing field margins for biocontrol services: The relative role of aphid abundance, annual floral resources, and overwinter habitat in enhancing aphid natural enemies. *Agriculture, Ecosystems & Environment*, 199, 94–104.
- Robinson, R.A. & Sutherland, W.J. (2002) Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*, 39, 157–176.

- Roschewitz, I., Hücker, M., Tschardtke, T. & Thies, C. (2005) The influence of landscape context and farming practices on parasitism of cereal aphids. *Agriculture, Ecosystems and Environment*, 108, 218–227.
- Schmidt, M.H., Lauer, A., Purtauf, T., Thies, C., Schaefer, M. & Tschardtke, T. (2003) Relative importance of predators and parasitoids for cereal aphid control. *Proceedings of the Royal Society of London B: Biological Sciences*, 270, 1905–1909.
- Schmitt, M. (1988) The Cricocerinae: biology, phenology and evolution. *Biology of Chrysomelidae* (eds P. Jolivet, E. Petitpierre, & T.H. Hsiao), pp. 475–495. Kluwer, Dordrecht, The Netherlands.
- Schneider, M.K., Lüscher, G., Jeanneret, P., Arndorfer, M., Ammari, Y., Bailey, D., Balázs, K., Báldi, A., Choisis, J.-P., Dennis, P., Eiter, S., Fjellstad, W., Fraser, M.D., Frank, T., Friedel, J.K., Garchi, S., Geijzendorffer, I.R., Gomiero, T., Gonzalez-Bornay, G., Hector, A., Jerkovich, G., Jongman, R.H.G., Kakudidi, E., Kainz, M., Kovács-Hostyánszki, A., Moreno, G., Nkwiine, C., Opio, J., Oschatz, M.-L., Paoletti, M.G., Pointereau, P., Pulido, F.J., Sarthou, J., Siebrecht, N., Sommaggio, D., Turnbull, L. a, Wolfrum, S. & Herzog, F. (2014) Gains to species diversity in organically farmed fields are not propagated at the farm level. *Nature communications*, 5, 4151.
- Statistisches Bundesamt. (2015) *Land- Und Forstwirtschaft, Fischerei - Bodenflächennutzung Nach Art Der Tatsächlichen Nutzung [Agriculture, Forestry and Fisheries - Land Use on the Type of Actual Utilisation]*. DeStatis, Wiesbaden.
- Sunderland, K. & Samu, F. (2000) Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: a review. *Entomologia Experimentalis et Applicata*, 95, 1–13.
- Sutherland, J.P., Sullivan, M.S. & Poppy, G.M. (2001) Distribution and abundance of aphidophagous hoverflies (Diptera: Syrphidae) in wildflower patches and field margin habitats. *Agricultural and Forest Entomology*, 3, 57–64.
- Thies, C., Haenke, S., Scherber, C., Bengtsson, J., Bommarco, R., Clement, L.W., Ceryngier, P., Dennis, C., Emmerson, M., Gagic, V., Hawro, V., Liira, J., Weisser, W.W., Winqvist, C. & Tschardtke, T. (2011) The relationship between agricultural intensification and biological control: experimental tests across Europe. *Ecological Applications*, 21, 2187–2196.
- Thies, C., Roschewitz, I. & Tschardtke, T. (2005) The landscape context of cereal aphid-parasitoid interactions. *Proceedings of the Royal Society B: Biological Sciences*, 272, 203–210.
- Thies, C. & Tschardtke, T. (1999) Landscape Structure and Biological Control in Agroecosystems. *Science*, 285, 893–895.
- Thompson, S.N. (1999) Nutrition and culture of entomophagous insects. *Annual Review of Entomology*, 44, 561–592.

- Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.M., Nouhuys, S. van & Vidal, S. (2007) Conservation biological control and enemy diversity on a landscape scale. *Biological Control*, 43, 294–309.
- Tscharntke, T., Karp, D.S., Chaplin-Kramer, R., Batáry, P., DeClerck, F., Gratton, C., Hunt, L., Ives, A., Jonsson, M., Larsen, A., Martin, E.A., Martínez-Salinas, A., Meehan, T.D., O'Rourke, M., Poveda, K., Rosenheim, J.A., Rusch, A., Schellhorn, N., Wanger, T.C., Wratten, S. & Zhang, W. (2016) When natural habitat fails to enhance biological pest control - Five hypotheses. *Biological Conservation*, 204, 449–458.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters*, 8, 857–874.
- Tscharntke, T., Rand, T.A. & Bianchi, F.J.J.A. (2005) The landscape context of trophic interactions: insect spillover across the crop-noncrop interface. *Annales Zoologici Fennici*, 42, 421–432.
- Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H. & Westphal, C. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, 87, 661–685.
- Tschumi, M., Albrecht, M., Bärtschi, C., Collatz, J., Entling, M.H. & Jacot, K. (2016) Perennial, species-rich wildflower strips enhance pest control and crop yield. *Agriculture, Ecosystems & Environment*, 220, 97–103.
- Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*. Springer, New York.
- Vollhardt, I.M.G., Tscharntke, T., Wäckers, F.L., Bianchi, F.J.J.A. & Thies, C. (2008) Diversity of cereal aphid parasitoids in simple and complex landscapes. *Agriculture, Ecosystems and Environment*, 126, 289–292.
- Wachmann, E., Melber, A. & Deckert, J. (2008) *Wanzen - Die Tierwelt Deutschlands*. Goecke & Evers, Keltern.
- Wäckers, F.L. & van Rijn, P.C.J. (2012) Pick and Mix: Selecting Flowering Plants to Meet the Requirements of Target Biological Control Insects. *Biodiversity and Insect Pests: Key Issues for Sustainable Management* (eds G.M. Gurr, S.D. Wratten, W.E. Snyder, & D.M.Y. Read), pp. 139–165. John Wiley & Sons, Chichester.
- Weber, U. (1992) *Freilandbeobachtung Und Laboruntersuchungen Zur Parasitierung von Eiern Und Larven Der Getreidehähnchen Oulema Lichenis (Voet) Und O. Melanopus (L.) Sowie Der Kokons von O. Lichenis*. Master's Thesis. Göttingen University.

- Winder, L., Alexander, C.J., Woolley, C., Perry, J.N. & Holland, J.M. (2013) The spatial distribution of canopy-resident and ground-resident cereal aphids (*Sitobion avenae* and *Metopolophium dirhodum*) in winter wheat. *Arthropod-Plant Interactions*, 7, 21–32.
- Wissinger, S. a. (1997) Cyclic colonization in predictably ephemeral habitats: A template for biological control in annual crop systems. *Biological Control*, 10, 4–15.
- Zahradnik, J. (1985) *Käfer Mittel- Und Nordwesteuropas*. Paul Parey, Berlin.
- Zhang, W., Ricketts, T.H., Kremen, C., Carney, K. & Swinton, S.M. (2007) Ecosystem services and dis-services to agriculture. *Ecological Economics*, 64, 253–260.
- Zhao, Z.-H., Hui, C., He, D.-H. & Ge, F. (2013) Effects of position within wheat field and adjacent habitats on the density and diversity of cereal aphids and their natural enemies. *BioControl*, 58, 765–776.
- Zhao, Z.-H., Hui, C., He, D.-H. & Li, B.-L. (2015) Effects of agricultural intensification on ability of natural enemies to control aphids. *Scientific Reports*, 5, 1–7.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer Science + Business Media LLC, New York.

Statement of Authentication

I herewith declare that I have written the present thesis on my own and that I have not used any other sources and materials than those indicated. I properly cited the materials I have relied upon. I have not submitted this document as a master's thesis elsewhere. The electronic version of this thesis is identical in content and layout to the printed versions.

[REDACTED]

[REDACTED]

Appendix

Table S 1: Heteroptera species caught via sweepnetting. Species classified as natural enemies (according to Wachmann, Melber & Deckert 2008) highlighted in red.

Species	Author (year)	Family	Carnivorous/ omnivorous	No. of individuals
<i>Aelia acuminata</i>	Linnaeus (1758)	Pentatomidae	no	1
<i>Amblytlyus nasutus</i>	Kirschbaum (1856)	Miridae	no	11
<i>Capsus ater</i>	Linnaeus (1758)	Miridae	no	3
<i>Closterotomus norwegicus</i>	Gmelin (1790)	Miridae	no	100
<i>Dolycoris baccarum</i>	Linnaeus (1758)	Pentatomidae	no	2
<i>Eurydema oleracea</i>	Linnaeus (1758)	Pentatomidae	no	1
<i>Eurydema</i> sp.		Pentatomidae	no	2
<i>Leptopterna dolobrata</i>	Linnaeus (1758)	Miridae	no	61
<i>Lygus gemellatus</i>	Herrich-Schäffer (1835)	Miridae	no	75
<i>Lygus pratensis</i>	Linnaeus (1758)	Miridae	no	3
<i>Lygus rugulipennis</i>	Poppius (1911)	Miridae	no	21
<i>Megaloceroea recticornis</i>	Geoffroy (1785)	Miridae	no	70
<i>Mirini</i> sp.		Miridae	no	78
<i>Nabis pseudoferus</i>	Remane (1949)	Nabidae	yes	7
<i>Nabis</i> sp.		Nabidae	yes	10
<i>Notostira elongata</i>	Geoffroy (1785)	Miridae	no	49
<i>Oncotylus punctipes</i>	Reuter (1875)	Miridae	no	23
<i>Pentatomidae</i> sp.	Leach (1815)	Pentatomidae	no	6
<i>Polymerus nigrita</i>		Miridae	no	41
<i>Polymerus unifasciatus</i>	Fabricius (1794)	Miridae	no	6
<i>Psallus falleni</i>	Fallén (1807)	Miridae	no	1
<i>Stenodema calcarata</i>	Fallén (1807)	Miridae	no	6
<i>Stenodema laevigata</i>	Linnaeus (1758)	Miridae	no	2
<i>Stenodemini</i> sp.		Miridae	no	47
<i>Stenotus binotatus</i>	Fabricius (1794)	Miridae	no	54
<i>Tingidae</i> sp.		Tingidae	no	1
sum individuals				681

Table S 2: Plant species for seed mixtures of annual flower strips in Lower Saxony (ML 2017). Species indigenous to Germany (according to BfN 2016) highlighted in green.

No.	Plant species	German trivial name	native
1	<i>Anethum graveolens</i>	Dill	no
2	<i>Avena sativa</i>	Hafer	no
3	<i>Borago officinalis</i>	Borretsch	no
4	<i>Brassica napus</i>	Raps, Futterraps	no
5	<i>Brassica oleracea</i>	Markstammkohl, Gemüsekohl	yes
6	<i>Brassica rapa</i>	Rübsen	yes
7	<i>Calendula officinalis</i>	Garten-Ringelblume	no
8	<i>Coriandrum sativum</i>	Echter Koriander	no
9	<i>Fagopyrum esculentum</i>	Buchweizen	no
10	<i>Helianthus annuus</i>	Sonnenblume	no
11	<i>Linum usitatissimum</i>	Saat-Lein	no
12	<i>Lupinus angustifolius</i>	Schmalblättrige Lupine	no
13	<i>Malva sylvestris</i> ssp. <i>Mauritiana</i> ssp. <i>Verticillata</i>	Mauretanische Malve, Bechermalve	yes
14	<i>Medicago sativa</i>	Luzerne	no
15	<i>Ornithopus sativus</i>	Serradella	no
16	<i>Phacelia tenacetifolia</i>	Rainfarn-Phazelle	no
17	<i>Pisum sativum</i>	Garten-Erbse	no
18	<i>Raphanus sativus</i> ssp. <i>Oleiformis</i>	Ölrettich	no
19	<i>Secale multicaule</i>	Ur-Roggen/ Waldstaudenroggen	no
20	<i>Setaria italica</i>	Kolbenhirse	no
21	<i>Sinapis alba</i>	Weißer Senf	no
22	<i>Trifolium alexandrinum</i>	Alexandrinischer Klee	no
23	<i>Trifolium resupinatum</i>	Persischer Klee	no
24	<i>Trigonella foenum-graecum</i>	Bockshornklee	no
25	<i>Vicia faba</i>	Acker-Bohne	no
26	<i>Melilotus officinalis</i>	Echter/ Gelber Steinklee	yes
27	<i>Melilotus albus</i>	Weißer Steinklee	yes
28	<i>Vicia sativa</i>	Sommerwicke	no