THE ROLE OF SOWN WILDFLOWER STRIPS FOR BIOLOGICAL CONTROL IN AGROECOSYSTEMS

Dissertation
zur Erlangung des Doktorgrades
der Fakultät für Agrarwissenschaften
der Georg-August-Universität Göttingen

vorgelegt von
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geboren in Saarbrücken

Göttingen, April 2010

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Tag der mündlichen Prüfung: 20.Mai 2010

CONTENTS

CHAPTER

1

INTRODUCTION:

THE ROLE OF SOWN WILDFLOWER STRIPS FOR BIOLOGICAL CONTROL IN AGROECOSYSTEMS

INTRODUCTION

Modern agriculture faces the challenge to supply the demands of the fast-growing world population for agricultural products on a limited area, thereby being economically efficient and ensuring human safety as well as the protection of the environment (Isaacs et al., 2009). This encompasses conflicts of different farming practices, e.g. the intensity of chemical applications and the integration of management practices. After times of inconsiderate exploitation of resources, leading to depleted landscapes shaped by monocultures and often only remnants of (semi-) natural habitat fragments (Krebs et al., 1999; Tillmann et al., 2002), the awareness of the need for a sustainable use strongly rose in the last decades. This change emerged as a huge amount of studies showed that landscapes lacking in a diversified matrix, are associated with a decline of biodiversity and related ecosystem functions such as pollination and biological control (Landis et al., 2000; Nentwig, 2003; Östman et al., 2003; Bianchi et al., 2006; Losey & Vaughan, 2006; Tscharntke et al., 2007; Isaacs et al., 2009; Gardiner et al., 2009; Musters et al., 2009; Zalucki et al., 2009), on which agricultural production strongly depends. Thus, EU agricultural policy – urged to establish directives considering all these concerns – developed so called agri-environment schemes, which provide incentives for farmers to operate in an environmentally sensitive way (Pfiffner & Luka, 2000; Duelli & Obrist, 2003; Kleijn et al., 2006) and to increase the abundance of non-crop habitats and biodiversity in agricultural landscapes (Kleijn & Sutherland, 2003; Herzog, 2005; Whittingham, 2007; Fiedler et al., 2008). The farmers, who are directly affected by such policy decisions, are interested in these options to e.g. reduce cost-intensive and environmentally unfriendly applications of chemicals against severe pest damage, especially as conservation biological control can decrease agricultural pests below an economic threshold level through the enhancement of natural pest enemies (Duelli & Obrist, 2003; Östman *et al*., 2003; Bianchi *et al*., 2006; Griffiths *et al.*, 2008). This is expressed by the growing number of contracts of and the increasing area under agri-environment schemes (BMELV, 2010; ML Niedersachsen, 2007, 2010a,b).

Nevertheless, successful biological control relies on sufficient numbers of natural enemies, which means, that natural enemy abundance determines the strength of the top-down control of pest populations (Halaj & Wise, 2001; Costamagna & Landis, 2007; Holland *et al*., 2008, 2009; Gardiner *el al*., 2009) and supporting natural enemy populations may contribute to an environmentally viable agriculture. Providing appropriate habitats and structures through the manipulation of habitats adjacent to crop fields, e.g. by measures of agri-environment schemes, improves conditions for natural enemies, and thus resulting in enhanced pest control through their spillover into agricultural fields (Wyss, 1996; Landis *et al.*, 2000; Eilenberg *et al.*, 2001; Meek *et al.*, 2002; Pfiffner & Wyss, 2004; Ma *et al.*, 2007; Fiedler *et al.*, 2008; Griffiths *et al.*, 2008; Gardiner *et al.*, 2009). It is crucial to know which group or species of natural enemies contributes most to the control of certain pest organisms, as it will determine the measures to be applied (Hawkins *et al.*, 1999; Lang, 2003; Schmidt *et al.*, 2003, 2004; Tenhumberg & Poehling, 1995). Several studies proved that the landscapes, in which such measures are employed, are perceived by the target species at different spatial scales (Thies *et al.*, 2003; Cronin & Reeve, 2005; Roschewitz *et al.*, 2005; Haenke *et al.*, 2009; Zaller *et al.*, 2009), and therefore achieve varying success. Hence, the surrounding landscape composition shaped by the variety of different (semi-) natural habitats is also decisive for successful biological control, based on the trophic rank, requirements and dispersal abilities of the natural enemy species.

Natural enemies of agricultural pests commute between crop and non-crop habitats providing resources at different times (Bianchi *et al.*, 2006; Tscharntke *et al.*, 2005, 2007). Ephemeral crop fields constitute suitable habitats only for a short period, and natural enemies need alternatives for shelter, overwintering and also for additional food and host/prey resources in non-crop habitats. As a variety of natural enemies of agricultural pests relies on floral resources such as nectar and pollen (Duelli & Obrist, 2003; Landis *et al.*, 2005; Kleijn & van Langenvelde, 2006; Fiedler *et al.*, 2008), sown flower habitats, a measure of agri-environment schemes (ML Niedersachsen, 2009, NAU A6), are considered to meet the needs of many natural enemies. Sown flower habitats represent stable habitats as they are implemented for a period of several years, during which they offer rich floral resources throughout the season, alternative food and host/prey and provide shelter and overwintering sites and can thus contribute to the preservation of natural enemy communities in agroecosystems (Wyss, 1996; Frank, 1999; Nentwig, 2000; Fiedler *et al.*, 2008; Griffiths *et al.*, 2008).

In this thesis, we bring together all these aspects to examine one of the most important issues in conservation biological control: how do landscape structure, natural enemies, and floral resources of sown flower habitats impact biological control. Wheat and rape are important crops in Europe and in much of the world (BMELV, 2010), and the community and impact of natural enemies of cereal aphids and rape pollen beetles, two major herbivore pests, are of great economic importance. Especially as more natural enemies in a refuge such as the sown flower habitats do not necessarily translate into reduced pest densities in the crop field (Bianchi *et al.*, 2006; Jonsson *et al.*, 2008), it is fundamental to know how to apply this management measure to improve biological control in adjacent crop fields (Isaacs *et al*., 2009).

With four studies we contribute to the questions, whether and which natural enemies belongig to different groups (i.e. ground-dwelling and vegetation-dwelling predators, parasitoids), are enhanced by sown flower habitats and are able to successfully suppress pest herbivores through spillover into adjacent crop fields. Thereto we analysed cereal aphids and rape pollen beetles and the trophic interactions with their natural enemies. This was done in differently structured landscapes to discriminate whether the patterns are driven by the local habitat management, by the influence of the surrounding landscape and whether these two scales interact.

Fig. 1: Landscapes in the vicinity of Göttingen. Left: complex landscape with high proportion on non-crop habitats (near Herberhausen). Right: simple landscape with high percentage of arable land (near Seeburg).

Study design & organisms

Study region & sites

All studies were carried out in the region around the city of Göttingen, southern Lower Saxony, Germany. The study area is dominated by intensive arable land use and covers landscapes with varying proportions of (semi-) natural habitats (Thies *et al*., 2005) (Fig. 1). The percentage of arable land is negatively correlated with the perimeter-area ratio (i.e. many field edges) and the diversity of habitat types shaping landscape configuration (Schmidt *et al*., 2004; Roschewitz *et al.*, 2005).

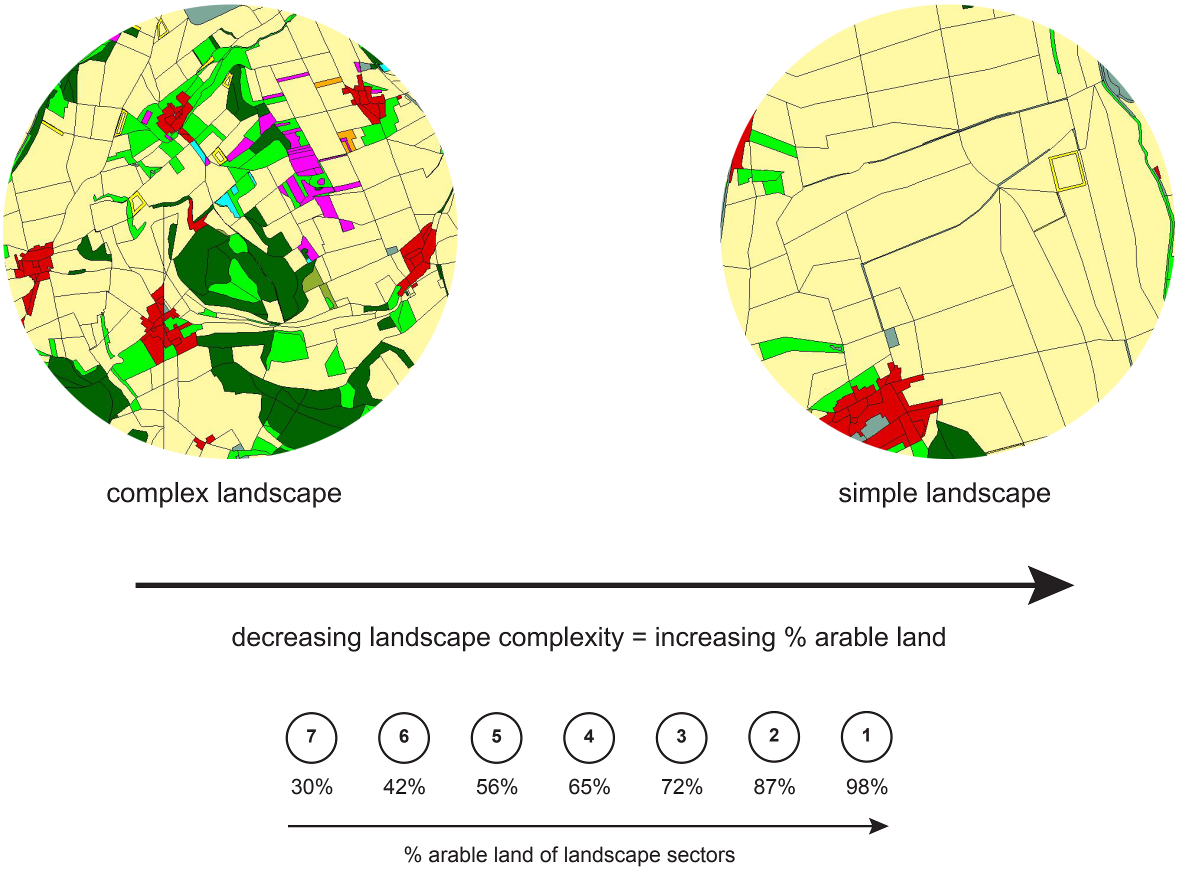

Fig. 2: Schematic drawing of the study design: we selected 7 landscape sectors of a 1000 m-radius along a gradient of varying landscape complexity, wich is associated with the percentage of arable land, showing the two extremes of complex and simple landscapes.

For the first three studies dealing with biological control of cereal aphids (chapters 2 – 4), we selected seven non-overlapping landscape sectors representing a gradient from structurally rich landscapes, i.e. only ~30% arable land, to structurally simple landscapes, i.e. up to 98% arable land in the surrounding of each study site in the range of a 1000 m-radius (Fig. 2). This radius is based on our experience of a functionally meaningful spatial scale for the insects studied (Thies *et al.*, 2003, 2005; see also Kleijn & van Langevelde, 2006). Within each of these landscape sectors, we selected four study sites in winter wheat fields 2 m distant to three different bordering habitat types. Broad sown flower fields and narrow sown flower strips were contrasted to grassy field margin strips and compared with wheat-wheat boundaries without any neighbouring habitat as controls (Fig. 3).

Sown flower habitats were established in 2005 and sown with a seed mixture of 13 flowering horticultural and 13 wildflower species with overlapping flower periods throughout the season (for the list of sown plant species, see Appendix A1 in chapter 2). Annuals in the seed mixture guaranteed the supply of flowers, nectar and pollen from the first year on. Flower strips and flower fields remained unmanaged all over the years, whereas grassy field margins, consisting of few flowering plants, but mainly of a variety of grasses, were cut once or more per year. We differentiated between sown flower strips with a similar width of ca. 3 m as the grassy field margins, and sown flower fields with a width of 12 – 25 m to test for size effects.

Fig. 3: Wheat field bordering habitat types (from left to right): sown flower fields, sown flower strips, grassy field margin strips and wheat-wheat boundaries.

The last study, dealing with biological control of the rape pollen beetle, was focused only on sown flower habitats, one each centred in a landscape sector of varying complexity. We selected 20 non-overlapping sectors, likewise covering a complexity gradient from structurally complex (~ 22% arable land) to structurally simple (~ 86% arable land). A radius of 1000 m is an appropriate scale also for the target species of this study (Thies *et al.*, 2003).

Study organisms

cereal aphids & natural enemies

In Germany, economically important herbivore pest populations in cereals mainly consist of three cereal aphid species, *Sitobion avenae* (Fabricius), *Metopolophium dirhodum* (Walker) and *Rhopalosiphum padi* (Linnaeus) (Homoptera, Aphididae). By phloem sucking and virus transmission they can cause severe crop damage in some years, but natural enemies can significantly regulate aphid densities below economic threshold level (Duelli & Obrist, 2003; Östman *et al*., 2003; Bianchi *et al*., 2006). Aphids are attacked by generalist ground-dwelling predators such as carabid beetles, rove beetles and spiders (Symondson *et al*., 2002; Lang, 2003; Schmidt *et al.*, 2003), as well as by specialist vegetation-dwelling predators such as the larvae and adults of ladybird beetles, larvae of syrphid flies, gall midges and lacewings and by specialist aphid parasitoids (mainly Aphidiidae) (Schmidt *et al.*, 2003; Griffiths *et al.*, 2008).

RAPE POLLEN BEETLE & PARASITOIDS

The rape pollen beetle *Meligethes aeneus* (Fabricius) (Coleoptera, Nitidulidae) is one of the major pests of rape crops (Borg & Ekbom, 1996; Alford *et al*., 2003; Zaller *et al*., 2009). Growing number and area of monocultures are susceptible to serious damage by this beetle and high amounts of insecticides are applied to keep this pest under control (Williams, 2006; Thies & Tscharntke, 2010). Parasitoids are known for their strong substantial biological control of pollen beetle abundances (Nilsson, 2003; Williams, 2006). The most common parasitoids in the study region attacking the beetles' larvae are *Phradis morionellus* (Holmgren), *P. interstitialis* (Thomson) and *Tersilochus heterocerus* (Thomson) (all Hymenoptera, Ichneumonidae) (Nilsson, 2003; Thies *et al*., 2003; Jönsson, 2005).

RESEARCH OBJECTIVES

We investigated the relative importance of different habitats adjacent to winter wheat fields, including sown flower habitats, grassy field margin strips and wheat controls, and of landscape complexity for biological control of cereal aphids through the enhancement of different groups of natural enemies (chapter 2), especially of syrphid flies (chapter 3), and – over the course of three years – of vegetation-dwelling predators and parasitoids (chapter 4). We also analysed the impact of sown flower habitats on the enhancement of specialized parasitoids of the rape pollen beetle (chapter 5).

CHAPTER OUTLINE

FLOWER POWER FOR BIOLOGICAL CONTROL OF CEREAL APHIDS ACROSS DIFFERENT LANDSCAPES – CHAPTER 2

In this study, we tested the effectiveness of sown flower habitats (broad and narrow) and grassy field margins for natural enemy impact on cereal aphids along a gradient from structurally simple to complex landscapes. Aphid population growth in cereal fields was analyzed under experimentally reduced densities of natural enemies by excluding each ground-dwelling predators, vegetation-dwelling predators and parasitoids and a combination of both compared to open controls, where no manipulation was done (Fig. 4). Aphid densities decreased most when all natural enemy groups were present, but vegetation-dwelling predators

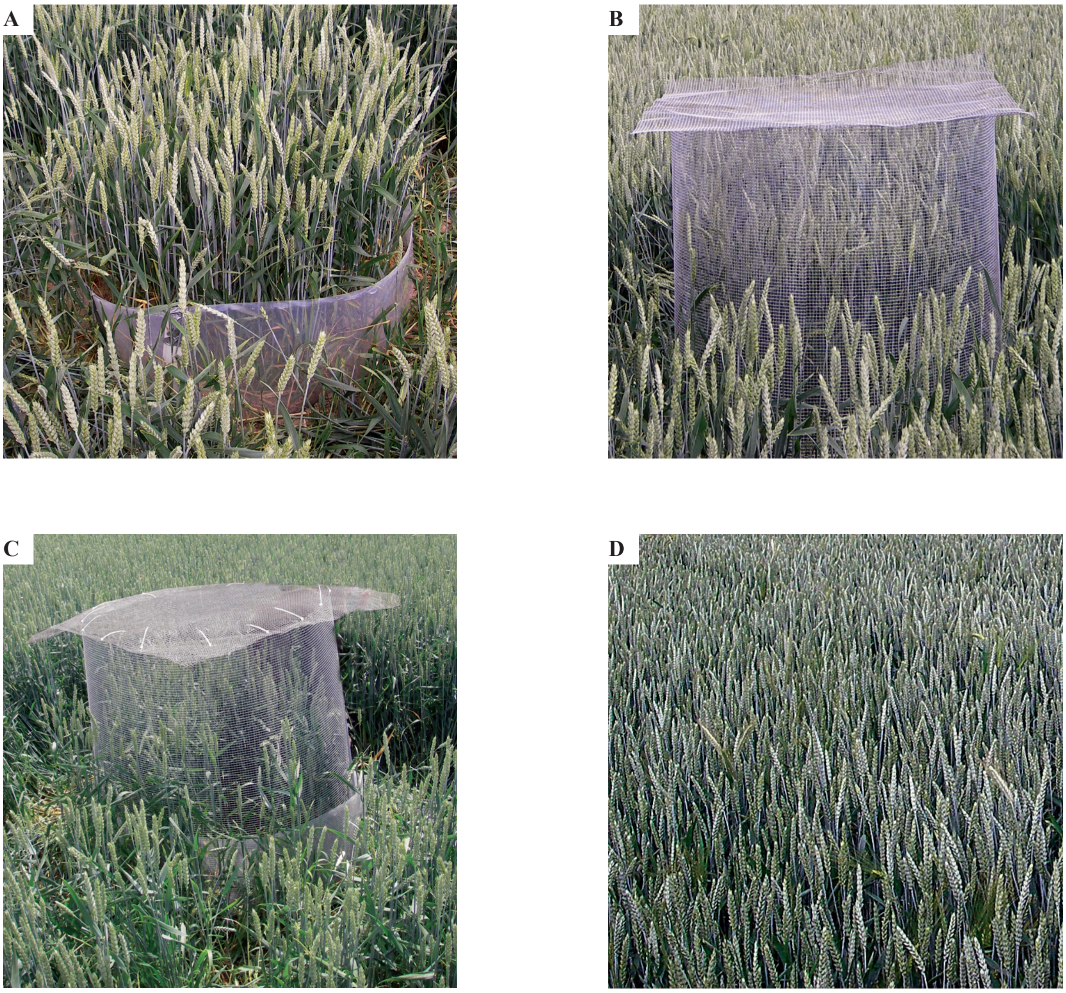

Fig. 4: Experimental aphid natural enemy exclusion: a) ground-dwelling predator exclusion; b) vegetation-dwelling predator and parasitoid exclusion; c) combination of both; d) control without any manipulation.

such as syrphid fly larvae and parasitoids contributed most to aphid control. Enhanced predator-prey ratios and parasitism rates strongly reduced aphid population growth in wheat fields adjacent to sown flower habitats, but this was not influenced by the complexity of the surrounding landscape. This study emphasizes the importance and potential of local habitat diversification enhancing beneficial insects relying on floral resources to improve biological control of cereal pests.

INCREASING SYRPHID FLY DIVERSITY AND DENSITY IN SOWN FLOWER STRIPS WITHIN SIMPLE VS. COMPLEX LANDSCAPES – CHAPTER 3

Syrphid fly (Diptera: Syrphidae) communities in broad and narrow sown flower habitats and in naturally developed grassy field margin strips, as well as their occurrence in adjacent wheat fields were analyzed along a landscape gradient. Densities and in particular, the density of aphidophagous species, was higher on both sown flower habitats compared to grassy strips and wheat–wheat boundary controls. In addition, species richness of aphidophagous syrphid flies within wheat fields adjacent to sown flower habitats was higher, indicating spillover between habitats and a positive effect of these sown flower habitats on potential biological control of cereal aphids. Species richness and abundance in sown flower habitats increased as the proportion of arable land in the surrounding landscape increased. This highlights the importance of the local creation of flower habitats in homogeneous, intensively managed arable landscapes for functionally important organisms such as syrphid flies benefiting from additional flowering resources.

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WHAT A DIFFERENCE A YEAR MAKES: INTER-ANNUAL VARIABILITY OF CEREAL APHID CONTROL BY FLOWER STRIPS AND LANDSCAPE COMPLEXITY – CHAPTER 4

Over the course of three years, we investigated the effects of local management of different wheat field-bordering habitat types and of landscape context on biological control of cereal aphids by vegetation-dwelling predators and parasitoids. Both local and landscape factors significantly influenced aphids and natural enemies, with most effective suppression of aphid populations adjacent to broad and narrow sown flower habitats compared to grassy field margins and wheat-wheat boundaries. These effects were pronounced in complex landscapes. Especially in a year with low aphid densities, strongly increased predator and parasitoid densities adjacent to sown flower habitats were able to suppress aphid populations successfully by 55 to 64% through 3 to 7 times higher predator-prey ratios and parasitism rates compared to grassy field margins and wheat-wheat-boundaries. This study accentuates the value of semi-natural habitats such as sown flower habitats for stronger biological aphid control by enhanced populations of parasitoids and predators. However, the high inter-annual variability of pest as well as natural enemy densities seems to be crucial for the success of such agri-environment schemes.

ENHANCING RAPE POLLEN BEETLE PARASITISM WITH SOWN FLOWER HABITATS IN COMPLEX LANDSCAPES – CHAPTER 5

We examined the potential of sown flower fields to enhance the abundance of specialized parasitoids thereby improving biological control of the rape pollen beetle *Meligethes aeneus*. 20 sown flower fields, each centred in a sector of varying landscape complexity and including one of the rape pollen beetles' host plant *Sinapis alba*, were selected to assess the influence of local (= plant) and landscape parameters on herbivory of *S. alba* plants by *M. aeneus* and on parasitism rates of *M. aeneus* larvae by the parasitoid *Tersilochus heterocerus*. We found herbivory to be determined by the local host plant density, whereas parasitism rate was determined by the structural complexity on the landscape scale with higher parasitism in landscapes with high proportions of semi-natural habitats. Moreover, sown flower fields with dense *S. alba* plant cover hosted higher parasitoid densities, sustained higher parasitism and suffered less from herbivory than sown flower fields with sparse *S. alba* plant cover. However, on all sites but three, parasitism stayed above the critical threshold of successful biological control. These results demonstrate that sown flower fields, offering constant and undisturbed habitats for parasitoids with a rich pollen and nectar supply and also abundant host densities for reproduction, are able to promote stable and numerous parasitoid populations, which can help to control rape pollen beetles in nearby rape crop fields.

CONCLUSIONS

All studies of this thesis showed that sown flower habitats are a promising tool of agri-environment schemes. Sown flower habitats promoted biological control of cereal aphids in adjacent winter wheat fields and reduced pest infestations successfully by enhancing natural enemy populations. Vegetation-dwelling predators and parasitoids, relying on floral food resources as adults, accounted most for cereal aphid control. Parasitoid populations of rape pollen beetles also benefited from the sown flower habitats. We ascribe these positive effects to the favourable conditions of the sown flower habitats for the beneficial insects: on the one hand they offer steady and undisturbed habitats as they are implemented for about five years. Moreover, during this period they provide a continuous supply of additional food (nectar and pollen) and prey/hosts for a variety of natural enemies of agricultural pests. Differently sized flower habitats achieved similar beneficial success in all studies, thus we can recommend both, narrow as well as broad flower habitats. However, continuity emerged to be of major importance as we proved highest benefit of the sown flower habitats after two years, when they were well established. So, to ensure constancy of sown flower habitats shows great promise aiming for the best possible outcome enhancing natural enemy populations of cereal aphids as well as parasitoids of rape pollen beetles in the long run.

The surrounding landscape matrix revealed heterogeneous effects for pest organisms, natural enemies and related trophic interactions. This highlights that the organisms studied perceive their environment with a different sensitivity and on different spatial scales based on their trophic rank, their requirements and dispersal abilities. Hence, our results imply that the local diversification with sown flower habitats in landscapes of various complexities provides strong potential to contribute to the build-up and maintenance of natural enemy populations, especially of nectar- and pollen-feeding enemies, and to facilitate their spillover into adjacent crop fields enhancing biological control of agricultural pests.

The sown flower habitats are established as a measure of the agri-environment scheme NAU A6 (ML Niedersachsen, 2010a), and are also part of the Partridge Conservation Project (www.rebhuhnschutzprojekt.de). This involved a special seed mixture (see above and Appendix A1 in chapter 2) to cope with the needs and to enhance grey partridge (*Perdix perdix* L.) populations, but apart from that were subject to the general requirements of the NAU A6. Our studies implicate sown flower habitats to be a promising multi-purpose agri-environmental practice to combine biodiversity conservation with ecosystem services such as biological control through “flower power” for a broad variety of beneficiaries.

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CHAPTER

2

FLOWER POWER FOR BIOLOGICAL CONTROL OF CEREAL APHIDS ACROSS DIFFERENT LANDSCAPES

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submitted to *Journal of Applied Ecology*

Summary

1. Much research is focussing on management practices enhancing natural enemies and conservation biological control, but little is known on the relative effects of different local and landscape changes. Here, we tested the effectiveness of wildflower strips for natural enemy impact on cereal aphids in a gradient from structurally simple to complex landscapes.
2. Aphid population growth in cereal fields was analyzed under experimentally reduced densities of ground-dwelling predators, flying predators and parasitoids and a combination of both compared to open controls. The exclusion experiment was applied in winter wheat fields adjacent to different types of neighbouring semi-natural habitats: sown flower strips, sown flower fields, naturally developed, grassy field margin strips and wheat-wheat boundaries as a control. These four exclusion and habitat treatments were located in landscapes along a gradient of varying land-use intensity, quantified as changing proportion of arable land (30 – 100%).
3. As hypothesized, aphid densities increased most when all natural enemies were excluded, with flying enemies such as syrphid flies and parasitoids contributing most to aphid control. Aphid densities were reduced ca. five times by natural enemies and were negatively related to flying predator-prey ratio and parasitism rate.
4. Adjacent to flower habitats lower aphid population growth was associated with enhanced predator-prey ratio and parasitism rate in the wheat fields. In contrast to our expectations, we did not detect any impact of the complexity of the surrounding landscape.
5. Synthesis and applications. Our experimental results show the potential of local habitat diversification for biological control. Natural enemies, in particular flying enemies such as syrphid flies and parasitoids, proved to be of major importance in cereal aphid control across different landscape types. Creating these flower habitats has been actually done to cope with the needs and to enhance populations of the grey partridge (*Perdix perdix* L.), but appears to be a promising multi-purpose agri-environmental practice (“flower power“) to combine biodiversity conservation with ecosystem services such as biological control alike.

Keywords

biological control, cereal aphids, natural enemies, sown flower strips, landscape context, area of field margin strips, parasitism, predator-prey ratio

Introduction

Landscape simplification through intensification of agriculture leads to a decline of natural habitats causing a dramatic decline of biodiversity and related functions (Landis *et al*., 2000; Pfiffner & Wyss, 2004; Bianchi *et al*., 2006; Cardinale *et al.*, 2006). Manipulation of habitats adjacent to crop fields has been shown to be a mean of improving the conditions of natural enemies, providing pest control through spillover into agricultural fields (Landis *et al.*, 2000; Pfiffner & Wyss, 2004; Ma *et al.*, 2007). Agri-environment schemes are implemented to reconstitute refuges outside (semi-) natural habitats to compensate for the decline of biodiversity in the increasingly depleted agricultural landscape (Nentwig, 2003; Musters *et al.*, 2009; but Kleijn *et al.*, 2001). Wildflower strips can offer necessary habitat structure for natural enemies by providing overwintering and nesting sites, shelter and food (hosts, prey, nectar, pollen, honeydew) (Müller & Godfray, 1999; Pfiffner & Luka, 2000; Duelli & Obrist, 2003; Griffiths *et al.*, 2008).

Jonsson *et al.* (2008) emphasize that increased densities of beneficial insects in the crop do not automatically translate into effective management of pests such as aphids, which are economically important pests causing serious damage in crops. Conservation biological control may decrease aphids below an economic threshold level and help to reduce cost-intensive and environmentally unfriendly application of insecticides (Duelli & Obrist, 2003; Östman *et al*., 2003; Bianchi *et al*., 2006; Griffiths *et al.*, 2008).

The main species of cereal aphids found in winter wheat in the study region are *Sitobion avenae* F., *Metopolophium dirhodum* Walk. and *Rhopalosiphum padi* L.. They are attacked by a diverse enemy group of predators and parasitoids. Although ground-dwelling predators like carabid beetles, rove beetles and spiders are generalists, they may significantly regulate aphid densities (Symondson *et al*., 2002; Lang, 2003; Schmidt *et al.*, 2003). Specialist aphid antagonists include parasitoid wasps and predators such as adults and larvae of ladybird beetles, larvae of syrphid flies, lacewing larvae and gall midge larvae (Schmidt *et al.*, 2003; Griffiths *et al.*, 2008). Because of the adult stages of these predators being flying insects, we refer to them as flying predators in the following.

Among the studies on the relative impact of the different enemy groups on aphid populations some studies emphasize the high impact of ground-dwelling predators (Lang, 2003), others report of successful aphid regulation by parasitoids (Hawkins *et al.*, 1999; Schmidt *et al.*, 2003) or further natural enemy groups (Tenhumberg & Poehling, 1995;

Schmidt *et al.*, 2004). Density of aphid antagonists is often linked to non-prey food such as nectar and pollen as additional resources, and flower strips, providing shelter, overwintering sites and alternative food resources, are suggested to be a management tool raising enemy population size (Frank, 1999; Duelli & Obrist, 2003; Bianchi *et al.*, 2006; Brewer *et al.*, 2008). In addition to local management, efficiency of aphid control seems to be influenced by the surrounding landscape with inconsistent effects depending on landscape complexity (Menalled *et al.,* 1999; Roschewitz *et al.,* 2005b; Thies *et al*., 2005; Tscharntke *et al.,* 2005; Rand & Tscharntke, 2007).

We brought together all these aspects to answer the questions whether flower strips improve biological control and whether this depends on the landscape context. In our study, aphid-enemy interactions were analyzed in winter wheat fields adjacent to different types of habitats, including sown flower strips, sown flower fields (to test for size effects), naturally developed grassy field margin strips and winter wheat fields (wheat-wheat boundaries without any flowering habitat) as controls. Further, cereal aphid performance was studied under experimentally reduced densities of (a) ground-dwelling predators, (b) flying predators and parasitoids, (c) a combination of (a) and (b), and (d) in open controls. To test for influences of the surrounding landscape, the winter wheat fields were located along a gradient of landscape complexity from structurally rich to structurally simple (i.e. 30 - 100% arable land; see Thies *et al.*, 2003).

We hypothesized that exclusion of both flying and ground-dwelling enemies would have the strongest effect on aphid population growth resulting in highest aphid densities, with specialist aphid enemies, foraging on nectar and pollen, being more effective than generalist predators, foraging on the ground (Schmidt *et al.*, 2003; Holland *et al.*, 2008). The flower habitats were expected to support a more diverse and abundant enemy community compared to naturally developed grassy field margin strips, thereby resulting in a stronger aphid control in adjacent winter wheat fields.

Densities of natural enemies are generally higher in structurally diverse and habitat-rich landscapes, independent of local habitat management (Bianchi *et al*., 2006). Duelli & Obrist (2003) argue that agri-environment schemes perform best in these complex landscapes when there are source populations in (semi-) natural habitats in the surrounding landscape. Tscharntke *et al*. (2005), however, hypothesize that effects of local habitat improvements are most effective in landscapes with intermediate complexity, because local management does often not improve the overall high biodiversity in complex landscapes, whereas simplified landscapes lacking in (semi-) natural habitats would perform worse, because of missing populations positively responding to changed management. So, local introduction of flower habitats can be hypothesized to be most effective in landscapes of intermediate structural complexity (Tscharntke *et al.*, 2005).

Materials and methods

The experiments were carried out in 2006 in 28 winter wheat fields in seven landscape sectors around the city of Göttingen. This region is characterized by intensive arable land-use interspersed with (semi-) natural habitats (Thies *et al.*, 2005). The complexity of each of the seven landscape sectors varied representing a gradient from structurally rich landscapes (~30% arable land) to structurally simple landscapes (up to 98% arable land) in the surrounding of the study site in a range of a 1000 m-radius (Fig. 1, here the actual proportions of arable land of each landscape sector are given). The percentage of arable land is negatively correlated with the perimeter-area-ratio (i.e. many field edges) and the diversity of habitat types (Schmidt *et al.*, 2004; Roschewitz *et al.*, 2005b).

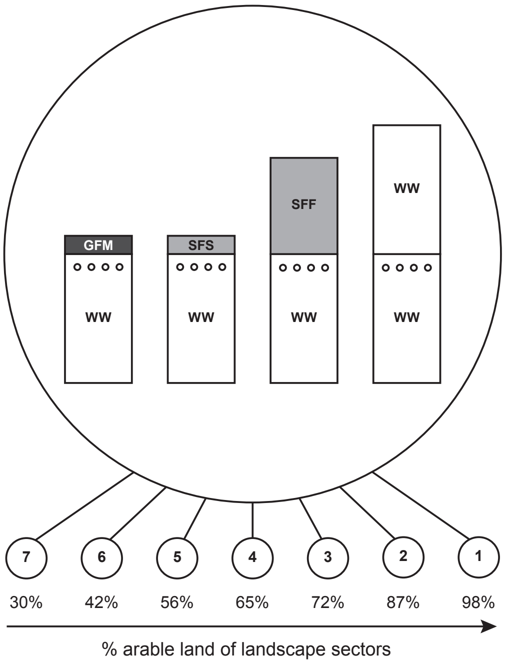


Fig 1: Schematic drawing of the experimental setup: four winter wheat fields, each with four exclusion treatment plots (small circles), which were set-up in a distance of 2 m adjacent to three different neighbouring habitat types and one wheat field control nested in each of the seven landscape sectors along a gradient of landscape complexity (i.e. proportion of arable land within the landscape sectors of a 1000 m – radius). Altogether we studied seven landscapes, 28 (7 × 4) wheat fields with 112 (7 × 4 × 4) samples. GFM = grassy field margin strips; SFS = sown flower strips; SFF = sown flower fields; WW = winter wheat fields.

In each of these landscape sectors, four winter wheat fields were situated closely together in a nested experimental setup (Fig. 1). All fields were managed conventionally but had left an insecticide-free area for the experimental treatments.

The experimental treatments were applied in winter wheat in a distance of 2 m adjacent to three different neighbouring habitat types (Fig. 1), i.e. adjacent to i) naturally developed, perennial field margins consisting of few flowering plants but mainly of a variety of grasses (“grassy field margin strips“). They had a width of approximately

3 m; ii) “sown flower strips“ with a similar width as the field margins (ca. 3 m; length 249.4 m ± 12.66 m) but composed of 13 flowering horticultural plant species and 13 wildflower species; iii) “sown flower fields“, sown with the same seed mixture as the sown flower strips but with a width of 12 – 25 m (length 212.0 m ± 20.2 m) (for the list of sown plant species for grey partridge (*Perdix perdix* L.) enhancement, see Appendix A1 in Supporting Information). This seed mixture guaranteed the presence of flowers throughout the vegetation period. Flower habitats were in the second year after establishing. Winter wheat fields without any neighbouring habitat, (iv) “wheat-wheat boundaries“, were examined as control sites (Fig. 1).

To quantify the potential biological aphid control, natural enemies were excluded from circular experimental plots with a diameter of 1 m (following Schmidt *et al.*, 2003). For the removal of ground-dwelling predators (“–G”) plastic barriers were set up. They were buried 10 cm into the soil and left 30 cm above soil surface. Inside this plastic barrier one pitfall-trap was placed to capture and remove ground-dwelling predators. Flying predators and parasitoids were reduced by setting wire cages over the plots (“–F”). These cages had a mesh size of 8 mm and were covered with glue to prevent flying insects from entering these cages (see also Costamagna *et al*., 2007). Ground-dwelling predators could enter these cages over the soil surface. To exclude both enemy groups the cage and plastic barrier were combined and set together over the plots (“–G–F”). Again one pitfall trap was set into these plots. Schmidt *et al.* (2003) showed that microclimate inside and outside the wire cages is identical. Control plots (“C”) were of the same size as the exclusion treatment plots, but just marked with bars and left unmanipulated. The distances between the four treatment plots were 15 m and plots were randomly assigned along the wheat field/neighbouring habitat border (Fig. 1).

Aphids and flying natural enemies, namely larvae of ladybirds (Coccinellidae), syrphid flies (Syrphidae), gall midges (Cecidomyiidae) and lacewings (Chrysopidae), and mummified aphids (indicating the abundance of parasitoids), were counted on 25 randomly chosen wheat shoots per treatment plot at wheat flowering stage (“wf“; BBCH-scale 65; Lancashire *et al*., 1991; Meier, 2001) in June, when aphids colonize the wheat fields, and at wheat milk-ripening stage (“wmr“; BBCH-scale 75–77) in July, when aphid population size was highest in the wheat fields. Pitfall traps of the exclusion plots “–G” and “–G–F” operated over the entire experimental period. They were emptied at the two sampling dates, when visual counts were made, and ground-dwelling predators caught in these pitfall traps were determined by counting individuals of carabid beetles, staphylinid beetles and spiders.

As pitfall traps were only placed in the "–G" and "–G–F" exclusion plots to reduce ground-dwelling predators' abundances, we have only indirect evidence of their effects on aphid population densities.

Because of negligible abundances and irregular distribution of lacewing larvae and the absence of gall midge larvae as well as larvae of ladybirds we present their means but did not include them in further statistical analyses. Parasitism rates were calculated as the ratio of mummies to total aphids present. Flying predator, mummy, and aphid counts as well as aphid population growth (i.e. difference of aphid numbers between the two counting dates) were log-transformed, whereas proportional data such as parasitism rate and predator-prey ratio, i.e. ratio numbers of predators (here syrphid fly larvae) to aphids present, were arcsine-square-root transformed to achieve assumptions of homogeneity of variance and normality of the residuals from the statistical models.

We did all statistical analyses and graphics using the software R 2.8.1 (R Development Core Team 2007). We fitted linear mixed-effects models ("lme"-function within the "nlme"-package, Pinheiro & Bates, 2000) with landscape complexity (i.e. the proportion of arable land in each landscape sector), adjacent habitat type and enemy-exclusion treatment plus their two-way interactions as fixed factors. We restricted the analyses to two-way interactions because more interactions become unwieldy, require a very large sample size and are hardly to interpret (Quinn & Keough, 2002). Treatments were nested within adjacent habitat type and adjacent habitat type within landscape sector by adding landscape sector and adjacent habitat type as random factors (blocks) in the order of nesting. For the analyses of aphid population growth we also included parasitism rate and predator-prey ratio separately as well as in interaction terms with the other fixed factors. Correlations between these two variables and aphid population growth can be difficult to interpret as they are non-independent, but following Brett (2004), page 653, this mathematical problem can be neglected here, because we aim at showing predictive relationships, but not causal ones. After calculating the maximal models, we performed stepwise backwards model selection by using the Akaike Information Criterion (AIC) removing non-significant terms during this procedure (Crawley, 2007; "stepAIC"-function within the "MASS"-package, Venables & Ripley, 2002). The minimal adequate model was the one with the lowest AIC (Burnham & Anderson, 2002). Multiple comparisons among factor levels of factors having a significant effect in the minimal model were calculated using Tukey contrasts with *P*-values adjusted by single-step method ("multcomp"-package, Hsu, 1996). In the text we give arithmetic means ± one SE.

Results

Overview

In total we found 21,269 aphids in the winter wheat fields. *Rhopalosiphum padi* reached the highest densities (37%), followed by *Metopolophium dirhodum* (33%) and *Sitobion avenae* (30%). Aphid abundances varied considerably between sampling dates with more than ten times higher numbers at wheat milk-ripening (176.7 ± 18.8, *n* = 112) than at wheat flowering (13.3 ± 1.2, *n* = 112) (Table 1). Aphid numbers in the open, unmanipulated plots ("C") amounted to 61.6 ± 4.4 individuals per 25 wheat shoots at wheat milk-ripening (Fig. 2) and did not reach the economic threshold level of five aphids per shoot (Giller *et al.*, 1995).

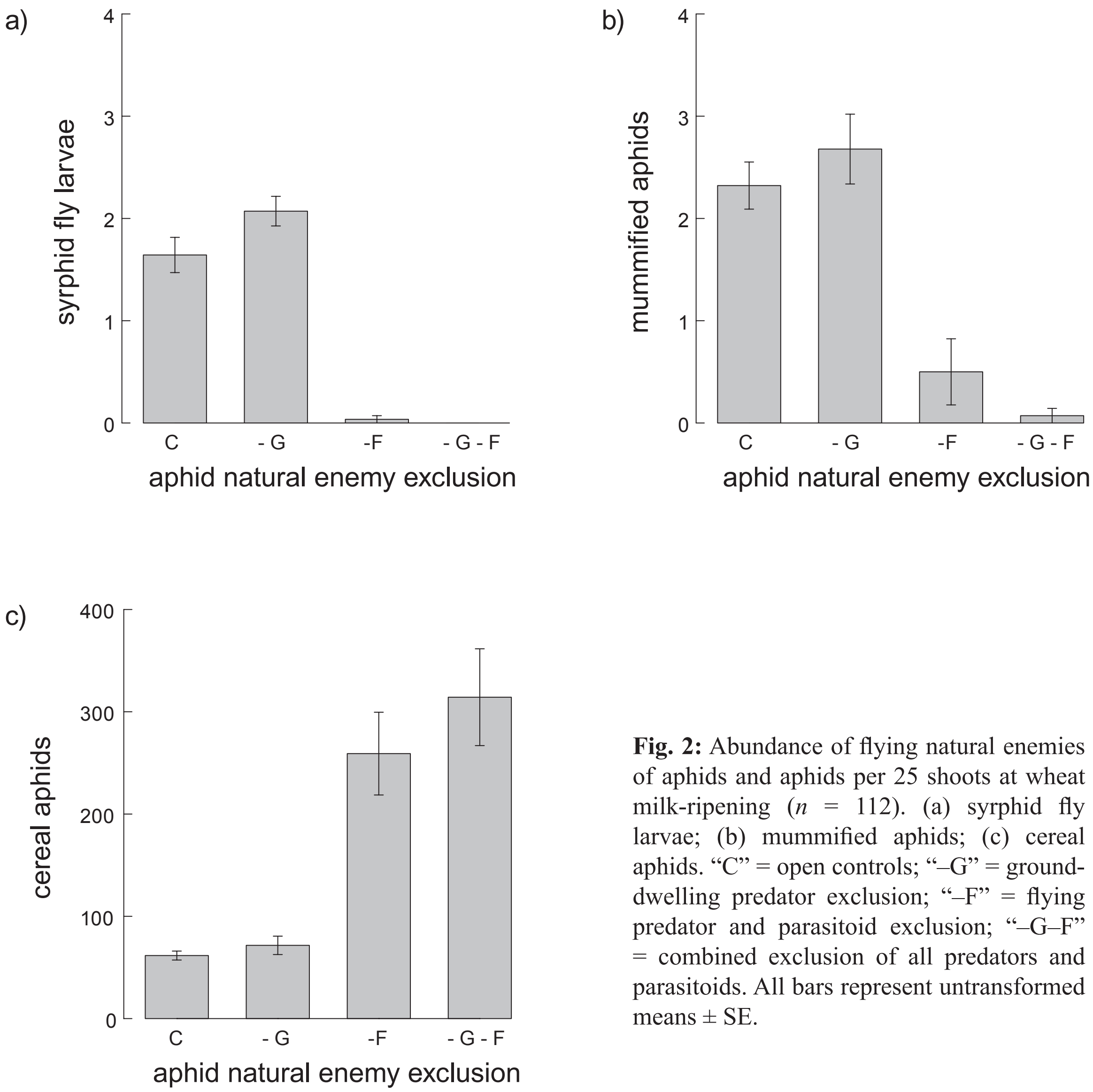


Fig. 2: Abundance of flying natural enemies of aphids and aphids per 25 shoots at wheat milk-ripening (*n* = 112). (a) syrphid fly larvae; (b) mummified aphids; (c) cereal aphids. "C" = open controls; "–G" = ground-dwelling predator exclusion; "–F" = flying predator and parasitoid exclusion; "–G–F" = combined exclusion of all predators and parasitoids. All bars represent untransformed means ± SE.

Table 1: Densities of aphids and their natural enemies (arithmetic means ± SE, minima and maxima of individuals per 25 shoots/pitfall trap) in all experimental treatments (*n* = 112)

	species	∑	$\bar{x}$	±	SE	min	max
aphids	all	21269					
	wheat flowering	1484	13.3	±	1.2	0	64
	wheat milk-ripening	19785	176.7	±	18.8	15	954
	Sitobion avenae	6229					
	wheat flowering	175	1.6	±	0.4	0	25
	wheat milk-ripening	6054	54.1	±	4.3	3	316
	Metopolophium dirhodum	7098					
	wheat flowering	1173	10.5	±	1.1	0	55
	wheat milk-ripening	5927	52.9	±	6.9	2	450
	Rhopalosiphum padi	7942					
	wheat flowering	138	1.2	±	0.4	0	30
	wheat milk-ripening	7804	69.7	±	11.8	1	734
parasitoids	Aphidiidae	215					
	wheat flowering	59	0.5	±	0.1	0	6
	wheat milk-ripening	156	1.4	±	0.2	0	8
flying predators	Syrphidae larvae	183					
	wheat flowering	78	0.7	±	0.1	0	4
	wheat milk-ripening	105	0.9	±	0.1	0	3
	Chrysopidae larvae	24					
	wheat flowering	2	0.0	±	0.0	0	1
	wheat milk-ripening	22	0.2	±	0.0	0	2
ground-dwelling predators	Carabidae	4109					
	wheat flowering	1468	26.2	±	3.9	0	110
	wheat milk-ripening	2641	47.2	±	5.1	0	190
	Staphylinidae	500					
	wheat flowering	289	5.2	±	0.7	0	24
	wheat milk-ripening	211	3.8	±	0.5	0	17
	Araneae	1571					
	wheat flowering	514	9.2	±	1.2	0	51
	wheat milk-ripening	1057	18.9	±	2.2	0	74

All flying aphid natural enemies were more common on the second sampling date. Aphid mummies had almost three times higher densities at wheat milk-ripening (1.4 ± 0.2, *n* = 112) compared to wheat flowering (0.5 ± 0.1, *n* = 112). Syrphid fly larvae densities increased about one third between sampling dates (0.7 ± 0.1 at wf, *n* = 112; 0.9 ± 0.1 at wmr, *n* = 112), whereas lacewing larvae (Chrysopidae) were rare (0.0 ± 0.0 at wf, *n* = 112; 0.2 ± 0.0 at wmr, *n* = 112) (Table 1) and larvae of ladybirds (Coccinellidae) and gall midges (Cecidomyiidae) were not found at all. Numbers of carabid beetles and spiders approximately doubled from first to second sampling date (carabids wf 26.2 ± 3.9, *n* = 112, wmr 47.2 ± 5.1, *n* = 112; spiders wf 9.2 ± 1.2, *n* = 112, wmr 18.9 ± 2.2, *n* = 112) (Table 1). Rove beetles decreased about one fourth from wheat flowering to wheat milk-ripening (wf 5.2 ± 0.7, *n* = 112, wmr 3.8 ± 0.5, *n* = 112) (Table 1).

WHEAT FLOWERING

At the beginning of the experiment at wheat flowering, when aphids colonize the wheat fields, aphid densities were nearly uniformly distributed all over the experimental treatment types, the habitat types adjacent to the wheat fields and landscapes (Table 2).

Aphid flying natural enemies responded differently to site conditions and adjacent habitats. While parasitoids (mummified aphids) did not reveal any differences between treatment types and adjacent habitat types (Table 2), syrphid fly larvae occurred in higher densities in the open controls and the plots where ground-dwelling predators were excluded (“C” 1.2 ± 0.2; “–G” 1.3 ± 0.2; “–F” 0.1 ± 0.1; “–G–F” 0.1 ± 0.1, each treatment *n* = 28), and in plots adjacent to sown flower habitats (Table 2; Appendix A2 in Supporting Information). Both, syrphid fly larvae and parasitoids, did not respond to landscape structure (Table 2). Carabid beetles and spiders were caught in lower densities in the pitfall traps in the combined exclusion plots than in the only ground-dwelling predator exclusion plots (carabids “–G–F” 21.4 ± 4.9, “–G” 31.0 ± 6.1, each treatment *n* = 28; spiders “–G–F” 8.4 ± 1.9, “–G” 10.0 ± 1.5; each treatment *n* = 28) (Table 2, treatments “–G” and “–G–F” only). Rove beetles showed only small differences between these two treatments (“–G–F” 4.1 ± 0.8, “–G” 6.2 ± 1.1, each treatment *n* = 28) (Table 2, treatments “–G” and “–G–F” only). All ground-dwelling predators were neither related to the adjacent habitat nor to landscape structure (Table 2, treatments “–G” and “–G–F” only).

Table 2: Results of linear mixed-effects models for aphids and their natural enemies at two sampling dates, describing the effects of landscape (i.e. the proportion of arable land in each of the seven landscape sectors), adjacent habitat type (sown flower fields, sown flower strips, grassy field margin strips, wheat-wheat boundaries) and treatment (exclusion of ground-dwelling predators ("–G"), of flying predators and parasitoids ("–F"), of both enemy groups ("–G–F") and open controls ("C")). NumDF = numerator degrees of freedom, DenDF = denominator degrees of freedom. Bold font indicates significant *P*-values.

	NumDF	DenDF	*F*-value	*P*-value
wheat flowering – all treatments				
aphids				
landscape	1	5	0.961	0.372
adjacent habitat type	3	18	0.384	0.766
treatment	3	81	1.683	0.177
mummified aphids				
landscape	1	5	0.004	0.953
adjacent habitat type	3	18	1.501	0.248
treatment	3	81	1.622	0.191
syrphid fly larvae				
landscape	1	5	0.174	0.694
adjacent habitat type	3	18	0.952	0.436
treatment	3	81	29.656	**< 0.0001**
adjacent habitat type × treatment	9	69	2.126	**0.039**
wheat flowering – treatments "–G" and "–G–F" only				
carabid beetles				
landscape	1	5	1.456	0.282
adjacent habitat type	3	18	0.522	0.673
treatment	1	27	7.103	**0.013**
rove beetles				
landscape	1	5	5.389	0.068
adjacent habitat type	3	18	1.833	0.177
treatment	1	27	3.914	0.058
spiders				
landscape	1	5	0.000	0.987
adjacent habitat type	3	18	0.136	0.937
treatment	1	27	6.150	**0.020**
wheat milk-ripening – all treatments				
aphids				
treatment	3	81	71.686	**< 0.0001**
aphid population growth				
treatment	3	81	44.720	**< 0.0001**
parasitism rate	1	83	36.552	**< 0.0001**
predator-prey ratio	1	83	41.428	**< 0.0001**
mummified aphids				
treatment	3	81	54.925	**< 0.0001**
syrphid fly larvae				
treatment	3	81	149.117	**< 0.0001**

(continued)

Table 2: Results of linear mixed-effects models for aphids and their natural enemies (*continued*)

	NumDF	DenDF	*F*-value	*P*-value
wheat milk-ripening – treatments “C“ and “–G“ only				
aphids				
treatment	1	27	0.641	0.43
aphid population growth				
treatment	1	27	0.798	0.38
parasitism rate	1	27	32.876	**< 0.0001**
predator-prey ratio	1	27	58.538	**< 0.0001**
adjacent habitat type × parasitism rate	3	24	4.862	**0.009**
adjacent habitat type × predator-prey ratio	3	24	3.639	**0.027**
syrphid fly larvae				
treatment	1	27	4.454	**0.044**
wheat milk-ripening – treatments “–F“ and “–G–F “ only				
aphids				
treatment	1	27	2.451	0.129
wheat milk-ripening – treatments “–G“ and “–G–F“ only				
carabid beetles				
treatment	1	27	56.844	**< 0.0001**
rove beetles				
treatment	1	27	0.068	0.796
spiders				
treatment	1	27	9.629	**0.005**

Wheat milk-ripening

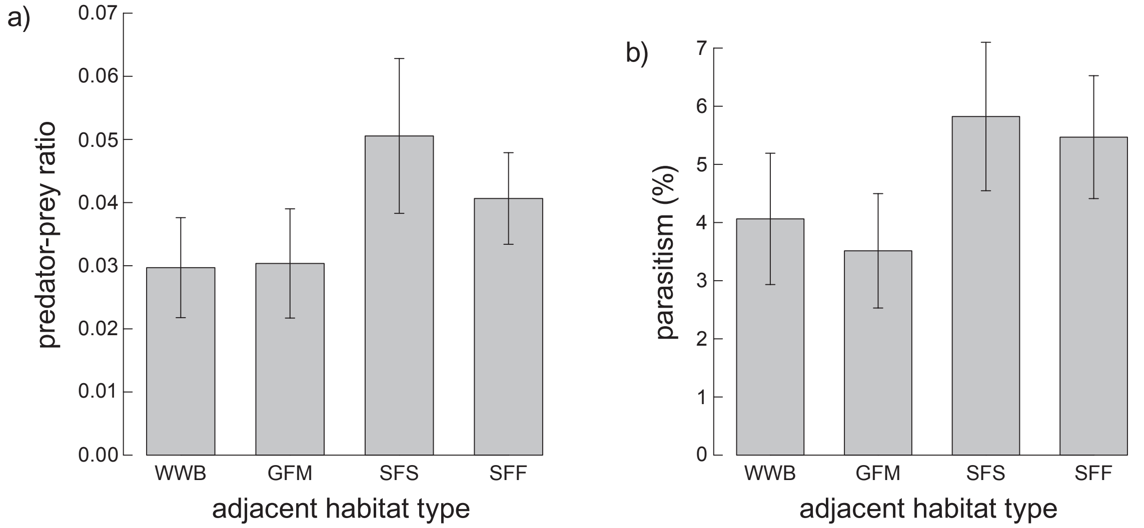
The wire cages and plastic barriers successfully excluded aphid natural enemies from the different treatment plots. In the flying predator and parasitoid exclusion plots (“–F”) as well as in the combined exclusion plots (“–G–F”) numbers of syrphid fly larvae were significantly lower than in the open control (“C”) and ground-dwelling predator removal plots (“–G”) (“–F” 0.0 ± 0.0; “–G–F” 0.0 ± 0.0; “–G” 2.1 ± 0.2 and “C”1.6 ± 0.2, each treatment *n* = 28) (Table 2, all treatments, Fig. 2a). Abundances of mummified aphids showed the same pattern with likewise significantly lower densities in the flying predator plus parasitoids exclusion plots (“–F” 0.5 ± 0.3, *n* = 28) just as in the combined exclusion treatment plots (“–G–F” 0.1 ± 0.1, *n* = 28) compared to the open control (“C” 2.3 ± 0.2, *n* = 28) and ground-dwelling predator removal plots (“–G” 2.7 ± 0.3, *n* = 28) (Table 2, all treatments, Fig. 2b). Both mummy and syrphid fly larvae densities were higher in plots where ground-dwelling predators were excluded compared to those open to all predators and parasitoids (Fig. 2a,b), but with significant differences only for the syrphid fly larvae (Table 2, treatments

"C" and "–G" only). Carabid beetles and spiders had higher densities in pitfall traps in the combined exclusion plots compared to the ground-dwelling exclusion plots (carabids "–G–F" 64.8 ± 7.9, "–G" 29.5 ± 4.3, each treatment *n* = 28; spiders "–G–F" 21.5 ± 3.4, "–G" 16.2 ± 2.6; each treatment *n* = 28) (Table 2, treatments "–G" and "–G–F" only). Rove beetles however did not show any significant reaction to the cage treatment ("–G–F" 3.4 ± 0.5, "–G" 4.1 ± 0.8; each treatment *n* = 28) (Table 2, treatments "–G" and "–G–F" only).

Aphid population densities were significantly influenced by natural enemy exclusion resulting in large differences between treatments (Table 2, all treatments). From the first sampling date to the second sampling date, aphid densities increased by 506% in the open control plots and by 467% in the ground-dwelling predator exclusion plots. In the flying predator and parasitoid exclusion cages aphid densities were 1709% higher and 1886% in the combined exclusion treatments after aphid reproduction.

Significantly reduced aphid densities were found in open control plots ("C"), where all predator groups were present. Aphid abundances did not differ significantly between plots where ground-dwelling predators were excluded and those where all natural enemies had access to, even though densities were slightly elevated in the "–G"-plots ("–G" 71.6 ± 9.0, *n* = 28; "C" 61.6 ± 4.4, *n* = 28) (Table 2, treatments "C" and "–G" only, Fig. 2c), indicating that aphid densities were only slightly affected by ground-dwelling predator exclusion. In contrast, exclusion of flying predators and parasitoids increased aphid densities significantly, while aphid numbers in the combined exclusion treatment ("–G–F") were even higher ("–F" 259.1 ± 40.5, *n* = 28; "–G–F" 314.3 ± 47.3, *n* = 28) (Fig. 2c). Analyzing aphid densities only of the flying predator exclusion plots ("–F") and the combined exclusion plots ("–G–F"), the presence of ground-dwelling predators ("–F"), alternatively the absence of ground-dwelling predators ("–G–F"), did not influence aphid densities (Table 2, treatments "–F" and "–G–F" only, Fig. 2c).

Aphid population growth was related to parasitism rate and to predator-prey ratio (Table 2, all treatments), as both were the remaining factors after stepwise backwards model selection by AIC. Analyses including only the plots that were accessible to flying predators and parasitoids (treatments "C" and "–G") also showed a highly significant relationship between aphid population growth and predator-prey ratio and parasitism rate, respectively (Table 2, treatments "C" and "–G" only, Fig. 4a,b). Aphid population growth was also related to the interaction between predator-prey ratio and parasitism rate, and the adjacent habitat type (Table 2, treatments "C" and "–G" only). Predator-prey ratios were highest at sown flower strips, followed by sown flower fields, grassy field margin strips and wheat-wheat



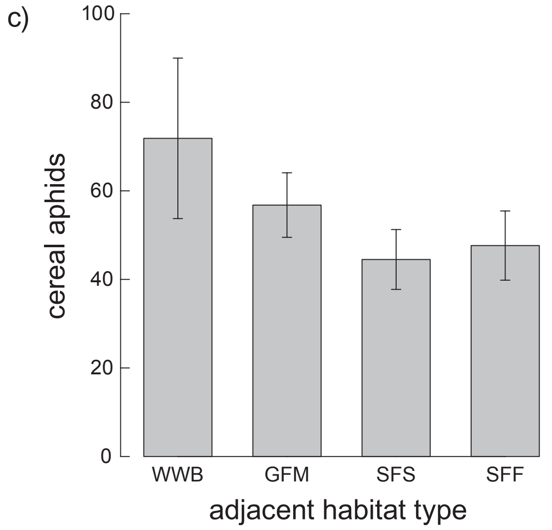


Fig. 3: Effects of different adjacent habitat types on (a) predator-prey ratios, (b) percent parasitism and (c) aphid population growth (difference of aphid densities between two sampling dates). Estimates per 25 shoots at wheat milk-ripening stage in winter wheat fields along the four adjacent habitats (data from the open control "C" and ground-dwelling predator exclusion "–G" plots; *n* = 56). All bars represent untransformed means ± SE.
(WWB = wheat-wheat boundaries; GFM = grassy field margin strips; SFS = sown flower strips; SFF = sown flower fields)

boundaries (Fig. 3a). Aphid population growth followed this pattern along the adjacent habitat types in reversed order with lowest numbers at the sown flower strips and increasing numbers at sown flower fields, grassy field margin strips and highest numbers in wheat-wheat bounderies (n.s.) (Fig. 3c). Parasitism rates displayed a just slightly different pattern with lowest rates neighbouring the grassy field margin strips, but having highest rates at sown flower strips as well (Fig. 3b).

Populations of aphids and natural enemies also varied among the study sites. However, the percentage of arable land around the study sites was neither related to aphid population growth nor to parasitism rate and predator-prey ratio, respectively.

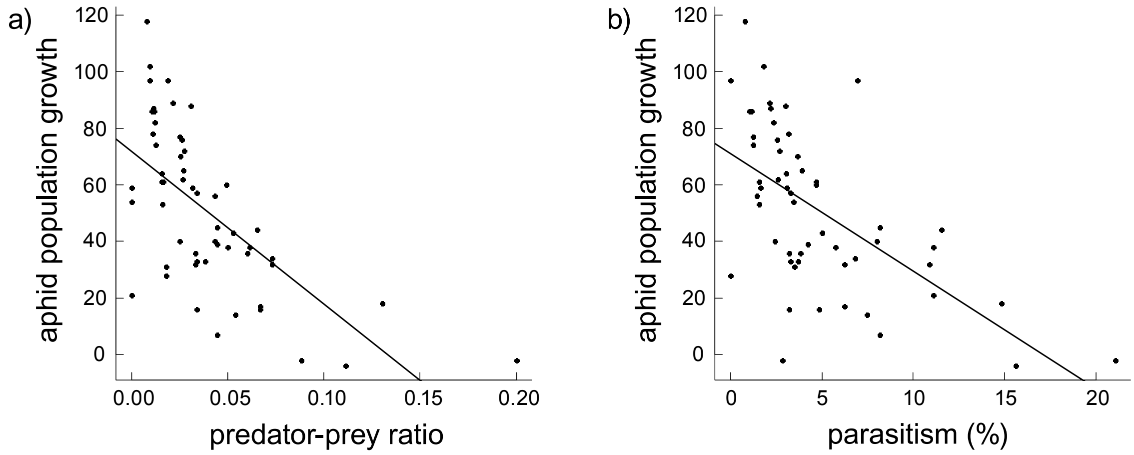


Fig. 4: Relation of aphid population growth (difference of aphid densities between two sampling dates) to (a) predator-prey ratio and to (b) percentage parasitism (data from the open control "C" and ground-dwelling predator exclusion "–G" plots; $n = 56$). parasitism: $r^2 = 0.362$, $y = 71.083 - 4.151\,x$, $P < 0.0001$; predator-prey ratio: $r^2 = 0.427$, $y = 71.916 - 541.275\,x$, $P < 0.0001$.

Discussion

In this study, we analyzed the potential of sown flower strips and sown flower fields to improve biological control of cereal aphids by enhancing the abundance and efficacy of aphid natural enemies. We further analyzed the strength of this effect for different groups of natural enemies using enemy exclusion techniques and tested whether this effect changed contingent on landscape type.

Aphid densities were reduced and densities of flying natural enemies were enhanced in wheat fields adjacent to sown flower strips and sown flower fields, compared to naturally developed grassy field margin stips and wheat-wheat boundaries. This is in line with other observations in our landscapes detecting lower aphid population densities adjacent to both flower habitats compared to grassy field margins (Erb, 2005). We found aphid population growth to be significantly influenced by the interaction of predator-prey ratio and parasitism rate with the adjacent habitat type. The effects on aphids and flying enemies as syrphid flies and parasitoids were independent of the complexity of the surrounding landscape.

Aphid population growth was highest in exclusion treatment plots without any impact of natural enemies ("–G–F"), independent of adjacent habitat types. But in the plots where natural enemies, namely flying enemies as syrphid flies and parasitoids, were allowed to prey on aphids ("C" and "–G"), the adjacent habitat type became important for aphid population growth. Wheat fields bordering sown flower strips and sown flower fields experienced the lowest increase in aphid population growth, showing a non-significant trend with respect to this main effect. Furthermore, aphid population growth was significantly related to the interaction between parasitism rate or predator-prey ratio and the adjacent habitat type, i.e. reduced aphid population growth was significantly attributed to increased predator-prey ratios and parasitism rates in wheat fields neighbouring sown flower strips and sown flower fields.

Both, sown flower strips and sown flower fields appeared to support a more abundant natural enemy community, compared to naturally developed grassy field margin strips, resulting in a stronger aphid control in adjacent winter wheat fields (see Hausammann, 1996, and Denys & Tscharntke, 2002, with similar results). Total abundance of flying aphid enemies in winter wheat fields was significantly enhanced in case of neighbouring flowering habitats ($F_{3,18} = 3.056, P = 0.055$). We found higher syrphid fly larvae and mummified aphid densities adjacent to sown flower strips and sown flower fields in contrast to wheat-wheat boundaries and grassy field margin strips. This supports findings showing the attractiveness of flowers for aphid natural enemies using nectar-resources (Frank, 1999; Pfiffner & Wyss, 2004; Lavandero *et al.*, 2006). Adjacent field margin strips, dominated by grasses, did not attract more syrphid flies and parasitoids than the wheat-wheat boundaries. Thus, flower habitats attracting syrphid flies and parasitoids appeared to provide higher predator-prey ratios and parasitism rates that strongly decreased aphid population growth. Our expectation that area (of flower habitat) is positively related to density (of flying insects) (Steffan-Dewenter & Tscharntke, 2000) could not be supported. The smaller flower strips promoted only slightly fewer numbers of parasitoids as the larger flower fields and even slightly higher numbers of syrphid fly larvae. These effects were measured 2 m distant from the adjacent habitats. We expect that these impacts translate further into the field (Salveter, 1998; Frank, 1999; Thies & Tscharntke, 1999; Pfiffner *et al.*, 2009), but future studies should expand experiments on a larger distance.

Our results are in line with results of studies from other countries and crops. For example, in New Zealand border planting with *Phacelia tanacetifolia* Benth. enhanced syrphid flies, which accounted for decreased aphid populations in cabbage fields (White *et al.*, 1995), and significantly enhanced parasitism rates were found in wheat fields bordered by buckwheat (*Fagoyprum esculentum* Moench) patches (Tylianakis *et al.*, 2004). Buckwheat borders and wildflower strips also provided higher parasitism rates of lepidopteran cabbage pests shown by studies in the US (buckwheat: Lee & Heimpel, 2005) and in Switzerland (wildflower strips: Pfiffner *et al.*, 2003; Pfiffner *et al.*, 2009). In addition, parasitoids released against the European corn borer persisted in wildflower strips and thus were abundant in the following year to colonize maize fields (Kuske *et al.*, 2003). Vegetable crops, such as potatoes, also profited from flower plantings next to the crop by augmented parasitism of the potato moth (Baggen & Gurr, 1998). Strip cropping with flowering plants also appears to be a favourable mean to enhance natural enemies (Zhao *et al.*, 1992; Vidal, 1997; Jones & Gillet, 2005) as well as parasitoid mass releases, which are applied successfully to control pests (Levie *et al.*, 2005). But especially the last measure is related to high efforts and costs, whereas bordering fields with flower strips is at present more cost-efficient (Levie *et al.*, 2005).

The effect of sown flower strips and sown flower fields on aphid population growth in the wheat fields was significant for predator-prey ratio and parasitism rate and thereby confirmed our hypotheses that (i) the natural enemy exclusion treatment increases aphid population growth and (ii) the nectar and pollen feeding specialist aphid enemies exert a stronger impact than the ground-dwelling generalist predators. The proportion of lower aphid population growth in the presence of ground-dwelling predators was not significant. However, both enemy groups appeared to act complementary and provided the highest level of aphid control (supporting Sunderland & Samu, 2000; Schmidt *et al.*, 2003; but see Holland *et al.*, 2008), although the contribution of ground-dwelling predators to aphid suppression was of minor importance (supporting results of Holland & Thomas, 1997; Snyder & Wise, 1999; Holland *et al.*, 2008; but not Lang *et al.*, 1999; Symondson *et al.*, 2002; Schmidt *et al.* 2004, Costamagna *et al.*, 2007).

The effect of the flying predator and parasitoid exclusion (“–F” and “–G–F”) on aphid populations could be attributed to syrphid fly larvae and parasitoids, because these two were the only flying natural enemies that were abundant during our experiment. The wire cages were highly effective in preventing these aphid enemies from entering the plots. They showed strongly reduced densities inside the cages compared to open plots (“C” and “–G”). Slightly higher densities of both flying natural enemy groups in the “–G”-plots suggest possible intraguild predation effects by ground-dwelling predators in the open control plots where those had access to and could feed on larvae as well as on mummified aphids (Wheeler *et al.*, 1968; Rosenheim *et al.*, 1995; Lang, 2003; Jonsson *et al.*, 2008; Straub *et al.*, 2008). Ferguson & Stiling (1996) could show a lesser influence of parasitoids on aphids in the presence of predators such as ladybird beetles which negatively interacted with the parasitoids. However, in our study this appeared to be quantitatively less important and did not result in disrupted biological control (Snyder & Ives, 2001; similar to the results of Schmidt *et al.*, 2003), as aphids were reduced most effectively in the open control plots where the entire natural enemy community was present. Our findings follow the results of Schmidt *et al.* (2003) who highlighted the importance of flying predators and parasitoids on cereal aphid control. With our results we expand these findings by the enhancement of flying predators and parasitoids through the agri-environment scheme of sown flower habitats. Besides, we show that this enhancement is consistent along the gradient of varying landscape complexity.

High proportions of (semi-) natural habitats in complex landscapes support diverse and abundant communities of beneficial arthropods (Duelli & Obrist, 2003; Pfiffner & Wyss, 2004; Bianchi *et al.*, 2006). Therefore we hypothesized local management effects to be more pronounced in intermediate landscapes, because in complex landscapes the overall high benefits of natural habitats may not be increased by local manipulations (Östman *et al.*, 2001; Tscharntke *et al.*, 2005), and simple landscapes were not expected to provide stable source populations benefiting from these practices. In contrast to our hypothesis, landscape context did not affect natural enemy density or biological aphid control (figures on the variability of landscape effects are shown for aphids, natural enemies and trophic interactions in Appendix A3 in Supporting Information), maybe because of just seven landscape replicates. Studies from the same study region that found significant landscape effects on aphids and natural enemies included almost double numbers of replicates (e.g. Roschewitz *et al.*, 2005b: 12 landscape replicates; Rand & Tscharntke, 2007: 14 landscape replicates). Although these studies took place in the same region in Lower Saxony, not exactly the same landscape sectors were used and populations of cereal aphids and their natural enemies are known to greatly fluctuate between years (e.g. Thies *et al.*, 2005).

In addition, specific characteristics of the surrounding landscape such as the availability of certain habitats (habitat type diversity) or certain habitat configurations (habitat isolation) might have superposed the expected effects of the landscape context (Andren, 1994). Our results support the findings of Vollhardt *et al.* (2008), who found aphid parasitoids to be in simple landscapes as species rich as in complex landscapes, but are in contrast to other work with evidence for the great importance of landscape context for local manipulation, e.g. introducing organic farming practices, with effects only in simple landscapes (e.g. Roschewitz *et al.*, 2005a; Holzschuh *et al.*, 2007). Similar densities of syrphid fly larvae over the entire landscape gradient may have been due to aggregation effects in cleared landscapes. Adult syrphid flies follow the concentrations of floral resources provided by the flower habitats (Sutherland *et al.*, 2001; Haenke *et al.,* 2009; Jauker *et al.*, 2009) and cross large distances thereby connecting isolated habitats and cereal fields (Krause & Poehling, 1996;

Meyer *et al.*, 2009). The sown flower habitats may therefore importantly compensate for the little flower availability (shown by Steffan-Dewenter *et al.*, 2002) in simple landscapes. In addition, syrphid flies select young aphid colonies as oviposition sites and neglect large, older colonies that stagnate in population growth (Kan, 1988; Hemptinne *et al.*, 1993). Hence, the behaviour of individual syrphid flies may also have contributed to the suppression of aphid population growth in the range of flower strips. Crowding (numerical response) and individual behaviour (functional response) shape the effectiveness of biological control (Landis *et al.*, 2000; Symondson *et al.*, 2002; Holland *et al.*, 2008) at the landscape level. Such large-scale trophic interactions are not well understood, and therefore are a matter of future research.

During this study the infestation rate of 2.5 aphids per shoot was below the economic threshold level of 5 aphids per shoot (Giller *et al.*, 1995) and in the lower range of the densities found in other studies in our region (0.1 – 13.7 aphids per shoot; Thies *et al.*, 2005). As aphid densities are known to underlie strong interannual variations, further investigations need to include years of severe aphid outbreaks to test for consistent effects of sown flower strips and fields.

Conclusions

The sown flower strips and flower fields used in this study were actually created to cope with the needs and to enhance populations of the grey partridge (*Perdix perdix*, see www.rebhuhnschutzprojekt.de). Our results show that flower habitats due to an agri-environment scheme with purpose to promote partridge populations can be also of benefit in terms of biological control (see also Olson & Wäckers, 2007).

The implementation of flowers in the agricultural landscape has been proven to encourage beneficial arthropods and thus to promote multiple ecosystem services as pollination and biological control (Pontin *et al.*, 2006; Isaacs *et al.*, 2009). Several studies document positive impacts of wildflower strips and flower abundance on pollinators such as bumblebees and wild bees (Pywell *et al.*, 2006; Carvell *et al.*, 2007; Holzschuh *et al.*, 2007; Westphal *et al.*, 2009) as well as on natural enemies (Frank, 1999; Pfiffner & Wyss, 2004; Heimpel & Jervis, 2005).

Creating flower habitats appears to be a promising tool of agri-environment schemes for conservation biological control, as flower strips in our study provided stronger aphid control than other crop-neighbouring habitats. Parasitoids and flying predators in the range of flower habitats were most important in the control of cereal aphids, but ground-dwelling predators also contributed to pest suppression. The landscape configuration did not modify the beneficial effects of flower habitats. “Flower power” enhancing biological control across different landscapes should be more implemented as a major management tool. Research on the relative role of local and landscape scales driving predator-prey interactions can contribute to a better understanding how to best manage resource subsidies for natural enemies in the cultural landscape.

Acknowledgements

We thank Eckhard Gottschalk and the Partridge Conservation Project (http://www.rebhuhnschutzprojekt.de) for collaboration, the farmers participating in this research project, and Eike Horn for help with field work. Many thanks go to Ines Vollhardt for helpful discussions and to Christoph Scherber for statistical advice. We also thank Jane Memmott, David Kleijn and three anonymous reviewers for valuable comments on an earlier version of the manuscript. Financial support came from the German Ministry of Research and Education (BMBF) and the German Science Foundation (DFG).

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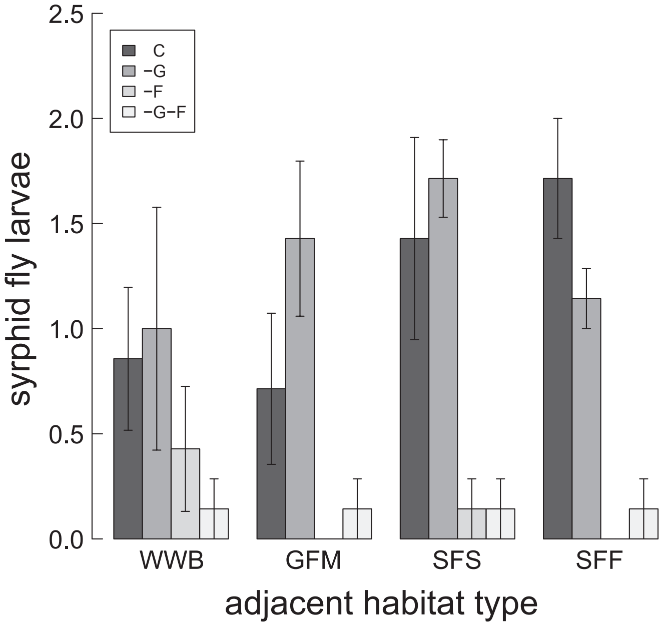
Appendix

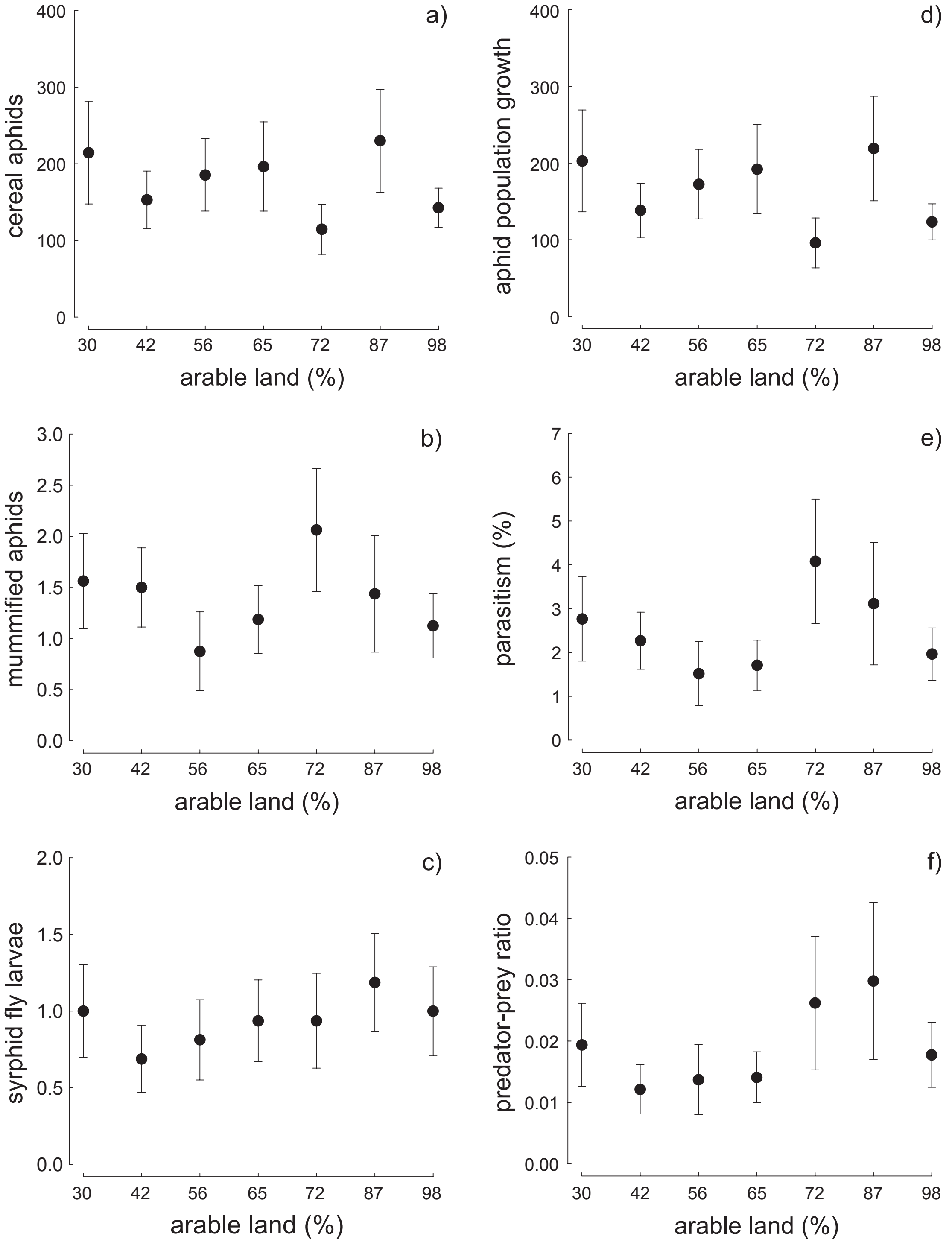
Appendix A1: Seed mixture of sown horticultural and wildflower plant species of the flower habitats for the grey partridge (*Perdix perdix*)

per cent by seed weight	species	horticultural (h)/wildflower (w)
30	*Linum usitatissimum* L.	h
10	*Helianthus annuus* L.	h
10	*Fagopyrum esculentum* Moench	h
6	*Lepidium sativum* L.	h
5	*Medicago sativa* L.	h
5	*Nigella sativa* L.	h
5	*Borago officinalis* L.	h
3	*Phacelia tanacetifolia* Benth.	h
3	*Raphanus sativus* L.	h
3	*Pisum sativum* L.	h
2	*Brassica oleracea* L.	h
1	*Sinapis alba* L.	h
1	*Foeniculum vulgare* Mill.	h
5	*Papaver rhoeas* L.	w
2.5	*Calendula arvensis* L.	w
2	*Leucanthemum vulgare* Lam.	w
1	*Isatis tinctoria* L.	w
1	*Pastinaca sativa* L.	w
1	*Carum carvi* L.	w
0.5	*Melilotus alba* Medic.	w
0.5	*Melilotus officinalis* (L.) Pall..	w
0.5	*Campanula rapunculoides* L.	w
0.5	*Hypericum perforatum* L.	w
0.5	*Cichorium intybus* L.	w
0.5	*Anthriscus sylvestris* (L.) Hoffm.	w
0.5	*Tanacetum vulgare* L.	w

Appendix A2: Abundances of syrphid fly larvae per 25 shoots at wheat flowering (n = 112). Natural enemy exclusion treatments are nested within adjacent habitat types. WWB = wheat-wheat boundaries; GFM = grassy field margin strips; SFS = sown flower strips; SFF = sown flower fields. “C” = open controls; “–G” = ground-dwelling predator exclusion; “–F” = flying predator and parasitoid exclusion; “–G–F” = combined exclusion of all predators and parasitoids. All bars represent untransformed means ± SE.



Appendix A3: Variability of response variables across 7 landscape sectors of a 1000 m–radius covering a gradient of varying proportions of arable land (30 – 98%) within the landscape sectors. Estimates per 25 shoots at wheat milk-ripening stage in winter wheat fields, averaged over the 4 adjacent habitat types (wheat-wheat boundaries; grassy field margin strips; sown flower strips; sown flower fields) and over 4 exclusion treatments (open controls; ground-dwelling predator exclusion; flying predator and parasitoid exclusion; combined exclusion of all predators and parasitoids) (each point *n* = 16). Points represent untransformed means ± SE.
(a) cereal aphids; (b) parasitoids (= mummified aphids); (c) syrphid fly larvae; (d) aphid population growth; (e) parasitism (%); (f) predator-prey ratio.



CHAPTER

3

INCREASING SYRPHID FLY DIVERSITY AND DENSITY IN SOWN FLOWER STRIPS WITHIN SIMPLE VS. COMPLEX LANDSCAPES

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in: *Journal of Applied Ecology* 2009, 46: 1106 – 1114.

doi: 10.1111/j.1365-2664.2009.01685.x

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Summary

1. The structural complexity of agricultural landscapes influences the local biodiversity and associated ecosystem services. Hence, developing effective biodiversity management requires a better understanding of the relative importance of local and landscape changes, especially for functionally important organisms such as hoverflies benefiting from flowering plants.
2. We examined hoverfly (Diptera: Syrphidae) communities in broad and narrow sown flower strips, in naturally developed grassy strips and in wheat fields (as a control). We also investigated the effects of these four habitat types on syrphid occurrence in the adjacent wheat fields.
3. The relative influence of local *vs*. landscape effects was tested by selecting study sites along a gradient of structural complexity from simple landscapes (~100% arable land) to complex landscapes (up to 70% semi-natural habitats such as fallows, field margins, hedges and grassland). Landscape complexity was assessed within landscape sectors of 0.5 – 4.0 km radius around strips.
4. Syrphid density and in particular, the density of aphidophagous species, was higher in narrow and broad sown flower strips compared to grassy strips and wheat–wheat boundary controls at the milk-ripening stage of the wheat. In addition, species richness of aphidophagous syrphids within wheat fields adjacent to broad sown flower strips was higher at the wheat peak-ripening stage. This indicates a spillover between habitats and a positive effect of these sown flower strips on potential biocontrol of cereal aphids. Flower densities and syrphid diversity and density, respectively, were closely related.
5. Species richness and abundance in the sown flower strips increased as the proportion of arable land in the surrounding landscape increased, suggesting that within structurally simple landscapes (at 0.5 – 1 km radius around the sites) syrphid flies concentrated on the most rewarding resources within the sown flower strips. Sown flower strips were more effective at increasing syrphid species richness and abundance in simple landscapes, presumably because the creation of flower resources made the greatest difference in such homogeneous, intensively managed arable landscapes.
6. Synthesis and applications: Agri-environment schemes should take the surrounding landscape characteristics into account when considering using sown flower strips to enhance syrphid density and diversity, and their biocontrol function, in arable landscapes. Creating locally such flower strips is more effective in simple landscapes containing a

high proportion of arable land, while in complex landscapes, keeping the overall diversity is important.

Keywords

agricultural intensification, biocontrol, concentration effects, flower strips, landscape complexity, semi-natural habitats, syrphids

Introduction

The loss and fragmentation of semi-natural habitats in modern agricultural landscapes leads to a reduction in species richness and abundance. This decrease in biodiversity may affect important ecosystem services such as biological control (Saunders *et al.*, 1991; Tews *et al.*, 2004). Habitat management that changes agricultural practices within crop fields, or the management of agricultural landscapes, such as natural habitat conservation, have been shown to mitigate the effects of agricultural intensification (Altieri, 1995; Burel & Baudry, 1995; van Driesche & Bellows, 1996; Matson *et al.*, 1997; Menalled *et al.*, 1999; Thies & Tscharntke, 1999; Tscharntke & Kruess, 1999; Tscharntke, 2000; Halaj & Wise, 2001; Östman *et al.*, 2001; van Nouhuys & Hanski, 2002; Tscharntke *et al.*, 2002; Wratten & van Emden, 1995). Field margins of various forms are found adjacent to arable fields (Marshall, 1988). In landscapes dominated by agriculture such ecotones may represent most semi-natural habitats (Bazin & Schmutz, 1994; Burel & Baudry, 1999). At the local scale, the introduction of sown flower strips and weed strips increases habitat diversity and numbers of both ground-dwelling and flying predators and parasitoids, thereby improving biological pest control (Lys & Nentwig, 1992; Salveter & Nentwig, 1993; Frank, 1999; Thies & Tscharntke, 1999). Improving habitat diversity at the landscape scale also enhances local biodiversity and such ‘matrix effects’ may be important for many groups of beneficial arthropods (Burel *et al.*, 1998; Weibull *et al.*, 2000; Atauri & de Lucio, 2001; Jeanneret *et al.*, 2003; Clough *et al.*, 2005; Schmidt *et al.*, 2005; Schweiger *et al.*, 2005; Thies *et al.*, 2005; Tscharntke *et al.*, 2005). However, different species/groups respond to landscape complexity at different spatial scales. For example, arable spider species show contrasting responses to landscape-scale modification with respect both to the direction and the spatial scale of the relationship (Schmidt *et al.*, 2008). The species richness of carabid beetles was shown to increase with percentage cover of grassland in the surrounding landscape, and activity density followed the same trend (Purtauf *et al*., 2005). Undisturbed perennial habitats appeared to enhance both cereal aphid pests and aphid parasitoids (Thies *et al*., 2005). Hence, the landscape matrix appears to be related to local patterns of diversity, selecting for species traits such as dispersal ability (Tscharntke & Brandl, 2004). The relative importance of natural enemy groups in the biological control of cereal aphids is little understood, but flying predators and parasitoids have been shown to be most effective in selective exclusion experiments (Schmidt *et al*., 2003; Holland *et al*., 2008). However, the relative abundance of naturally occurring enemy species differs greatly among years and regions (Krause & Poehling, 1996; Östman *et al*., 2001; Schmidt *et al*., 2003; Thies *et al*., 2005). Syrphid flies (Diptera Syrphidae) are a species-rich group involving over 500 phytophagous, saprophagous and zoophagous species in Europe (van Veen, 2004). The natural habitats of these functional groups are related to the availability of larval food resources. Aphidophagous species, which represent the dominant group, use a wide range of habitat types including arable fields harbouring aphid pests, whereas phytophagous and saprophagous species predominantly are restricted to non-crop habitats because of their specific food resource requirements (Raskin *et al.*, 1992; Frank, 1999). The adults of all functional syrphid groups feed on pollen and nectar of flowering plants. Therefore, they are expected to benefit from flowering plants, e.g. flower rich field margins (Chambers & Aikman, 1988; Cowgill *et al.*, 1992; Hickman & Wratten, 1996). The role of aphidophagous syrphid species in suppressing cereal aphid outbreaks and methods of increasing the population size through local and landscape diversification has been reported in previous studies (Chambers & Adams, 1986; Chambers *et al*., 1986; Tenhumberg & Poehling, 1995; Schmidt *et al*., 2003; Brewer & Elliott, 2004). However, the influence of, and the interaction between, local and landscape scale diversity on syrphid populations is little known, because most studies have been conducted at one scale only. In this study, we analysed the relative importance of local and landscape structural diversity on syrphid fly species richness and abundance by comparing four types of ecotone habitats adjacent to winter wheat fields occurring across a gradient of landscape complexity (~30 – 100% arable land): broad sown flower strips (BFS), narrow sown flower strips (NFS), naturally developed grassy strips (GS) and the boundary of adjoining wheat fields lacking such strips (as a control). Syrphids are an interesting group for the study of effects of agricultural intensification as they are very mobile compared with many other insect groups; and therefore, may contribute to the preservation of ecosystem services such as biocontrol and pollination in intensified agricultural landscapes (Jauker *et al*., 2009). We expected that

(i) species richness and abundance of syrphids would be increased in flower strips compared with naturally developed field margins and wheat fields and that (ii) this effect would be more pronounced in structurally simple landscapes compared with complex landscapes (hypothesized by Tscharntke *et al*., 2005).

Materials and methods

Study area and study design

The study was conducted in the vicinity of the city of Göttingen (51°54’N, 9°93’E), Lower Saxony (North Germany). The area is under intensive agricultural use (ca. 75%) dominated by arable fields and interspersed with fragments of semi-natural habitats such as forests, hedges and grasslands (Steffan-Dewenter *et al*., 2002). The average temperature and total rainfall during the study period in June and July 2006 was 17.9°C and 0 mm (20 – 23 June), 20.9°C and 44.6 mm (11 – 14 July) and 22.3°C and 11.1 mm (27 – 28 July); data from the Meteorological Station, Göttingen. We analysed syrphid species richness and abundance in five types of habitats: GS (ca. 3 m wide, $n = 7$); NFS (ca. 3 – 6 m wide, $n = 7$); BFS (ca. 12 – 25 m wide, $n = 7$); the boundary of adjoining wheat fields lacking such strips (as a control and which we refer to as wheat–wheat boundary, $n = 7$); and within the wheat fields adjacent to each of the preceding habitats ($n = 4 \times 7 = 28$). Agri-environmental schemes in Lower Saxony include incentives for the creation of NFS and BFS in the agricultural landscapes. For this study, we selected strips adjacent to wheat fields that were located along a gradient of surrounding landscape complexity, ranging from ca. 30% to 100% arable land, with a mean distance of 18.3 km between study fields. We measured the proportion of arable land in circular sectors at four spatial scales (radii of 0.5, 1, 2 and 4 km) around each study site using official digital thematic maps (ATKIS–Digitales Landschaftsmodell 25⁄1; Landschaftsvermessung und Geobasisinformation, Hannover, Germany 1991 – 1996) and the Geographical Information System ArcView 3.1 (ESRI Geoinformatik GmbH, Hannover, Germany). The proportion of arable land has been shown to be a simple predictor of landscape complexity in our study area because of its close correlation with other landscape metrics such as habitat type diversity and habitat isolation (Thies & Tscharntke, 1999; Steffan-Dewenter *et al*., 2002).

Sampling of syrphid flies

Syrphids were captured along 100 m transects by sweep netting (ca. one sweep per footstep) (i) within the strip habitats and (ii) within the adjacent winter wheat field along a transect parallel to the strips (6 m distance to strips) and at a distance of 6 m from the edge of the strip habitat. The wheat–wheat controls were sampled in a similar way along transects running directly along the boundary between the two fields (within 3 m of the boundary at both sides). Sampling was carried out at three consecutive periods: (i) at wheat flowering stage (20 – 23 June); (ii) at wheat milk-ripening stage (11 – 14 July); and (iii) at winter wheat peak-ripening stage (27 – 28 July). All invertebrates collected were placed in 3 liter plastic bags, cooled, and then taken to the laboratory. The syrphid species were separated from all other arthropod genera and identified, where possible, to species level using identification keys (van Veen, 2004). Species were sorted into two trophic groups according to their larval feeding type: aphidophagous feeding type and saprophagous, detrivourous and bacteria eating feeding type (a list of species is available in Appendix A1, Supporting Information).

Flower densities in ecotones

Flower density in each of the 28 habitats was measured, at the same time as syrphids were sampled using a standardized estimation procedure for each strip. Flowers within the conventional managed wheat fields were almost absent, so flower density was around zero. A ring with an area of ca. 0.75 m^2 was placed on the ground 10 times per strip at 10 m–intervals per habitat at the same locations used for the syrphid samplings. The number of flowers of all flowering plants was counted and the flower density was calculated for an area of 1 m^2. Plants were identified up to species level using Rothmaler (1994) (a list of plant species is available in Appendix A2, Supporting Information).

Statistical analyses

We analysed syrphid species richness and abundance (per 100 m transect) using general linear models (GLM) to test the influence of (i) habitat type (NFS, BFS, GS and control fields) nested in site; (ii) site (wheat field vs. adjacent habitat); and (iii) landscape complexity (the proportion of arable land at four spatial scales, 0.5 – 4 km radius of landscape sector). Model assumptions were tested by examining the Gaussian distribution of the residuals. All non-significant main effects and interactions were removed from the models by using a backwards selection procedure using Statistica, Version 6 for Windows (StatSoft, Inc. 2003).

Rarefaction methods using R 2.8.0 were used to consider any effects on syrphid sampling success of sampling in different habitat types featuring different vegetation structures. However, the species richness from field samples and the species richness resulting from rarefaction curves, rescaled by the number of individuals, was highly correlated ($P < 0.001$). Therefore, the analyses were conducted using the original field data. Data on syrphid densities and quantities of flowers were log-transformed to compensate for the skewness and/or kurtosis of the data. These models were performed separately for each of the three sampling dates and each of four spatial scales (0.5 – 4 km radius) of landscape complexity. To test for differences between habitat types post hoc Tukey highest significant differences tests (with $P < 0.05$ as level of significance) were performed. In addition, we compared regression lines relating total species richness and the abundance of the most abundant syrphid species, *Episyrphus balteatus*, to the proportion of arable land, distinguishing between wheat-fields and adjacent strip habitats. Moreover, species richness and abundance of syrphids were related to the number of flowers per square metre using simple regression models. In the text, arithmetic means ± standard errors are given.

Results

A total of 20 syrphid species and 829 individuals were collected during the three sampling periods. They averaged 1.7 ± 2.0 species and 5.2 ± 11.0 individuals per 100 m transect. The community was dominated by aphidophagous species (1.3 ± 1.5) and individuals (4.2 ± 9.8), followed by syrphids with other larval feeding types such as saprophagous, detrivorous and bacteria-eating, phytophagous and fungivorous species (0.37 ± 0.91) and (0.92 ± 3.60) individuals. The abundance of these trophic groups during the three sampling periods is given in Appendix A3, Supporting Information.

EFFECTS OF SOWN FLOWER STRIPS

Total species richness and abundance differed between sampling dates, and was highest at the wheat milk-ripening stage. Total richness and abundance increased from wheat–wheat boundaries (control; without any strip) through GS to NFS and BFS (Fig. 1). Total species richness and abundance was generally higher within field margin strips compared with adjacent wheat fields (black and white bars in Fig. 1) giving a highly significant site effect

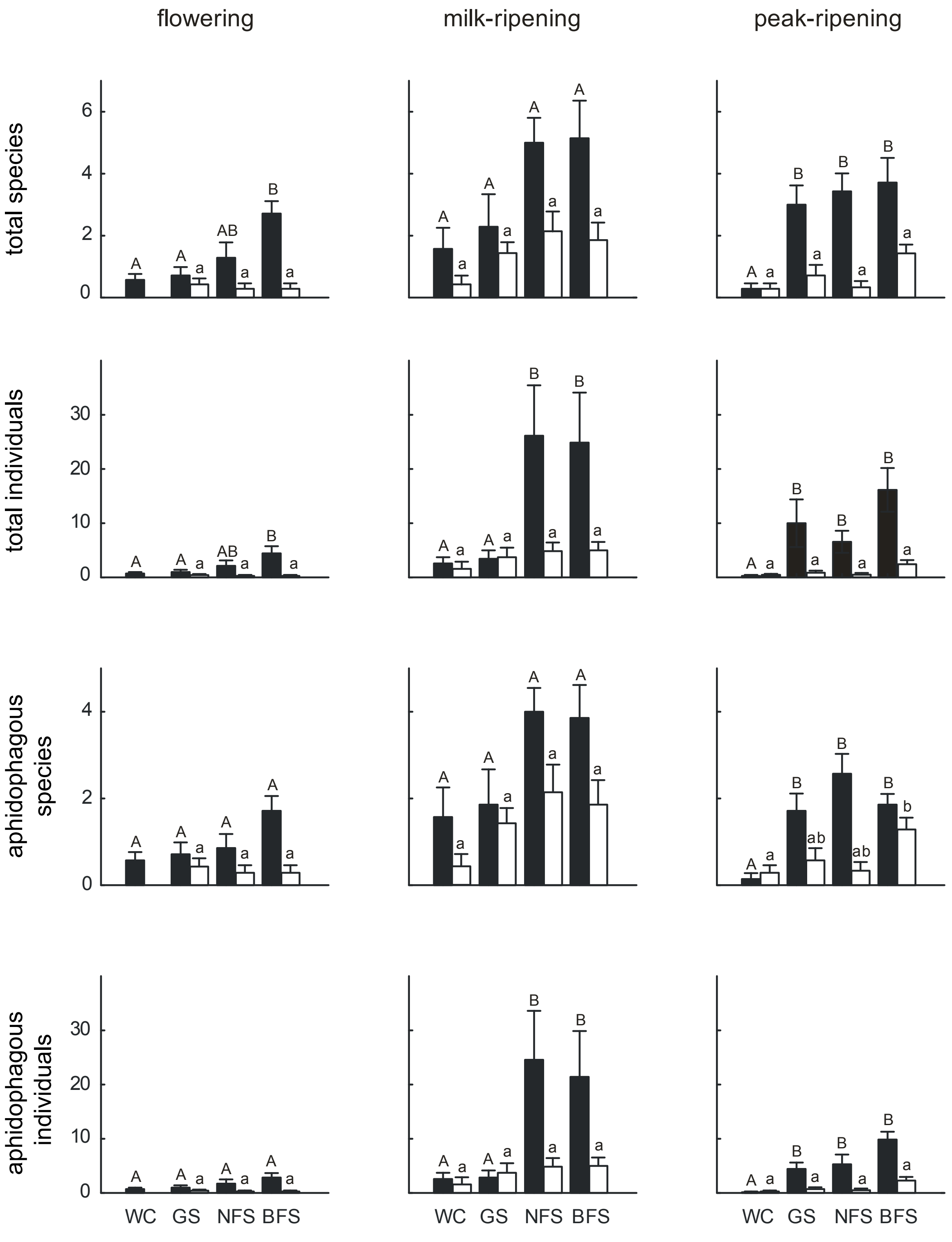

Fig. 1: Total species number and total individual number of syrphids as well as total aphidophagous species number and individual number of aphidophagous syrphids for three consecutive sampling dates at wheat flowering, wheat milk-ripening and wheat peak-ripening (mean numbers and standard deviation is given). Dissimilar capital letters above black bars show significant differences between habitats adjacent to wheat fields, which are grassy strips (GS), narrow flower strips (NFS), broad flower strips (BFS) and wheat-wheat boundary (WC). Dissimilar lower case letters above white bars show significant differences between wheat fields adjacent to the four strip types.

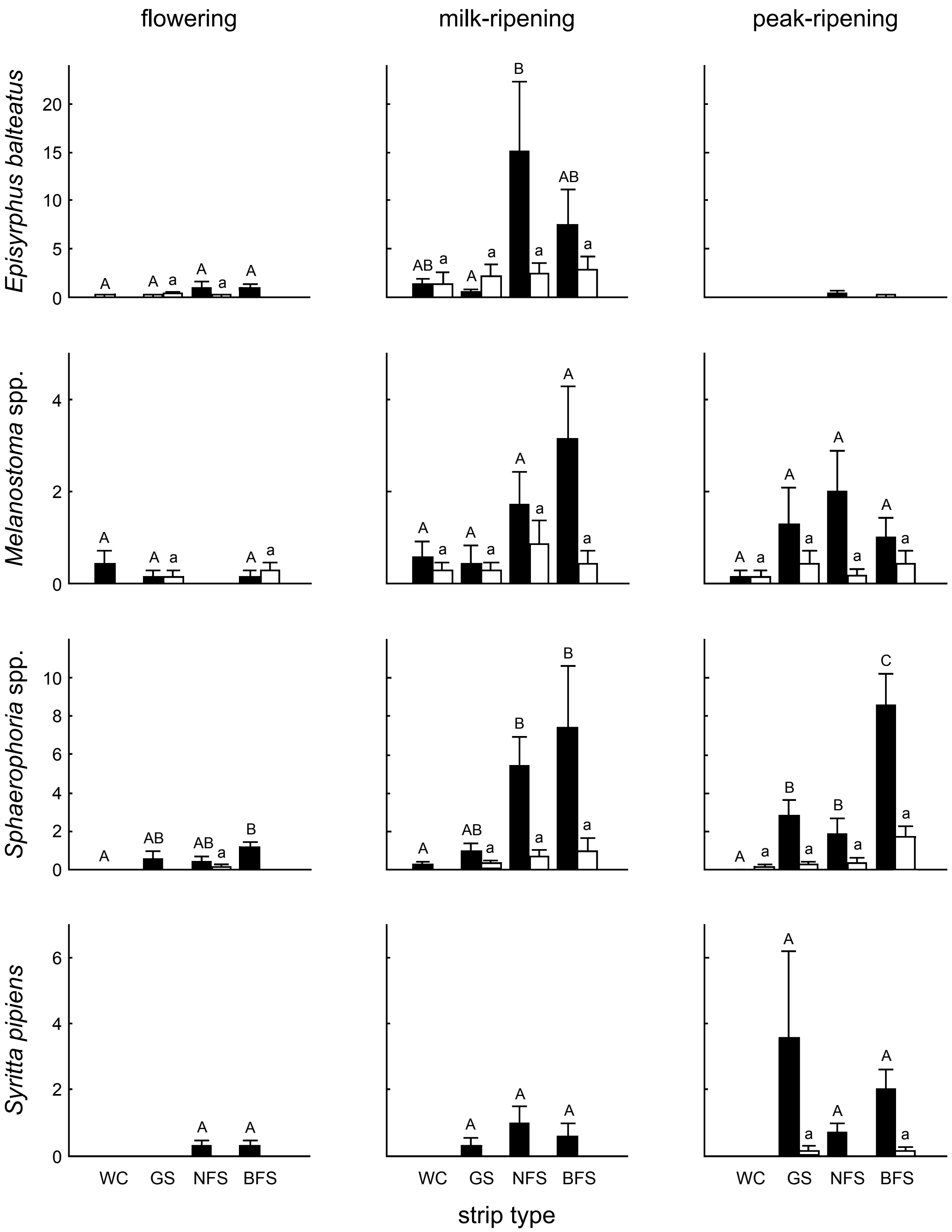

Fig. 2: Total number of individuals of *Episyrphus balteatus*, *Melanostoma* spp., *Sphaerophoria* spp. and *Syritta pipiens* for three consecutive sampling dates at wheat flowering, wheat milk-ripening and wheat peak-ripening (mean number and standard deviation is given). Dissimilar capital letters above black bars show significant differences among habitats adjacent to wheat fields, which are grassy strips (GS), narrow flower strips (NFS), and broad flower strips (BFS) and wheat-wheat boundary (WC). Dissimilar lower case letters above white bars show significant differences between wheat fields adjacent to the four strip types.

Table 1: *F*-values and levels of significance from general linear models relating syrphid densities to three predictive factors: (i) percentage of arable land per landscape sector, (ii) site, which indicates the dichotomy between strip habitats and adjacent wheat fields, and (iii) habitat type nested in site at wheat flowering, wheat milk-ripening and at wheat peak-ripening at 0.5 - 4 km scale (radius of landscape sector). Note that the percentage of arable land was positively correlated with total species richness, total number of individuals, total number of apphidophagous species, total number of individuals and *Episyrphus balteatus*, whereas it was negatively correlated with numbers of *Syritta pipiens*.

	wheat flowering				wheat milk-ripening				wheat peak-ripening			
					radius of landscape sector (km)							
	0.5	1	2	4	0.5	1	2	4	0.5	1	2	4
total species												
arable land %	n.s.	n.s.	n.s.	n.s.	6.0*	7.1*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
site	17.2***	17.2***	17.2***	17.2***	9.1**	9.3**	8.3**	8.3**	37.6***	37.6***	37.6***	37.6***
habitat type (site)	3.8**	3.8**	3.8**	3.8**	3.7**	3.3**	3.0*	3.0*	9.6***	9.6***	9.6***	9.6***
model	6.1***	6.1***	6.1***	6.1***	4.3***	4.6***	3.7**	3.7**	13.5***	13.5***	13.5***	13.5***
total individuals												
arable land %	n.s.	n.s.	n.s.	n.s.	8.0**	7.9**	n.s.	n·s.	n.s.	n.s.	n.s.	n.s.
site	17.6***	17.6***	17.6***	17.6***	8.6**	8.6**	7.5**	7.5**	47.6***	47.6***	47.6***	47.6***
habitat type (site)	3.2**	3.2**	3.2**	3.2**	5.3***	4.6***	4.0**	4.0**	11.4***	11.4***	11.4***	11.4***
model	5.7***	5.7***	5.7***	5.7***	5.5***	5.5***	4.5***	4.5***	16.5***	16.5***	16.5***	16.5***
aphidophagous species												
arable land %	n.s.	n.s.	n.s.	n.s.	6.1*	6.5*	n.s	n.s.	n.s.	n.s.	n.s.	n.s.
site	8.7**	8.7**	8.7**	8.7**	6.6*	6.6*	5.9*	5.9*	21.2***	21.2***	21.2***	21.2***
habitat type (site)	n.s.	n.s.	n.s.	n.s.	3.4**	2.9*	2.6*	2.6*	9.5***	9.5***	9.5***	9.5***
model	8.7**	8.7**	8.7**	8.7**	3.8**	3.8**	3.1**	3.1**	11.1***	11.1***	11.1***	11.1***
aphidophagous individuals												
arable land %	n.s.	n.s.	n.s.	n.s.	8.3**	7.7**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
site	12.2**	12.2**	12.2**	12.2**	7.5**	7.5**	6.5*	6.5*	36.2***	36.2***	36.2***	36.2***
habitat type (site)	n.s.	n.s.	n.s.	n.s.	5.2***	4.5**	4.0**	4.0**	12.0***	12.0***	12.0***	12.0***
model	12.2**	12.2**	12.2**	12.2**	5.4***	5.3***	4.3***	4.3***	15.3***	15.3***	15.3***	15.3***
Episyrphus balteatus												
arable land %	n.s.	n.s.	n.s.	n.s.	18.8***	18.3***	9.7**	9.3**	n.s.	n.s.	n.s.	n.s.
site	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
habitat type (site)	n.s.	n.s.	n.s.	n.s.	3.5**	2.8*	2.4*	2.3*	n.s.	n.s.	n.s.	n.s.
model	n.s.	n.s.	n.s.	n.s.	4.8***	4.7***	3.3**	3.2**	n.s.	n.s.	n.s.	n.s.
Melanostoma spp.												
arable land %	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
site	n.s.	n.s.	n.s.	n.s.	4.1*	4.1*	4.1*	4.1*	5.3*	5.3*	5.3*	5.3*
habitat type (site)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
model	n.s.	n.s.	n.s.	n.s.	4.1*	4.1*	4.1*	4.1*	5.3*	5.3*	5.3*	5.3*
Sphaerophoria spp.												
arable land %	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
site	7.7**	7.7**	7.7**	7.7**	14.4***	14.4***	14·4***	14·4***	29.8***	29.8***	29.8***	29.8***
habitat type (site)	2.8*	2.8*	2.8*	2.8*	3.9**	3.9**	3.9**	3.9**	13.4***	13.4***	13.4***	13.4***
model	3.6**	3.6**	3.6**	3.6**	5.4***	5.4***	5.4***	5.4***	15.6***	15.6***	15.6***	15.6***
Syritta pipiens												
arable land %	n.s.	n.s.	6.1**	6.6**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
site	n.s.	n.s.	n.s.	n.s.	6.7*	6.7*	6.7*	6.7*	10.5**	10.5**	10.5**	10.5**
habitat type (site)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
model	n.s.	n.s.	6.1**	6.6**	6.7*	6.7*	6.7*	6.7*	10.5**	10.5**	10.5**	10.5**

***$P < 0.001$; **$P < 0.01$; *$P < 0.05$

(Table 1). Strip type did not affect total species richness and abundance within adjacent wheat fields. Aphidophagous species richness and abundance showed a similar pattern (Fig. 1, Appendix A1, Supporting Information), but at wheat peak-ripening aphidophagous species richness was significantly higher in wheat fields adjacent to BFS (Fig. 1). The four most abundant syrphid species, the aphidophagous *Episyrphus balteatus*, *Melanostoma* spp. and *Sphaerophoria* spp. and the saprophagous *Syritta pipiens* were analysed separately. The abundance of *E. balteatus* was highest at wheat milk-ripening and was significantly higher in BFS and NFS compared with wheat–wheat boundaries and GS (Fig. 2). The abundance of *Melanostoma* spp. increased from wheat flowering to wheat milk-ripening, and did not respond to strip types on any sampling date (Fig. 2). The abundance of *Sphaerophoria* spp. strongly increased from wheat flowering to wheat milk-ripening and was higher in BFS at wheat flowering; within NFS and BFS at wheat milk-ripening; and within BFS and NFS and

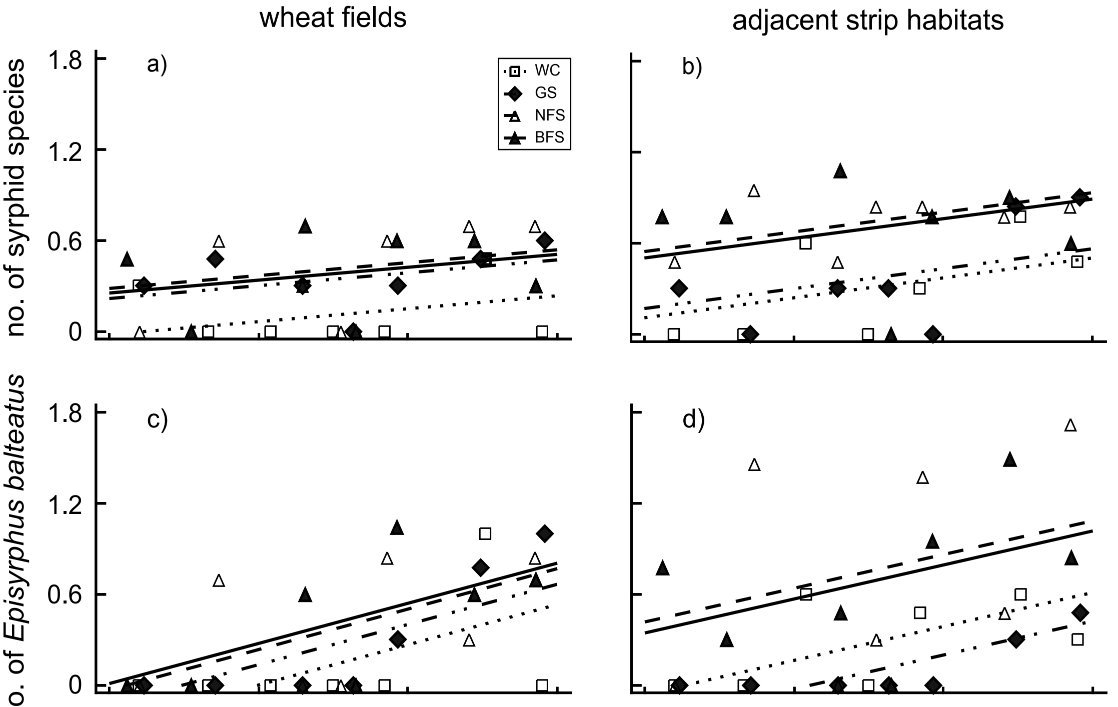

Fig. 3: Total number of syrphid species (no. of syrphid species) and number of *Episyrphus balteatus* (no. of *Episyrphus balteatus*) in relation to the proportion of arable land (%) at 1 km radius at wheat milk-ripening. Regressions are separated for each type of adjacent strip habitat (WC= wheat-wheat control [blank squares], GS= grassy strip [black squares], NFS = narrow flower strip [blank triangles], BFS= broad flower strip [black triangles]). All *F*-ratios and *P*-levels describe differences between intercepts of the regression lines. (a) No. of syrphid species within wheat fields (*F*-ratio = 2.17, $P = 0.119$; N = 28), (b) No. of syrphid species within adjacent strip habitats (*F*-ratio = 4.06, $P = 0.019$; N = 28). (c) no. of Episyrphus balteatus within wheat fields (*F*-ratio: 0.97, $P = 0.4218$; N = 28), (d) no. of *Episyrphus balteatus* within adjacent strip habitats (*F*-ratio = 3.81, $P = 0.024$; N = 28).

GS at wheat peak-ripening (Fig. 2). The abundance of *Syritta pipiens* also increased from wheat flowering to wheat milk-ripening, with no effects of the availability of strip habitats adjacent to wheat fields (Fig. 2).

Effects of landscape complexity

At wheat milk-ripening stage, total species richness and abundance, and aphidophagous species richness and abundance, correlated positively with the proportion of arable land in adjacent strip habitats occurring within a radius of 0.5 – 1 km centred on the location of the sites, but not with the proportion of arable land occurring within larger spatial scales (Table 1, Fig. 3). At wheat milk-ripening the abundance of *E. balteatus* correlated positively with the proportion of arable land in adjacent strip habitats occurring within a radius of 0.5 – 4 km centred on the location of the sites (Table 1, Fig. 3). The abundance of *Melanostoma* spp. and *Sphaerophoria* spp. did not respond to the proportion of arable land at any spatial scale (Table 1). The abundance of *Syritta pipiens* correlated negatively with the proportion of arable land at spatial scales of 2 – 4 km at wheat flowering stage (Table 1).

Importance of flower resources

Total species richness and abundance as well as aphidophagous species richness and abundance, and species richness and abundance of all other larval feeding types together, were positively correlated with flower densities for each of the three sampling periods, this being strongest at wheat peak-ripening (Fig. 4; statistics in Appendix A4, Supporting Information).

Discussion

Both narrow and broad flower strips enhanced syrphid densities and particularly the density of aphidophagous species in comparison to grassy strips and wheat–wheat boundaries at the wheat milk-ripening stage. In addition, species richness of aphidophagous syrphids was higher in wheat fields adjacent to broad at wheat peak-ripening stage (when flower density was highest in the strips), indicating a potential spillover across habitats and a positive effect of the broad strips on the potential biocontrol of cereal aphids. Moreover, the number of species and individuals was higher in strips occurring in structurally simple as

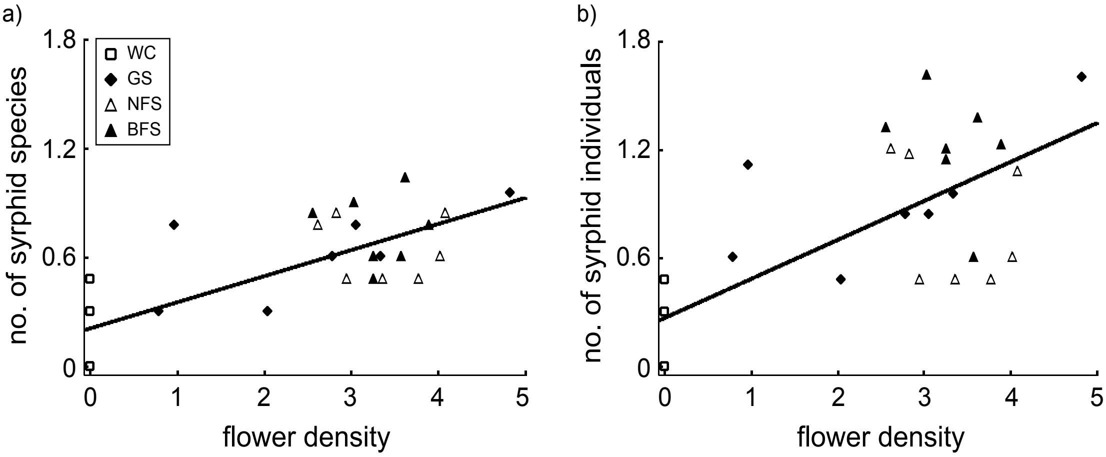

Fig. 4: Flower density in relation to syrphid numbers, (a) total number of syrphid species (no. of syrphid species; $F = 33.0$, $P = 0.000$, N = 28) and (b) total number of syrphid individuals (no. of syrphid individuals; $F = 24.6$, $P = 0.000$, N = 18) in relation to flower densities per square metre at wheat peak-ripening (see Supporting Inofrmation, Appendix A4 for additional results on the relation of number of species and individuals of total syrphids, aphidophagous syrphids, and all non-aphidophagous syrphids and flower densites at three consecutive dates). Different symbols are indicating the affiliation of the results to a certain strip habitat (WC= wheat-wheat control [blank squares], GS= grassy strip [black squares], NFS= narrow flower strip [blank triangles], BFS= broad flower strip [black triangles]).

opposed to complex landscapes. This appeared to be as a result of concentration of syrphids in flower strips occurring within structurally simple, intensively managed arable landscapes. This concentration effect was strongest at smaller spatial scales, i.e. within a radius of 0.5 – 1 km of the study sites. Aphidophagous syrphids represented the dominant group in all habitat types (similar to the results found by Raskin *et al.*, 1992, and Frank, 1999), whereas the non-aphidophagous larval feeding types were only found in non-crop habitats, which may be related to better food-resource availability in such habitats. Aphidophagous syrphid densities increased from wheat flowering to wheat milk-ripening and then decreased to wheat peak-ripening stage. These temporal changes of aphidophagous syrphids appeared to be associated with the development of aphid colonies within wheat fields, which usually reach their maximum at wheat milk-ripening stage and then collapse suddenly (Rabbinge *et al.*, 1979). Syrphids appeared to have profited from the high availability of nectar and pollen resources in sown flower habitats supporting previous findings that flowering weeds attract hoverflies (Schneider, 1948; Gilbert, 1981; Weiss & Stettmer, 1991; Salveter & Nentwig, 1993; Bianchi *et al.*, 2006). The patch size of flower resources (narrow *vs.* broad sown strips) did not influence syrphid abundance. This is in contrast to expectations from area-density effects (Steffan-Dewenter & Tscharntke, 2000), and suggests that narrow sown flower strips may provide sufficient amounts of pollen and nectar for adult syrphids (Sutherland *et al.*, 2001). Syrphids were hypothesized to profit from a high proportion of semi-natural habitats in structurally complex landscapes, following the patterns exhibited by other pollen and nectar feeding insects in the agricultural landscape (Jonsen & Fahrig, 1997; Steffan-Dewenter & Tscharntke, 1999; Steffan-Dewenter *et al.*, 2002; Weibull *et al.*, 2003). However, we found higher densities of syrphids with an increasing proportion of arable land. This result probably reflects crowding effects on flower resources that are rare in structurally simple landscapes. Such crowding of natural enemies in response to local concentrations of flower resources is little known, but can be expected to exert a high influence on local biodiversity and food web interactions (Thies *et al.*, 2008). Therefore, the opportunistic resource use of syrphids in combination with their high dispersal ability may (temporally) connect isolated habitats in intensified agricultural landscapes. For example, the dominant species, *E. balteatus*, is known to exhibit high mobility with high dispersal rates (Krause & Poehling, 1996; Lundberg & Moberg, 2003; Rand *et al.,* 2006; Hondelmann & Poehling, 2007). This pattern resembles the situation where social honey bees concentrate in flower patches in simple landscapes based on an opportunistic exploitation of resources at large spatial scales (Steffan-Dewenter *et al.*, 2002). These findings have consequences for the implementation of agri-environment measures for syrphid flies. In complex landscapes, the effects of sown flower strips are hardly visible, whereas in simple landscapes, they are most effective. These results support the general idea that promoting landscape heterogeneity might be economically more efficient in simple landscapes (Roschewitz *et al.*, 2005; Tscharntke *et al.*, 2005; Holzschuh *et al.*, 2007). The species richness and abundance of both total and aphidophagous syrphid species responded to the landscape context at the smallest spatial scales of 0.5 – 1 km (radius of landscape sector). This result is surprising given the fact that syrphids are highly vagile organisms with excellent vision abilities (Bernard & Stavenga, 1979; Lunau & Wacht, 1994) easily detecting remote resource patches in monotonous, non-nutritious environments. However, the findings of Harwood *et al.* (1994) suggest that hoverflies are less likely to cross areas with breaks in vegetation ground cover. Furthermore, only small landscape sectors may be expected to become ecologically effective for the concentration effect on patchy resources such as the flower strips. At larger spatial scales these small patches may become increasingly less attractive. An alternative explanation may be that landscapes become more similar when larger sectors are considered, thereby reducing potential explanatory power. However, previous results in the same landscapes showed that bumblebees experienced their surrounding landscape at different spatial scales dependent on their body sizes (from 100 to 3000 m radius, Westphal *et al.*, 2006). Similarly, honey bees responded to landscape resources at spatial scales of 3000 m radius, while solitary bees respond to at scales of just 500 m radius (Steffan-Dewenter *et al.*, 2002). These studies provide evidence that these spatial scales (radii from 500 to 4000 m) are biologically meaningful.

Conclusion

Agriculture is a major land-use type in Europe, and the maintenance of biodiversity in agroecosystems is of great importance for ecosystem functioning (Foley *et al*., 2005; Tscharntke *et al*., 2005). Our results show that sown flower strips in agricultural landscapes can enhance the diversity and abundance of syrphid flies, with the potential to improve the biological control of aphid pests. Sown flower strips are therefore an element of current, mainly locally orientated, agri-environmental schemes. However, our results showed that the local importance of sown flower strips is mediated by landscape context. The concentration of syrphid species and individuals in structurally simple landscapes supports the idea that agri-environmental measures are most effective in structurally simple landscapes, with spillover of aphidophagous species from sown flower strips to adjacent wheat fields. Understanding how landscape composition affects the efficiency of environmental measures is important for the optimization of agri-environment schemes, including the value of sown flower strip habitats as sources of beneficial arthropods.

Acknowledgements

Financial support was provided by the BIOLOG research program of the German Federal Ministry of Education and Research (BMBF, http://www.uni-giessen.de/bioplex) and the German Research Foundation (DFG). We gratefully acknowledge the helpful comments of Davy McCracken and all reviewers.

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Appendix

Appendix A1: Syrphid species: mean and standard deviation for three consecutive dates: (i) wheat flowering (wf), (ii) wheat milk-ripening (wmr) and (iii) wheat peak-ripening (wpr).

species	mean ±SD wf	mean ±SD wmr	mean ±SD wpr
Cheilosia spec. [b] (Antiqua G.)	0.000 ± 0.000	0.000 ± 0.000	0.018 ± 0.134
Cheilosia spec. [b] (Bergenstammi G.)	0.107 ± 0.679	0.304 ± 1.747	0.054 ± 0.227
Cheilosia spec. [b] (Canicularis G.)	0.000 ± 0.000	0.018 ± 0.134	0.000 ± 0.000
Episyrphus balteatus [a] (Degeer) 1776	0.304 ± 0.851	4.018 ± 9.114	0.054 ± 0.297
Eristalis abusiva [c] (Collin) 1931	0.018 ± 0.134	0.036 ± 0.267	0.000 ± 0.000
Eristalis abustorum [c] (Linnaeus) 1758	0.018 ± 0.134	0.018 ± 0.134	0.446 ± 2.296
Eristalis jugorum [c] (Egger) 1858	0.000 ± 0.000	0.054 ± 0.227	0.018 ± 0.134
Eristalis pertinax [c] (Scopoli) 1763	0.000 ± 0.000	0.018 ± 0.134	0.000 ± 0.000
Eristalis tenax [c] (Linnaeus) 1758	0.018 ± 0.134	0.000 ± 0.000	0.339 ± 0.920
Eupeodes corollae [a] (Fabricius) 1794	0.125 ± 0.470	0.232 ± 0.687	0.000 ± 0.000
Eupeodes latifasciatus [a] (Macquart) 1829	0.000 ± 0.000	0.018 ± 0.134	0.000 ± 0.000
Helophilus trivittatus [c] (Fabricius) 1805	0.018 ± 0.134	0.018 ± 0.134	0.000 ± 0.000
Melanostoma mellinum [a] (Linnaeus) 1758	0.000 ± 0.000	0.250 ± 0.796	0.000 ± 0.000
Melanostoma scalare [a] (Fabricius) 1794	0.000 ± 0.000	0.268 ± 0.820	0.000 ± 0.000
Melanostoma spec [a] (Schiner) 1860	0.125 ± 0.334	0.893 ± 1.723	0.679 ± 1.390
Platycheirus albimanus [a] (Fabricius) 1781	0.000 ± 0.000	0.018 ± 0.134	0.000 ± 0.000
Platycheirus angustatus [a] (Zetterstedt) 1843	0.000 ± 0.000	0.018 ± 0.134	0.036 ± 0.187
Platycheirus clypeatus [a] (Meigen) 1822	0.000 ± 0.000	0.089 ± 0.345	0.089 ± 0.438
Platycheirus europaeus [a] (Goeldlin, Maibach & Speight) 1990	0.000 ± 0.000	0.018 ± 0.134	0.000 ± 0.000
Platycheirus fluviventris [a] (Macquart) 1829	0.000 ± 0.000	0.000 ± 0.000	0.018 ± 0.134
Platycheirus spec. [a] (Lepeletier & Serville) 1828	0.018 ± 0.134	0.232 ± 0.539	0.054 ± 0.227
Sphaerophoria spec. [a] (Lepeletier & Serville) 1828	0.286 ± 0.680	2.000 ± 4.260	1.964 ± 3.330
Syritta pipiens [b] (Linnaeus) 1758	0.071 ± 0.260	0.232 ± 0.738	0.821 ± 2.797
Syrphus ribesii [a] (Linnaeus) 1758	0.000 ± 0.000	0.054 ± 0.297	0.000 ± 0.000
Syrphus vittripennis [a] (Meigen) 1822	0.018 ± 0.134	0.018 ± 0.134	0.018 ± 0.134
Xanthogramma laetum [a] (Fabricius) 1794	0.018 ± 0.134	0.000 ± 0.000	0.000 ± 0.000

[a] aphidophagous; [b] saprophagous; [c] detrivorus and bacteria-eating

Appendix A2: Plant species recorded during transect walks at wheat flowering (wf), wheat milk-ripening (wmr) and wheat peak-ripening (wpr).

species	mean ± SD wf	mean ± SD wmr	mean ± SD wpr
Achillea millefolium [b] L. (Asteraceae)	0.097 ± 0.496	0.229 ± 0.826	0.346 ± 1.099
Anchusa officinalis [b] L. (Boraginaceae)	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
Anthriscus sylvestris [a] L. (Apiaceae)	0.213 ± 0.840	0.366 ± 1.033	0.761 ± 1.389
Borago officinalis [a] L. (Boraginaceae)	0.000 ± 0.000	0.241 ± 0.470	0.177 ± 0.390
Brassica oleracea [a] L. (Brassicaceae)	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
Calendula arvensis [a] L. (Asteraceae)	0.000 ± 0.000	0.040 ± 0.167	0.000 ± 0.000
Campanula rapunculoides [a] L. (Campanulaceae)	0.000 ± 0.000	0.000 ± 0.000	0.147 ± 0.452
Carum carvi [a] L. (Apiaceae)	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
Centaurea cyanus [b] L. (Asteraceae)	0.000 ± 0.000	0.019 ± 0.099	0.000 ± 0.000
Chrysanthemum leucanthemum [a] L.(Asteraceae)	0.747 ± 1.081	0.396 ± 0.654	0.164 ± 0.381
Cichorium intybus [a] L. (Cichorioidae)	0.000 ± 0.000	0.079 ± 0.285	0.000 ± 0.000
Cirsum arvense [b] L. (Asteraceae)	0.033 ± 0.166	0.404 ± 0.698	0.753 ± 0.814
Convolvulus arvensis [b] L. (Convolvulaceae)	0.009 ± 0.048	0.278 ± 0.621	0.000 ± 0.000
Daucus carota [b] L. (Apiaceae)	0.000 ± 0.000	0.155 ± 0.803	0.000 ± 0.000
Epilobium spp. [b] L. (Onagraceae)	0.135 ± 0.688	0.187 ± 0.409	0.000 ± 0.000
Fagopyrum esculentum [a] MOENCH (Polygonaceae)	0.000 ± 0.000	0.055 ± 0.287	0.000 ± 0.000
Foeniculum vulgare [a] MILL. (Apiaceae)	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
Galium aparine [b] L. (Rubiaceae)	0.103 ± 0.362	0.000 ± 0.000	0.000 ± 0.000
Galium spp. [b] L. (Rubiaceae)	0.061 ± 0.311	0.000 ± 0.000	0.000 ± 0.000
Geranium dissectum [b] L. (Geraniaceae)	0.137 ± 0.396	0.059 ± 0.181	0.000 ± 0.000
Glechoma hederacea [b] L. (Lamiaceae)	0.036 ± 0.182	0.000 ± 0.000	0.000 ± 0.000
Helianthus annuus [a] L. (Asteraceae)	0.000 ± 0.000	0.000 ± 0.000	0.037 ± 0.112
Heracleum sphondylium [b] L. (Apiaceae)	0.000 ± 0.000	0.136 ± 0.707	0.000 ± 0.000
Hypericum perforatum [a] L. (Hypericaceae)	0.033 ± 0.166	0.155 ± 0.358	0.264 ± 0.490
Isatias tinctoria [a] L. (Brassicaceae)	0.051 ± 0.260	0.000 ± 0.000	0.000 ± 0.000
Lamium album [b] L. (Lamiaceae)	0.090 ± 0.258	0.057 ± 0.295	0.077 ± 0.305
Lepidium sativum [a] L. (Brassicaceae)	1.336 ± 1.649	0.306 ± 0.782	0.000 ± 0.000
Linum usitatissimum [a] L. (Linaceae)	0.000 ± 0.000	0.078 ± 0.293	0.014 ± 0.075
Lotus corniculatus [b] L. (Fabaceae)	0.041 ± 0.208	0.354 ± 1.027	0.000 ± 0.000
Matricaria recutita [b] L. (Asteraceae)	0.348 ± 0.726	0.489 ± 0.896	0.434 ± 0.753
Matricaria spp. [b] L. (Asteraceae)	0.000 ± 0.000	0.184 ± 0.474	0.000 ± 0.000
Medicago lupulina [b] L. (Fabaceae)	0.332 ± 0.940	0.000 ± 0.000	0.000 ± 0.000
Medicago sativa [a] L. (Fabaceae)	0.000 ± 0.000	0.059 ± 0.305	0.076 ±0.403
Meliotus albus [a] MED. (Fabaceae)	0.148 ± 0.586	0.563 ± 1.216	0.872 ± 1.551
Meliotus officinalis [a] L. (Fabaceae)	0.098 ± 0.502	0.802 ± 1.292	0.703 ± 1.334
Myosotis arvensis [b] L. (Boraginaceae)	0.568 ± 0.993	0.300 ± 0.744	0.000 ± 0.000
Nigella sativa [a] L. (Ranunculaceae)	0.000 ± 0.000	0.059 ± 0.305	0.000 ± 0.000

[a] sown crop and wild plants (seed mixture); [b] not contained in the seed mixture. *(continued)*

Appendix A2: Plant species recorded during transect walks at wheat flowering (wf), wheat milk-ripening (wmr) and wheat peak-ripening (wpr). *(continued)*

species	mean ± SD wf	mean ± SD wmr	mean ± SD wpr
Papaver rhoeas [a] L. (Papaveraceae)	0.084 ± 0.199	0.209 ± 0.337	0.142 ± 0.329
Pastinaca sativa [a] L. (Apiaceae)	0.000 ± 0.000	0.076 ± 0.397	0.000 ± 0.000
Phacelia tanacetifolia [a] BENTH. (Hydrophyllaceae)	0.982 ± 1.493	1.063 ± 1.456	0.450 ± 0.887
Pisum sativum [a] L. (Fabaceae)	0.000 ± 0.000	0.100 ± 0.332	0.022 ± 0.114
Plantago lanceolata [b] L. (Plataginaceae)	0.000 ± 0.000	0.036 ± 0.186	0.000 ± 0.000
Ranunculus spp. [b] L. (Ranunculaceae)	0.079 ± 0.305	0.009 ± 0.047	0.000 ± 0.000
Raphanus sativus [a] L. (Brassicaceae)	0.646 ± 1.037	0.769 ± 1.126	0.343 ± 0.709
Sinapis alba [a] L. (Brassicaceae)	0.980 ± 1.241	0.462 ± 0.901	0.212 ± 0.563
Stellaria spp. [b] L. (Caryophyllaceae)	0.153 ± 0.564	0.089 ± 0.332	0.000 ± 0.000
Tanacetum vulgare [a] L. (Asteraceae)	0.000 ± 0.000	0.443 ± 0.872	0.698 ± 1.135
Trifolium pratense [b] L. (Fabaceae)	0.000 ± 0.000	0.064 ± 0.331	0.000 ± 0.000
Trifolium repens [b] L. (Fabaceae)	0.049 ± 0.144	0.296 ± 0.577	0.106 ± 0.321
Veronica persica [b] POIR. (Scrophulariaceae)	0.079 ± 0.288	0.000 ± 0.000	0.000 ± 0.000
Vicia spp. [b] L. (Fabaceae)	0.191 ± 0.707	0.076 ± 0.395	0.000 ± 0.000
Viola spp. [b] L. (Violaceae)	0.055 ± 0.214	0.000 ± 0.000	0.000 ± 0.000

[a] sown crop and wild plants (seed mixture); [b] not contained in the seed mixture.

Appendix A3: Mean numbers, minima and maxima of species and individuals for (i) total syrphids, (ii) aphidophagous syrphids and (iii) syrphids with other feeding types at three consecutive dates. Mean numbers and standard deviation is given.

	mean + SE	min	max
wheat flowering			
number of all species	0.898 ± 1.160	0	4
number of all individuals	1.327 ± 0.321	0	12
number of aphidophagous species	0.694 ± 0.114	0	3
number of aphidophagous individuals	1.041 ± 0.220	0	7
number of species (other larval feeding type)	0.204 ± 0.077	0	2
number of individuals (other larval feeding type)	0.286 ± 0.124	0	5
wheat milk-ripening			
number of all species	2.482 ± 0.340	0	11
number of all individuals	9.018 ± 2.114	0	75
number of aphidophagous species	2.143 ± 0.260	0	6
number of aphidophagous individuals	8.321 ± 1.959	0	72
number of species (other larval feeding type)	0.339 ± 0.126	0	6
number of individuals (other larval feeding type)	0.696 ± 0.354	0	19
wheat peak-ripening			
number of all species	1.673 ± 0.249	0	7
number of all individuals	4.709 ± 1.092	0	39
number of aphidophagous species	1.109 ± 1.153	0	4
number of aphidophagous individuals	2.982 ± 0.554	0	14
number of species (other larval feeding type)	0.564 ± 0.151	0	5
number of individuals (other larval feeding type)	1.727 ± 0.734	0	30

Appendix A4: Blossom densities per square metre in relation to species richness and abundance of (i) total syrphids, (ii) aphidophagous syrphids and (iii) syrphids with other larval feeding type.

	function	*F*	*P*	r
total syrphids				
wheat flowering				
no. of individuals	Y = 0.09 X + 0.23	9.4	0.005	0.516
no. of species	Y = 0.07 X + 0.21	9.8	0.004	0.524
wheat milk-ripening				
no. of individuals	Y = 0.18 X + 0.52	7.7	0.010	0.477
no. of species	Y = 0.11 X + 0 40	7.5	0.011	0.473
wheat peak-ripening				
no. of individuals	Y = 0.22 X + 0.27	24.6	0.000	0.697
no. of species	Y = 0.14 X + 0.21	33.8	0.000	0.752
aphidophagous syrphids				
wheat flowering				
no. of individuals	Y = 0.06 X + 0.24	6.2	0.019	0.440
no. of species	Y = 0·04 X + 0.22	4.6	0.042	0.387
wheat milk-ripening				
no. of individuals	Y = 0.17 X + 0.52	7.3	0.012	0.468
no. of species	Y = 0.09 X + 0.40	6.8	0.015	0.445
wheat peak-ripening				
no. of individuals	Y = 0.17 X + 0.25	16.4	0.000	0.622
no. of species	Y = 0.11 X + 0.20	19.2	0.000	0.652
all non-aphidophagous				
wheat flowering				
no. of individuals	Y = 0.06 X - 0.02	8.5	0.007	0.496
no. of species	Y = 0.05 X - 0.02	10.1	0.004	0.529
wheat milk-ripening				
no. of individuals	Y = 0.08 X + 0.01	5.3	0.030	0.410
no. of species	Y = 0.06 X + 0.01	6.1	0.021	0.435
wheat peak-ripening				
no. of individuals	Y = 0.16 X - 0.01	11.8	0.002	0.559
no. of species	Y = 0.10 X + 0.01	12.9	0.001	0.576

CHAPTER

4

WHAT A DIFFERENCE A YEAR MAKES: INTER-ANNUAL VARIABILITY OF CEREAL APHID CONTROL BY FLOWER STRIPS AND LANDSCAPE COMPLEXITY

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(in prep.)

Abstract

Sown flower strips are implemented to promote biodiversity and ecosystem services in agricultural landscapes, but their efficiency may vary in space and time. We simultaneously investigated the effects of local management of sown flower strips and landscape complexity on biological control of cereal aphids by natural enemies and parasitoids in a three year study. The impact of broad sown flower fields and narrow sown flower strips on cereal aphids in adjacent winter wheat fields was compared to grassy field margins and wheat-wheat controls. Both local and landscape factors significantly influenced aphids and natural enemies, with most effective suppression of aphids adjacent to both sown flower habitats, and with pronounced effects in complex landscapes. But these effects were very susceptible to a high inter-annual variability. Especially in a year of low aphid densities, adjacent to sown flower fields and sown flower strips, aphid densities were reduced by 64% and 55%, compared to aphid densities at wheat-wheat boundaries. Strongly increased predator and parasitoid densities adjacent to both sown flower habitats resulted in parasitism rates being 3 to 5 times higher adjacent to flower strips and fields compared to wheat-wheat boundaries and grassy field margins, and predator-prey ratios being 3 to 7 times higher, respectively.

Keywords

conservation biological control; agri-environment scheme; parasitism rate; vegetation-dwelling predators; predator-prey ratio; inter-annual variability

Introduction

Biological control of herbivore pests by natural enemies is an important ecosystem service (e.g. Losey & Vaughan, 2006; Swinton *et al*., 2006; Straub *et al*., 2008; Isaacs *et al*., 2009), and is based upon the potential of naturally occurring predators and parasitoids to control crop pests (Eilenberg *et al*., 2001; Halaj & Wise, 2001; Schmidt *et al*., 2004; Gardiner *et al*., 2009). (Semi-) natural habitats support populations of such beneficial insects (Wyss, 1996; Menalled *et al*., 1999; Frank, 2000; Landis *et al*., 2000; Meek *et al*., 2002; Zurbrugg & Frank, 2006), while simple agricultural landscapes with large fields, few (semi-) natural habitats and little crop-habitat connectivity are expected to support only few beneficial insects (Elliott *et al*., 1998; Bianchi *et al*., 2006; Gardiner *et al*., 2009). The consequences are declining ecosystem services and more insecticide applications against pest infestations (Östman *et al*., 2003; Losey & Vaughan, 2006; Zalucki *et al*., 2009). Effective biological control depends on sufficient numbers of natural enemies, which provide strong top-down regulation of pest populations (Costamagna & Landis, 2007; Griffiths *et al*., 2008; Holland *et al*., 2008, 2009). Therefore it is essential to enhance their abundance and diversity to restore pest regulation, e.g. by habitat management and the implementation of agri-environment schemes (Wyss, 1996; Landis *et al*., 2000; Eilenberg *et al*., 2001; Meek *et al*., 2002; Fiedler *et al*., 2008; Griffiths *et al*., 2008; Gardiner *et al*., 2009). Agri-environment schemes provide incentives for farmers to operate in an environmentally sensitive way (Pfiffner & Luka, 2000; Duelli & Obrist, 2003; Kleijn *et al*., 2006), including management to increase the abundance of non-crop habitats and biodiversity in agricultural landscapes (Kleijn & Sutherland, 2003; Herzog, 2005; Whittingham, 2007; Fiedler *et al*., 2008).

Wildflower strips represent a measure of agri-environment schemes providing pollen and nectar, alternative food and prey, shelter as well as overwintering sites for many insects and the food-webs building on them (Wyss, 1996; Frank, 1999; Nentwig, 2000; Fiedler *et al*., 2008; Griffiths *et al*., 2008), resources which are generally limited in simple agricultural landscapes (Landis *et al*., 2000; Duelli & Obrist, 2003; Isaacs *et al*., 2009). Improving habitat availability and quality, especially by the provision of flowers, they are expected to promote beneficial insect abundance and diversity near crop environments (MacLeod, 1999; Landis *et al*., 2000; Meek *et al*., 2002; Swinton *et al*., 2006, Fiedler *et al*., 2008; Griffiths *et al*., 2008; Holland *et al*., 2009; Isaacs *et al*., 2009). Additionally to these local measures, other studies particularly emphasize the importance of the landscape context for the distribution and abundance of insects and related pest control (Thies & Tscharntke, 1999; Landis *et al*., 2000; Kleijn & Sutherland, 2003; Östman *et al*., 2003; Thies *et al*., 2003; Tscharntke & Brandl, 2004; Bianchi *et al*., 2006; Fiedler *et al*., 2008; Griffiths *et al*., 2008; Isaacs *et al*., 2009), and also for applying habitat management practices like agri-environment schemes (Duelli & Obrist, 2003; Gurr *et al*., 2003; Bianchi *et al*., 2006; Fiedler *et al*., 2008). As (semi-) natural habitats support populations of beneficial insects, complex landscapes are assumed to provide diverse and abundant source populations to recolonize newly established habitats such as wildflower strips (Lee *et al*., 2001; Duelli & Obrist, 2003; Isaacs *et al*., 2009). On the other hand, simple landscapes with restricted habitat diversity and connectivity are expected to suffer from reduced natural enemy diversity and abundance (Tscharntke *et al*., 2005; Isaacs *et al*., 2009).

In this study, we quantified populations of cereal aphids and aphid natural enemies in winter wheat fields in the range of different semi-natural habitats over three years to simultaneously assess the efficiency of agri-environment schemes at local and landscape scales. Large sown flower fields were compared with small sown flower strips to test for size effects (Holt *et al*., 1999; Isaacs *et al*., 2009) and were contrasted to naturally developed grassy field margin strips with respect to their potential biological control. The survey was concentrated on vegetation-dwelling enemies only, because they are expected to be the enemy group mostly attracted by the flowering plants of the flower habitats (Cowgill *et al*., 1993; Hickman & Wratten, 1996; Wyss, 1996; Landis *et al*., 2000; Meek *et al*., 2002; Kleijn & van Langevelde, 2006; Fiedler *et al*., 2008; Isaacs *et al*., 2009), since they depend on pollen and nectar in parts of their life time. The wheat fields featuring these different neighbouring habitats were located in seven different landscape sectors across a gradient of landscape structural complexity ranging from simple to complex. In each landscape we also tested winter wheat fields without any neighbouring semi-natural habitat (“wheat-wheat boundaries”) as controls.

We hypothesized the landscape context to influence insect abundances, with higher aphid densities and lower natural enemy densities in simple landscapes, whereas complex landscapes should support higher numbers of natural enemies and lower numbers of aphids, causing higher predator-prey ratios and parasitism rates, respectively (Landis *et al*., 2000; Duelli & Obrist 2003). We expected flower habitats to promote a more abundant natural enemy community and lower herbivore densities in the adjacent wheat fields than grassy field margins and wheat-wheat boundaries (Meek *et al*., 2002) and hence provide better biological control in terms of higher predator-prey ratio and parasitism rate. Furthermore, we assumed that flower fields provide most efficient ecosystem services, because they offer more resources to beneficial insects than flower strips (Welling & Kokta, 1988). Local influences of the differently managed adjacent habitat types were supposed to become stronger with progression of the study period as flower fields and flower strips should be fully established and colonized by insects over the three years and therefore be able to exert a stronger local impact. Moreover, we assumed an interaction of landscape context and local management in terms of simple landscapes profiting more by the effects of the flower habitats, whereas complex landscapes already should provide more and stable (semi-) natural habitats (Gabriel *et al*., 2005; Roschewitz *et al*., 2005).

Methods

In Germany, economically important pest populations in cereals consist of mainly three cereal aphid species, *Sitobion avenae* F., *Metopolophium dirhodum* Walk. and *Rhopalosiphum padi* L. (Hom., Aphididae). They are attacked by generalist ground-dwelling predators such as carabid beetles, rove beetles and spiders as well as by specialist vegetation-dwelling aphid predators such as the larvae and adults of ladybird beetles, larvae of syrphid flies, gall midges and lacewings and by specialist aphid parasitoids (mainly Aphidiidae). Because we only considered vegetation-dwelling natural enemies, we refer to them as “predators” further on. We examined the abundance of cereal aphids and their predators and parasitoids based on 84 samples distributed in the region around the city of Göttingen (Northern Germany) in three consecutive years from 2005 to 2007 (*n* = 28 plots in each of the three years).

STUDY AREA AND STUDY SITES

The study area is dominated by intensively managed cereal crops with varying proportions of (semi-) natural habitats. Average annual temperature reaches 8.7°C and annual rainfall amounts to 645 mm on average (www.wetterstation-goettingen.de). Mean temperatures did not differ largely between the three years (2005: 9.4°C; 2006: 9.7°C; 2007: 10.1°C), but variations between the study periods from May to July were even stronger, especially in July 2007 temperature was relatively low compared to previous years (Appendix A1). Total rainfall in 2007 highly exceeded the amounts of the two previous years with about one third more rainfall in 2007 than in 2005, and about one fourth more than in 2006, respectively. Particularly May and June had extremely higher amounts of rainfall compared to 2005 and 2006 (Appendix A1). This is the time of aphids' colonization of the fields and of aphid reproduction.

The study sites were situated in conventionally managed winter wheat fields, which were located adjacent to three different habitat types in seven non-overlapping landscape sectors of a 1000 m–radius representing different grades of landscape complexity (Fig. 1). Landscape composition was quantified within this radius around the study sites as the proportion of arable land following the classification of the ATKIS-data ("Amtliches Topographisch-Kartographisches Informationssystem") and revised by hand-mapping in the field during each field season. The landscape sectors covered seven different landscapes from structurally complex (~34% arable land) to structurally simple (up to 95% arable land) along the landscape complexity gradient. We selected a radius of 1000 m based on our experience of a functionally meaningful scale for the insects studied (Thies *et al*., 2005; see also Kleijn & van Langevelde, 2006). In several cases we had to consider different fields across years due to crop rotation, but they remained in the same landscape context.

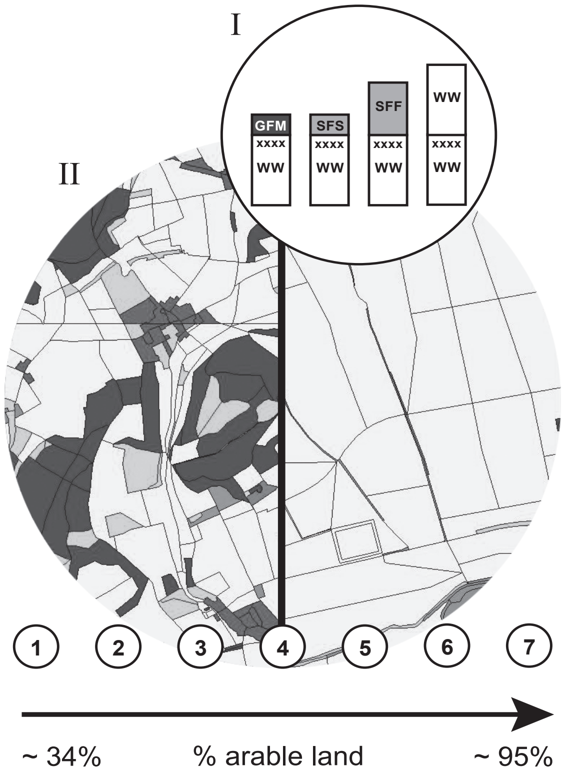

Fig. 1: Schematic drawing of the study design: four winter wheat fields (WW), each with four sampling plots (x) in a distance of 2 m adjacent to three different neighbouring habitat types (GFM: grassy field margins; SFS: sown flower strips; SFF: sown flower fields) and one wheat field control (circle I). Study sites were nested in each of seven landscape sectors of a 1000 m–radius along a gradient of landscape complexity (i.e. % arable land within landscape sector) (circle II). Altogether we studied seven landscapes, 28 (7 × 4) wheat fields over three years (*n* = 84).

In each of the seven landscape sectors, four winter wheat fields with different neighbouring habitat types were grouped in a nested design (Fig. 1). Neighbouring habitat types consisted of i) sown flower fields, ii) sown flower strips and iii) naturally developed grassy field margin strips ("grassy field margins"). Additionally, another winter wheat field without any neighbouring habitat, (iv) the wheat-wheat boundary, was selected as control. Sown flower habitats were established in 2005 and sown with a seed mixture of 13 flowering horticultural and 13 wildflower species with overlapping flower periods throughout the season (for the list of sown plant species, see Appendix A2). Annuals in the seed mixture guaranteed the supply of flowers, nectar and pollen in the first year after sowing. Flower strips and flower fields remained unmanaged all over the years, whereas grassy field margins, consisting of few flowering plants, but mainly of a variety of grasses, were cut once per year. We differentiated between sown flower strips with a similar width of ca. 3 m as the grassy field margins, and sown flower fields with a width of 12 – 25 m to test for size effects.

Insect sampling

Aphids and aphid natural enemies were quantified visually on 4 × 25 shoots in insecticide-free areas in each winter wheat field in a distance of ca. 2 m to the adjacent habitat type (Fig. 1). Counting was done twice a year; first in June at wheat flowering stage (BBCH-scale 65; Lancashire *et al.*, 1991; Meier, 2001) (2005: June 22nd to 23rd; 2006: June 20th to 23rd; 2007: June 14th to 16th), when aphids colonize the fields, and second in July at wheat milk-ripening stage after aphid reproduction (BBCH-scale 75 – 77) (2005: July 11th to 13th; 2006: July 11th to 14th; 2007: July 2nd to 4th). We recorded three cereal aphid species, mummified aphids, indicating the abundance of parasitoids, syrphid fly larvae, larvae of lacewings, gall midges, and ladybird beetles. Due to negligible abundances and irregular distributions, larvae of gall midges and ladybird beetles were not included in statistical analysis. Larvae of syrphid flies and lacewings were pooled as "predators".

Statistical analyses

All statistical analyses and graphics were carried out using the software R 2.9.1 (R Development Core Team 2009; http://www.r-project.org). Predator, parasitoid, and aphid counts were log-transformed; proportion data such as predator-prey ratio (i.e. ratio of numbers of syrphid fly and lacewing larvae to aphids present) and parasitism rates (i.e. ratio of mummies to the sum of aphids and mummies) were arcsine-square root-transformed before all analyses. We fitted linear mixed-effects models ("lme"-function in package "nlme"; Pinheiro & Bates, 2000) using maximum likelihood. The factors "year" (2005, 2006, 2007), "% arable land" (proportion of arable land of each landscape sector) and "adjacent habitat type" (sown flower fields, sown flower strips, grassy field margins, wheat-wheat boundaries) plus their two-way interactions were included as fixed effects.

Because different fields were used in each of the three years (see *2.1. Study sites*), we created a "sector ID"-variable consisting of "landscape sector" and "year" (e.g. "sector 7 – 2005") that was included as a random effect in the model. In addition, "adjacent habitat type" was nested within the "sector ID" random effect. When analysing data separately for each year, the models were fitted accordingly, but only "% arable land" and "adjacent habitat type" were included as fixed effects, and "landscape sector" as the only random effects term. We inspected the residuals for constant variance and normality and used variance functions (Pinheiro & Bates, 2000) to account for heteroscedasticity. Models were then simplified using stepwise backwards model selection based on AIC (Akaike's Information Criterion; "stepAIC"-function, "MASS"-package, Venables & Ripley, 2002; Crawley, 2007). Models were considered minimal adequate when AIC reached a global minimum (Burnham & Anderson, 2002). Multiple comparisons for main effects were performed using Tukey´s all-pair comparisons with *P*-values adjusted by the single-step method ("multcomp"-package, Hsu, 1996). In the text we give arithmetic means ± one SE.

Results

Overview

A total of 23,415 aphids were counted showing a great variability of aphid densities across years (Table 1). High variation was also found between sampling dates within each year, with higher numbers at second sampling date at wheat milk-ripening in July after aphid reproduction (Table 1). Abundances of the three aphid species were also distributed differently over the three years. In 2005 and 2006 *M. dirhodum* was the most abundant aphid species, while being the least abundant species in 2007, when *S. avenae* reached the highest densities, followed by *R. padi*, which was the less abundant in the two other study years (Table 1). Predators and parasitoids also varied considerably between years as well. For parasitoids and syrphid fly larvae, we found highest densities in 2006, whereas lacewing larvae were most abundant in 2005, and larvae of lady bird beetles in 2007, respectively (Table 1). Gall midge larvae were only found in 2006 with just four individuals (Table 1).

Table 1: Densities of three cereal aphid species and their natural enemies (arithmetic means ± SE, minima and maxima of individuals per 100 shoots) (*n* = 84)

		2005				**2006**				**2007**			
	species	∑	$\overline{x}$	±	SE	∑	$\overline{x}$	±	SE	∑	$\overline{x}$	±	SE
aphids	all	14744				8004				667			
	wheat flowering	3141	112.18	±	20.46	1140	40.71	±	7.86	115	4.11	±	0.59
	milk ripening	11603	414.39	±	41.43	6864	245.14	±	18.42	552	19.71	±	2.53
	Sitobion avenae	4899				2672				397			
	wheat flowering	90	3.21	±	2.00	68	2.43	±	1.15	48	1.71	±	0.32
	milk ripening	4809	171.75	±	19.03	2604	93.00	±	10.25	349	12.46	±	1.33
	Metopolophium dirhodum	7899				3100				125			
	wheat flowering	2136	76.29	±	12.17	904	32.29	±	6.75	26	0.93	±	0.15
	milk ripening	5763	205.82	±	27.34	2196	78.43	±	7.81	99	3.54	±	0.67
	Rhopalosiphum padi	1946				2232				145			
	wheat flowering	915	32.68	±	13.52	168	6.00	±	4.38	41	1.46	±	0.28
	milk ripening	1031	36.82	±	17.17	2064	73.71	±	10.38	104	3.71	±	0.28
parasitoids	Aphidiidae	183				308				104			
	wheat flowering	11	0.39	±	0.12	48	1.71	±	0.88	35	1.25	±	0.19
	milk ripening	172	6.14	±	0.85	260	9.29	±	0.92	69	2.46	±	0.32
vegetation-dwelling predators	Syrphidae (larvae)	105				200				110			
	wheat flowering	17	0.61	±	0.16	52	1.86	±	0.56	30	1.07	±	0.23
	milk ripening	88	3.14	±	0.68	148	5.29	±	0.62	80	2.86	±	0.31
	Chrysopidae (larvae)	112				44				29			
	wheat flowering	55	1.96	±	0.45	0	0.00	±	0.00	3	0.11	±	0.06
	milk ripening	57	2.04	±	0.56	44	1.57	±	0.43	26	0.93	±	0.15
	Coccinellidae (larvae)	5				4				34			
	wheat flowering	5	0.18	±	0.12	0	0.00	±	0.00	15	0.54	±	0.12
	milk ripening	0	0.00	±	0.00	4	0.14	±	0.14	19	0.68	±	0.13
	Aphidoletes spp.(larvae)	0				4				0			
	wheat flowering	0	0.00	±	0.00	0	0.00	±	0.00	0	0.00	±	0.00
	milk ripening	0	0.00	±	0.00	4	0.14	±	0.14	0	0.00	±	0.00

THREE YEARS: FIRST SAMPLING DATE - WHEAT FLOWERING

At the first sampling date at wheat flowering, variability of aphid densities between years was very high as was the variability of numbers of parasitoids and predators (Table 2). At this early stage, no effect of adjacent habitat type and of proportion of arable land in the surrounding of the study site was observed, neither for the aphids nor for the natural enemies.

THREE YEARS: SECOND SAMPLING DATE - WHEAT MILK-RIPENING

The strong significant effect of "year" was consistent for aphid densities (Fig. 2a) as well as for numbers of parasitoids and predators on the second sampling date (Table 2). Aphids reached highest numbers in 2005, whereas parasitoids and predators had highest numbers in 2006. All were least abundant in 2007 (Table 1). This high variability between years was also reflected by parasitism rate (Fig. 2b) and predator-prey ratio (Fig. 2c) (Table 2), both being strongest in 2007. Parasitism rate and predator-prey ratio were sensitive to neighbouring habitat type (Table 2). Adjacent to flower fields both reached highest levels, followed by likewise high levels adjacent to flower strips, whereas they were significantly lower adjacent to grassy field margins and at wheat-wheat boundaries (Fig. 3b,c). Aphid populations displayed a contrasting pattern with significantly reduced densities adjacent

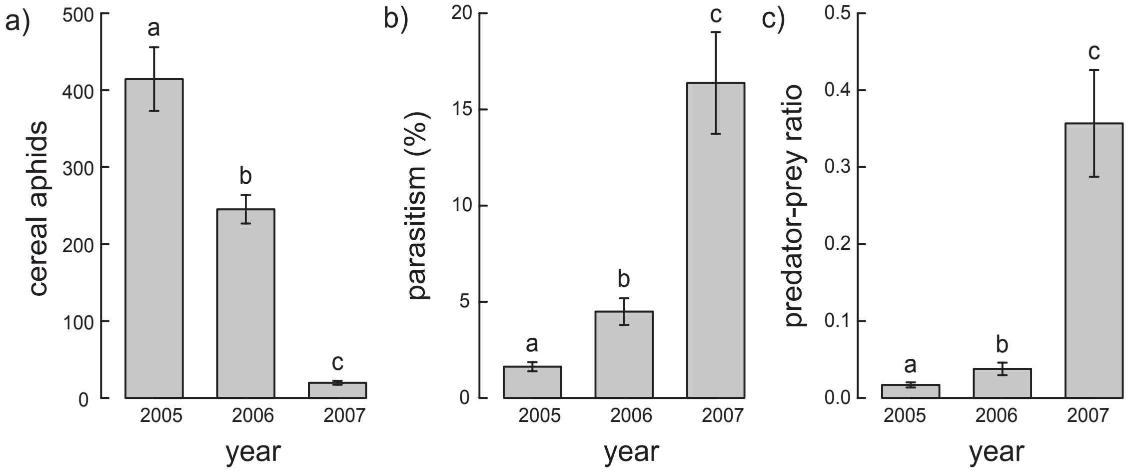

Fig. 2: Inter-annual variability of (a) aphid numbers, (b) percent parasitism, and (c) predator-prey ratio. Estimates per 100 shoots at wheat milk-ripening stage in winter wheat fields averaged over all 7 landscapes and 4 different adjacent habitats (each year *n* = 28). All bars represent untransformed means ± SE. Significant differences between years are indicated by different letters.

Table 2: Results of linear mixed-effects models for aphids and their natural enemies at two sampling dates for three years, describing the effects of study year, the proportion of arable land in each of the seven landscape sectors, and adjacent habitat type (sown flower fields, sown flower strips, grassy field margin strips, wheat-wheat boundaries). NumDF = numerator degrees of freedom, DenDF = denominator degrees of freedom.

3 years	NumDF	DenDF	*F*-value	*P*-value
wheat flowering				
aphids				
year	2	18	71.26	< 0.0001
parasitoids				
year	2	17	3.86	0.0414
predators				
year	2	15	4.17	0.0364
wheat milk-ripening				
aphids				
year	2	15	452.32	< 0.0001
% arable land	1	15	8.15	0.0121
adjacent habitat type	3	54	12.32	< 0.0001
year × % arable land	2	15	13.27	0.0005
year × adjacent habitat type	6	54	2.87	0.0169
parasitoids				
year	2	15	59.69	< 0.0001
adjacent habitat type	3	53	9.14	0.0001
year × adjacent habitat type	6	53	5.94	0.0001
predators				
year	2	17	9.38	0.0018
adjacent habitat type	3	51	5.52	0.0023
year × adjacent habitat type	6	51	3.08	0.0120
parasitism rate				
year	2	15	70.36	< 0.0001
% arable land	1	15	4.50	0.0509
adjacent habitat type	3	54	8.75	0.0001
year × % arable land	2	15	10.00	0.0017
year × adjacent habitat type	6	54	7.41	< 0.0001
predator-prey ratio				
year	2	15	21.04	< 0.0001
% arable land	1	15	12.50	0.0030
adjacent habitat type	3	51	12.70	< 0.0001
year × % arable land	2	15	11.73	0.0009
year × adjacent habitat type	6	51	10.51	< 0.0001

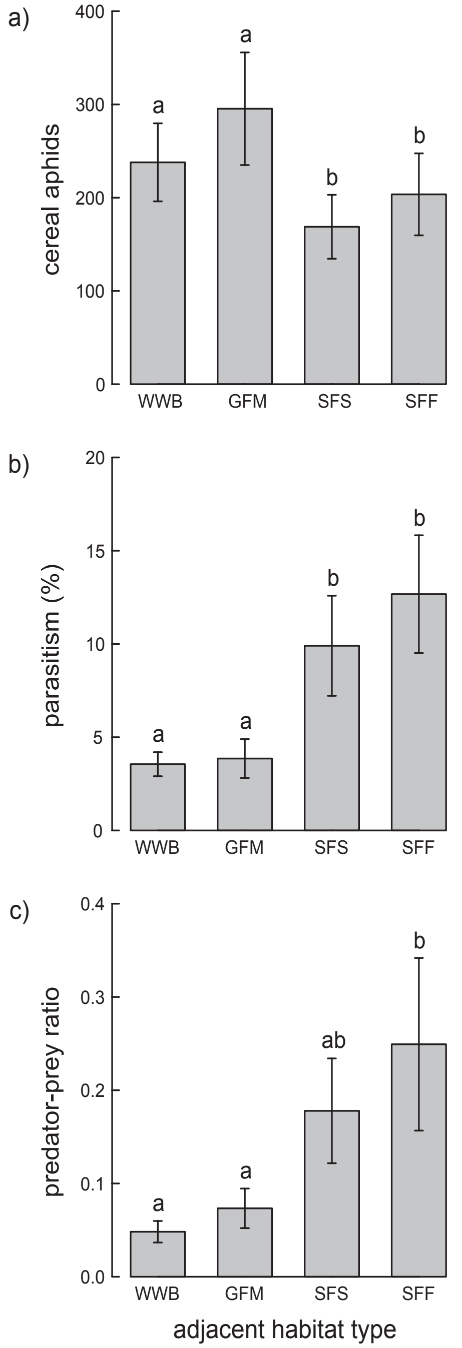

Fig. 3: Effects of wheat-wheat boundaries (WWB), grassy field margin strips (GFM), sown flower strips (SFS), and sown flower fields (SFF) on (a) aphid densities, (b) percent parasitism, and (c) predator-prey ratio. Estimates per 100 shoots at wheat milk-ripening stage in winter wheat fields along the four adjacent habitats, averaged over all 7 landscapes and the 3 years (each adjacent habitat type *n* = 21). All bars represent untransformed means ± SE. Significant differences between habitat types are indicated by different letters.

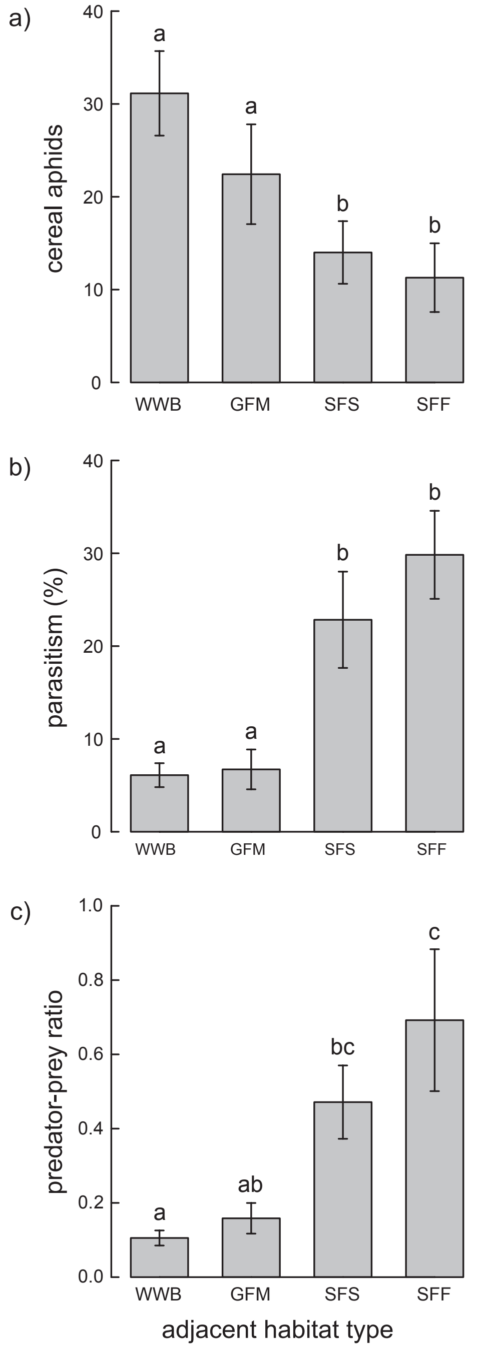

Fig. 4: Effects in 2007 of wheat-wheat boundaries (WWB), grassy field margin strips (GFM), sown flower strips (SFS) and sown flower fields (SFF) on (a) aphid densities, (b) percent parasitism, and (c) predator-prey ratio. Estimates per 100 shoots at wheat milk-ripening stage in winter wheat fields along the four adjacent habitats, averaged over all 7 landscapes (each adjacent habitat type *n* = 7). All bars represent untransformed means ± SE. Significant differences between habitat types are indicated by different letters.

to both flower habitat types (Fig. 3a). Significant interactions between the factors "year" and "adjacent habitat type" for aphid densities, parasitism rate, as well as for predator-prey ratio (Table 2) imply that the impact of the adjacent habitat type changes throughout the three years. The same applies for the also strong interaction of "year" and "% arable land". Even though the factor "% arable land" (the proportion of arable land in the surrounding of the study site), by itself explained the distribution of aphids and also the generation of parasitism rate and predator-prey ratio (Table 2), the interaction with "year" was even stronger (Table 2). Again, this gives evidence, that there is a high variation between the three years. When differentiating between years, it becomes clear, that these influences are most effective at wheat milk-ripening in 2007.

The year 2007

In 2007 local and landscape influences became of major importance for aphids and aphid natural enemies (Table 3). Aphid numbers were decreasing and parasitism rate as well as predator-prey ratio were increasing in wheat fields neighbouring habitat types in the order from wheat-wheat boundaries, grassy field margins, flower strips and flower fields (Table 3; Fig. 4 a,b,c). Both, aphid numbers and the strength of trophic interactions differed considerably between the "grassy" habitats (wheat-wheat boundaries and grassy field margins) and the

Table 3: Results of linear mixed-effects models for aphids and their natural enemies at wheat milk-ripening in 2007, describing the effects of the proportion of arable land in each of the seven landscape sectors and adjacent habitat type (sown flower fields, sown flower strips, grassy field margin strips, wheat-wheat boundaries). NumDF = numerator degrees of freedom, DenDF = denominator degrees of freedom.

2007	NumDF	DenDF	*F*-value	*P*-value
wheat milk-ripening				
aphids				
% arable land	1	5	19.46	0.0069
adjacent habitat type	3	18	17.51	< 0.0001
parasitism rate				
% arable land	1	5	9.94	0.0253
adjacent habitat type	3	18	62.85	< 0.0001
% arable land × adjacent habitat type	3	15	3.26	0.0513
predator-prey ratio				
% arable land	1	5	39.77	0.0015
adjacent habitat type	3	15	25.73	< 0.0001
% arable land × adjacent habitat type	3	15	7.49	0.0027

two types of flower habitats (aphids $F_{1,6} = 33.11$, $P = 0.0012$; parasitism rate $F_{1,6} = 32.81$, $P = 0.0012$; predator-prey ratio $F_{1,6} = 19.73$, $P = 0.0044$). Moreover, in 2007 the structure of the surrounding landscape turned out to be significantly relevant for populations of aphids. In structurally complex landscapes with only low proportions of arable land aphids performed worse compared to structurally simple landscapes with high proportions of arable land (Table 3; Fig. 5a). Over the entire gradient of the seven (differently structured) landscapes aphids always had higher densities adjacent to grassy field margins and at wheat-wheat boundaries, and showed considerably lower densities in wheat fields adjacent to flower strips and flower fields and in complex landscapes (Fig. 5a). Additionally, complex landscapes supported significantly higher levels of parasitism rate and predator-prey ratio than intermediate or simple landscapes (Table 3; Fig. 5b,c). These levels were strikingly higher when wheat fields were neighboured by flower fields and flower strips (Table 3; Fig. 5b,c).

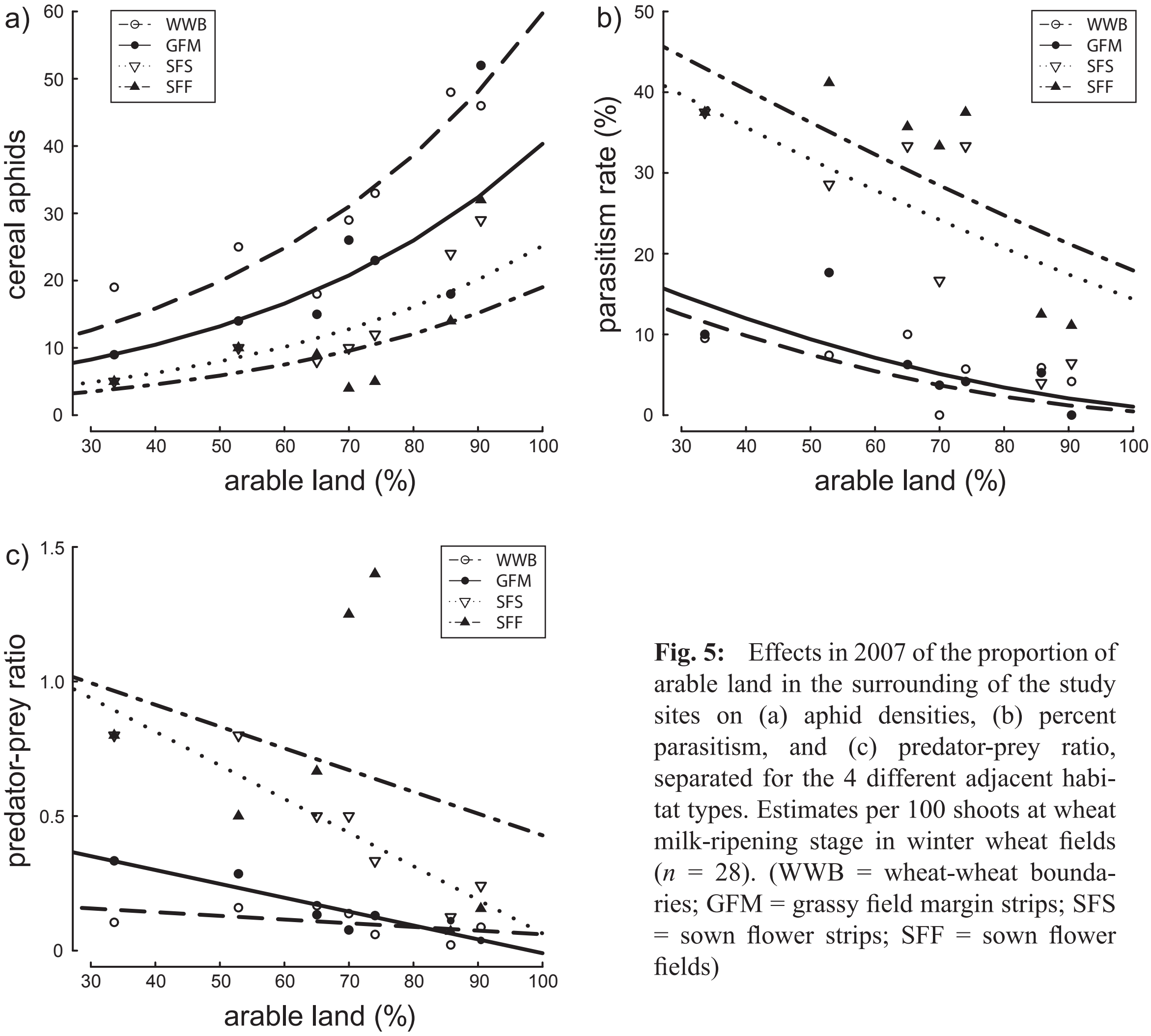

Fig. 5: Effects in 2007 of the proportion of arable land in the surrounding of the study sites on (a) aphid densities, (b) percent parasitism, and (c) predator-prey ratio, separated for the 4 different adjacent habitat types. Estimates per 100 shoots at wheat milk-ripening stage in winter wheat fields (*n* = 28). (WWB = wheat-wheat boundaries; GFM = grassy field margin strips; SFS = sown flower strips; SFF = sown flower fields)

Discussion

In this three year study, we showed that a high inter-annual variation determines the effectiveness of local and landscape-scale management for biological control. Predators like syrphid flies and lacewings as well as parasitoids appeared to suppress cereal aphid populations successfully when enhanced by adjacent flower habitats and by structurally complex landscapes, but mainly in just one of the three years studied. Covering the three years of the study, numbers of aphids and parasitoids as well as predators were essentially influenced by main effects of adjacent habitat type and landscape complexity, but with a high inter-annual variability. Both those effects were most obvious in the last year. In 2007, we found strong responses of aphid numbers and natural enemies to neighbouring habitat types with sown flower fields and sown flower strips lowering aphid population densities and enhancing natural enemy population densities compared to grassy field margins and wheat-wheat boundaries. The same holds for parasitism rate and predator-prey ratio, which were also significantly higher adjacent to both flower habitats.

Our results are in accordance to the habitat needs and foraging behaviour of parasitoids and predators feeding on nectar and pollen of flowering plants (Salveter, 1998; Frank, 1999; Landis *et al*., 2000; Araj *et al*., 2009). While flower habitats were left undisturbed over the entire study period and provided stable environments after the three years for natural enemies (as in Frank *et al*., 2007; Holland *et al*., 2008), naturally developed field margins are mown at least once per year and these disturbances may account for lower natural enemy densities adjacent to these habitats (Meek *et al*., 2002; Schmidt-Entling & Döbeli, 2009). Several studies found increased natural enemy densities (MacLeod, 1999; Langer & Hance, 2004; Haenke *et al*., 2009) as well as reduced aphid densities (Hickman & Wratten, 1996; Flückiger & Schmidt, 2006) in wheat fields adjoining flower habitats and also showed an increased parasitism rate (Pfiffner *et al*., 2003; Tylianakis *et al*., 2004; Araj *et al*., 2009) and predator-prey ratio (Hickman & Wratten, 1996; Salveter, 1998) when providing multiple flower resources. Flower strips and fields have been reported to favour alternative prey and hosts (Wyss, 1996; Schmidt-Entling & Döbeli, 2009), e.g. other than cereal aphid species, which constitute an essential resource for the build-up of natural enemy populations (Pfiffner & Wyss, 2004; Thies *et al*., 2005). Parasitoids' fitness, fecundity and longevity profit from additional nectar resources resulting in substantially enforced biological control (Tylianakis *et al*., 2004; Landis *et al*., 2005; Lavandero *et al*., 2006; Banks *et al*., 2008), which is reflected by higher parasitism rates adjacent to flower strips and flower fields in our study and led to decreased aphid population densities. Thus, our expectation of enhanced predator-prey ratios and parasitism rates in fields adjoining flower habitats was confirmed. As expected, the broad sown flower fields provided even stronger aphid control by higher predator-prey ratios and parasitism rates than the small sown flower strips, presumably because they cover bigger areas and thereby offer more resources and niches for the beneficial insects (Welling & Kokta, 1988; Denys & Tscharntke, 2002; Meek *et al*., 2002; Griffiths *et al.*, 2008).

According to our second hypothesis aphid densities increased as landscape complexity decreased. Higher proportions of arable land in the surrounding of the study site promoted higher aphid densities than landscapes with high proportions of (semi-) natural habitats. This response was expected as aphids concentrate in cereal fields and increasing crop area should support higher aphid population densities (Östman *et al*., 2001; Flückiger & Schmidt, 2006; but see Thies *et al*., 2005). On the other hand, increasing parasitism rates and predator-prey ratios were associated with increasing landscape complexity. Complex landscapes provide a broad range of non-crop habitats suitable for overwintering and offer refuges and alternative food for beneficial insects (Landis *et al*., 2000; Thies *et al*., 2005; Tscharntke *et al*., 2007) and thereby may support higher parasitoid and predator densities (for an overview see Bianchi *et al.*, 2006). This is in line with findings from several studies, which also found higher rates of parasitism in complex than in simple landscapes (Thies & Tscharntke, 1999; Östman *et al*., 2001; Menalled *et al*., 2003; Schmidt *et al*., 2003; Roschewitz *et al*., 2005; Boccaccio & Petacchi, 2009). Similar results are documented for generalist aphid predators such as spiders (Schmidt *et al*., 2005; Schmidt & Tscharntke, 2005) and carabid beetles (Purtauf *et al*., 2005; Batary *et al*., 2008), which also occurred in higher abundances in complex landscapes compared to simple landscapes (but see Rand & Tscharntke, 2007). In complex landscapes, high availability of (semi-) natural habitats have been shown to facilitate spillover from non-crop to crop habitats supporting natural enemies to invade crop fields and to respond quickly to the herbivore population (Marshall & Moonen, 2002; Bianchi *et al*., 2006; Tscharntke *et al.*, 2007). Resources required by natural enemies such as parasitoids, syrphid flies and lacewings (aphids as hosts and larval prey; pollen and nectar for adults) are often spatially separated (Bianchi *et al*., 2006; Banks *et al*., 2008), so only a complex mixture of (semi-) natural habitats and crop habitats provides a sound basis for an effective biological control (Griffiths *et al*., 2008).

Our expectation of an interaction between local management and landscape context, providing stronger aphid control adjacent to flower habitats in simple landscapes was partially confirmed: we found sown flower strips and sown flower fields to support higher predator-prey ratios and parasitism rates and lower aphid densities compared to the grassy field margins and wheat-wheat boundaries. But in contrast to our expectation, this effect was apparent in each of the seven different landscapes (Fig. 5a-c), indicating sown flower habitats to be profitable in simple and complex landscape types. Nevertheless, differences of considerably lower aphid densities in fields adjacent to flower habitats (Fig. 5a, two lower lines) compared to grassy field margins and wheat-wheat boundaries (Fig. 5a, two upper lines) were more pronounced in simple landscapes, indicating the importance of the flower habitats when (semi-) natural habitats in the surrounding landscape are lacking.

We ascribe the high inter-annual variability of habitat and landscape effects basically to the high inter-annual variability of aphid numbers. Although densities of natural enemies also varied considerably between the three years, differences in aphid densities were much higher. Such variations are often reported (Jones, 1979; Sigsgaard, 2002; Thies *et al*., 2005; Honek *et al*., 2006) and mostly attributed to weather conditions with low temperatures and high precipitation negatively affecting aphid populations mainly during the reproduction period (Lang, 2003; Thies *et al*., 2005; Frere *et al*., 2007; Houlahan *et al*., 2007). In 2005, average numbers of 4.1 aphids/tiller almost reached the economic threshold level of 3 to 5 aphids/tiller (Giller *et al*., 1995), especially at wheat-wheat boundaries (4.2/tiller) and adjacent to grassy field margins (5.8/tiller), but in the two consecutive years aphid densities remained well below threshold level (2006: 2.5 aphids/tiller; 2007: 0.2 aphids/tiller). So, in 2007 aphid densities were significantly lower and possibly suffered heavily from extreme rainfall events in May and June (Appendix A1), when they colonize the fields and start to proliferate. As densities of natural enemies did not vary as strong as aphid densities, we conclude that the influences of the surrounding landscape complexity and of the different adjacent habitat types are only effective on aphid control when aphid densities are rather low as they were in 2007, so that natural enemies exert dominating influence on aphid populations (Thies *et al*., 2005). On the other hand, high densities as in 2005 seem to outperform these impacts.

Different responses (and thus different contribution to aphid suppression) of syrphid flies, lacewings and parasitoids to the adjacent habitats during the three years of this study support the idea of the insurance hypothesis (Yachi & Loreau, 1999; Loreau *et al*., 2001), where different species respond in different ways to environmental fluctuations. Higher numbers of species per functional group mean a higher chance to have species included that are able cope with the changing environment (Naeem & Li, 1997; Ives *et al*., 2000; Hobbs *et al*., 2007; Bruelheide & Luginbühl, 2009). More generally, it is evident, that maximizing the pool of functionally complementary species should lead to most effective biological control (Griffiths *et al*., 2008).

Conclusions

Our results emphasize the importance of complex landscapes but also the importance of semi-natural habitats such as flower strips for stronger biological control by enhanced populations of parasitoids and predators. Creating flower habitats contributes to the diversification of the landscape, especially in simple landscapes (Schmidt *et al*., 2004; Bianchi *et al*., 2006; Isaacs *et al*., 2009). Flower habitats fulfil a variety of purposes as agri-environment schemes, e.g. the increase of the landscape diversification, supply of additional structures and resources and enhancement of biodiversity (Kleijn & Sutherland, 2003; Fiedler *et al*., 2008; Holland *et al*., 2009). The creation of flower habitats had also positive impacts on biological control of aphids in adjacent winter wheat fields as they were able to reduce pest infestations successfully by enhancing natural enemy populations through the offer of alternative habitat, food and prey resources. However, the high inter-annual variability of pest as well as natural enemy densities seems to be crucial for the success of such agri-environment schemes. In years with high pest densities, natural enemies could not completely suppress but still reduce aphid infestations in fields adjacent to flower habitats, while in years with stable and rather balanced pest densities, natural enemies obviously succeed in controlling the pest (cf. Levie *et al*., 2005; Thies *et al*., 2005).

Farmers can easily implement sown flower strips around crop fields to increase positive impacts of natural enemies (Landis *et al*., 2000; Östman *et al*., 2001; Pfiffner & Wyss, 2004; Tscharntke *et al*., 2007), and this measure is financially supported in many regions. We found the highest benefit of the flower habitats in complex and simple landscapes after two years, when these flower habitats were well established. The subsequent implication is to ensure the constancy of those habitats to promote natural enemies in the long run (Frank & Nentwig, 1995; Frank *et al*., 2007, 2009), and thus to maximize the “outcome” and most integrating benefit. Also, increasing the amount of flower habitats at a larger spatial scale may lead to more stable ecosystem functioning by spatio-temporal complementarity through promoting different enemy species (Loreau *et al*., 2001; Tscharntke *et al*., 2007). However, the strength of the effects and thus the success of biological control spilling over to the field centres depend on the dispersal ability of the natural enemies (MacLeod, 1999; Thies &

Tscharntke, 1999; Nicholls & Altieri, 2004; Tylianakis *et al*., 2004). Collectively, our results emphasize the need for long-term and large-scale observations to evaluate the implications of the great variability of pests and ecosystem functions in order to give reliable and sustainable recommendations for habitat management promoting biological control.

Acknowledgements

We thank Eckhard Gottschalk and all farmers participating in the Partridge Conservation Project (www.rebhuhnschutzprojekt.de) for providing the fields and flower habitats, Matthias Erb for help with field work, and Ines Vollhardt for discussions. Financial support came from the German Ministry of Research and Education (BMBF) and the German Science Foundation (DFG).

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Appendix

Appendix A1 Meteorological data from 2005 – 2007 (www.wetterstation-goettingen.de)

	mean temperature (°C)	total rainfall (mm)	sunshine duration (h)
May 2005	12.5	81.7	216.6
May 2006	13.1	96.5	227.8
May 2007	14.2	153.4	222.1
June 2005	15.7	54.9	258.1
June 2006	16.6	94.7	280.4
June 2007	17.3	141.6	221.8
July 2005	18.1	55.7	225.7
July 2006	21.8	82.6	337.0
July 2007	17.1	94.5	208.4

Appendix A2: List of plant species mixture of sown flower habitats for the grey partridge (*Perdix perdix*)

species	percent by seed weight	horticultural (h)/wildflower (w)
Linum usitatissimum L.	30	h
Helianthus annuus L.	10	h
Fagopyrum esculentum Moench	10	h
Lepidium sativum L.	6	h
Medicago sativa L.	5	h
Nigella sativa L.	5	h
Borago officinalis L.	5	h
Phacelia tanacetifolia Benth.	3	h
Raphanus sativus L.	3	h
Pisum sativum L.	3	h
Brassica oleracea L.	2	h
Sinapis alba L.	1	h
Foeniculum vulgare Mill.	1	h
Papaver rhoeas L.	5	w
Calendula arvensis L.	2.5	w
Leucanthemum vulgare Lam.	2	w
Isatis tinctoria L.	1	w
Pastinaca sativa L.	1	w
Carum carvi L.	1	w
Melilotus alba Medic.	0.5	w
Melilotus officinalis (L.) Pall..	0.5	w
Campanula rapunculoides L.	0.5	w
Hypericum perforatum L.	0.5	w
Cichorium intybus L.	0.5	w
Anthriscus sylvestris (L.) Hoffm.	0.5	w
Tanacetum vulgare L.	0.5	w

CHAPTER

5

ENHANCING RAPE POLLEN BEETLE PARASITISM WITH SOWN FLOWER FIELDS IN VARYING LANDSCAPES

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Abstract

1. Sown flower habitats are a tool of agri-environment schemes in the European Union, which are hypothesized to contribute to the biological control of pests such as the rape pollen beetle *Meligethes aeneus* by improving habitat and resource availability for its specialized parasitoid.
2. In this study, we selected 20 sown flower fields, including one of the pollen beetles' host plants *Sinapis alba*, each centred in a landscape sector of varying complexity, to test the influence of the surrounding landscape structure on parasitism rate and herbivory by *M. aeneus*. Additionally, plant cover of *Sinapis alba* plants on the sown flower fields and numbers of flowers were also included in the analyses.
3. Landscapes with high proportions of (semi-) natural habitats supported higher parasitism rates and sown flower fields with dense *S. alba* plant cover hosted more parasitoids (and suffered from less herbivory), thus sustaining higher parasitism rates than sown flower fields with sparse *S. alba* plant cover.
4. We conclude that sown flower fields, offering constant and undisturbed habitats for parasitoids with a rich pollen and nectar supply and abundant host densities for reproduction, contribute to the build-up and maintenance of parasitoid populations, which can help to control rape pollen beetles in nearby rape crop fields.

Keywords

Meligethes aeneus, *Tersilochus heterocerus*, *Sinapis alba*, herbivory, parasitism rate, biological control, agri-environment scheme

Introduction

In Germany, the area under oilseed rape production (*Brassica napus* Linnaeus) for bioenergy crop and vegetable oil production is strongly increasing over recent years (BMELV, 2010). Growing numbers and areas of monocultures are susceptible to high damage by rape pollen beetle *Meligethes aeneus* Fabricius (Coleoptera, Nitidulidae), one of the major pests of rape plants (Borg & Ekbom, 1996; Alford *et al*., 2003; Zaller *et al*., 2009), and large amounts of insecticides are applied to keep this pest under control (Williams, 2006; Thies & Tscharntke, 2010). However, parasitoids are known for their substantial biological control of pollen beetle abundances (Nilsson, 2003; Williams, 2006), but spatio-temporal coincidence with their host is important for successful pest suppression (Tscharntke *et al*., 2005; Williams, 2006). Parasitoids are strongly influenced by the matrix of the surrounding landscape (Marino & Landis, 1996; Cronin & Reeve, 2005; Thies *et al*., 2008), and several studies have shown higher parasitism rates in landscapes of high complexity, i.e. with high proportions of (semi-) natural habitats (Menalled *et al*., 1999; Thies & Tscharntke, 1999; Schmidt *et al*., 2003; Thies *et al*., 2003; Bianchi *et al*., 2005). This is ascribed to the higher availability of habitats for refuge, shelter and the supply of alternative and additional resources such as flowers providing pollen and nectar for adult parasitoids (Steffan-Dewenter *et al*., 2001).

There are nine parasitoid species attacking *M. aeneus* in Europe (Nilsson, 2003; Jönsson, 2005), from which two species of the genus *Phradis* (*P. morionellus* Holmgren, *P. interstitialis* Thomson) and *Tersilochus heterocerus* Thomson (all Hymenoptera, Ichneumonidae) are the most common in Germany (Thies *et al*., 2003). They all attack rape pollen beetle larvae in the rape buds and flowers (Thies *et al*., 2008). The adult rape pollen beetle damages the plant by feeding on pollen of buds and flowers, resulting in podless stalks (Borg & Ekbom, 1996; Zaller *et al*., 2009). Adults oviposit into flower buds, where the developing larvae also feed on pollen (Billqvist & Ekbom, 2001; Alford *et al*., 2003). First instar larvae are attacked by *P. interstitialis*, whereas *P. morionellus* and *T. heterocerus* attack mostly second instar larvae, before these drop from the rape flower to pupate in the soil (Nilsson, 2003; Zaller *et al*., 2009; Thies & Tscharntke, 2010). The parasitoid develops to adult stage and remains inside the cocoon in diapause and emerges the following spring. Instead, unparasitized rape pollen beetles hatch after 45 to 55 days (Borg & Ekbom, 1996) and the new generation again feeds on *Brassica* crops but also on autumn flowers before hibernation (Borg & Ekbom, 1996; Jönsson, 2005).

Sown flower strips and fields, implemented as a component of agri-environment schemes in the study region (ML Niedersachsen, 2010, NAU A6), are sown with 13 horticultural and 13 wildflower species, among them the Brassicaceae *Sinapis alba* Linnaeus. Several studies showed that *S. alba* is also accepted as a host plant by the rape pollen beetle, but it is less susceptible to infestations than *Brassica* spp., implying that flower habitats do not explicitly encourage the rape pollen beetle (Ekbom & Borg, 1996; Hopkins *et al*., 1998; Billqvist & Ekbom, 2001). Modifying habitats adjacent to crops are supposed to facilitate natural enemy populations to spillover into crop fields (Gurr *et al*., 2004; Cronin & Reeve, 2005; Bianchi *et al*., 2006). In this study, we investigated whether such sown flower habitats can contribute to the biological control of *M. aeneus* by improving habitat and resource availability for specialized parasitoids and increasing parasitism rates of *M. aeneus*. We tested the influence of landscape parameters such as the proportion of arable land and rape crop in the surrounding of the study sites, hypothesizing that landscapes with high proportions of (semi-) natural habitats would support higher parasitism rates (Thies & Tscharntke, 1999, 2010; Landis *et al*., 2000; Tscharntke *et al*., 2005) and that flower fields with dense *S. alba* plant cover host more parasitoids and thus sustain higher parasitism rates than flower fields with sparse *S. alba* plant cover (Ekbom & Borg, 1996; Ferguson *et al*., 2006).

Methods

Study sites

In the study region around Göttingen, Germany, 20 non-overlapping landscape sectors with a 1000 m–radius were selected. This radius is supposed to be an appropriate scale as former studies in this region showed strong reactions of the target species up to this scale (Thies *et al.*, 2003). The landscape sectors are characterized by varying proportions of arable land and (semi-) natural habitats with a sown flower field as a central study site, and covered a gradient of landscape complexity from structurally complex (~ 22% arable land) to structurally simple (~ 86% arable land). The ATKIS-data ("Amtlich Topographisch-Kartographisches Informations-System") provided a basis for an update hand-mapping of the current land-use of each sector, especially assessing rape fields and sown flower fields.

The sown flower fields are sown with a seed mixture of 13 horticultural and 13 wildflower species, and had a width of approximately 6 to 25 m (see Appendix A1 for plant species mixture of sown flower fields). In a first approach we tested for influences of different sizes of narrow *vs*. broad flower habitats, but as the size did not account for the explanation of response variables, we left this aspect unconsidered in further analysis. In one of the 20 landscape sectors we did not find any rape pollen beetle larvae, thus this site was excluded from all statistical analysis.

INSECT AND PLANT SAMPLING

Sampling of plants and insects from flower fields began with bud development of *S. alba* and when plants began to flower (BBCH scale 60 – 65; Lancashire *et al*., 1991; Meier, 2001). Covering the whole area of each flower field, 100 racemes of randomly chosen plants were cut off, stored in a plastic bag and transferred into a freezer. In the laboratory, numbers of buds and flowers of the 100 racemes/site were counted and examined under a binocular for infestation by rape pollen beetle larvae. Adults of rape pollen beetles, caught with the racemes on the flower fields, were also counted.

Parasitism of *M. aeneus* larvae by one of the three parasitoid species was determined by dissecting second instar larvae (≥ 3 mm; see Thies & Tscharntke, 1999; Billqvist & Ekbom, 2001). Dissections were carried out within a drop of water in a Petri dish under a binocular microscope. Parasitism rates were calculated by counting the larvae infested by black eggs of *T. heterocerus* and white eggs of *Phradis* spp., respectively.

Additionally, 10 randomly chosen plants on each flower field were cut off (BBCH scale 77 - 79) to assess plant damage caused by herbivory of adult rape pollen beetles. The number of pods and blind stalks indicating buds, which did not develop into pods because of rape pollen beetles' feeding, were counted and percentage of blind stalks in relation to total number of pods was calculated (= herbivory).

Plant density measures of *S. alba* were done by estimation of percentage cover of *S. alba* plants on each flower field.

STATISTICAL ANALYSES

The statistical analyses and graphics were carried out using the software R, Version 2.9.1 (R Development Core Team 2009). We fitted generalized linear models (GLM) with a quasipoisson error distribution to overcome overdispersion of models. Count data were log-transformed; proportion data such as parasitism rate and herbivory were arcsine-square root-transformed before all analyses for meeting the assumptions of normality and homoscedasticity. We examined the effects of landscape parameters, i.e. percentage of arable land and of rape crop, and of plant parameters, i.e. plant cover on flower fields and numbers of buds and flowers per raceme, on the distribution of *M. aeneus* larvae and their parasitoids, as well as on herbivory and parasitism.

Results

From 2749 collected larvae only 23% were second instar larvae suitable for dissection. Mean parasitism of these larvae was 51.9 ± 6.2% (n = 19). As *Phradis* spp. was only encountered four times, we refer to *T. heterocerus* parasitism. Plant damage by feeding of adult rape pollen beetles (= herbivory) led to a mean of 43.5 ± 2.1% (n = 19) of buds destroyed.

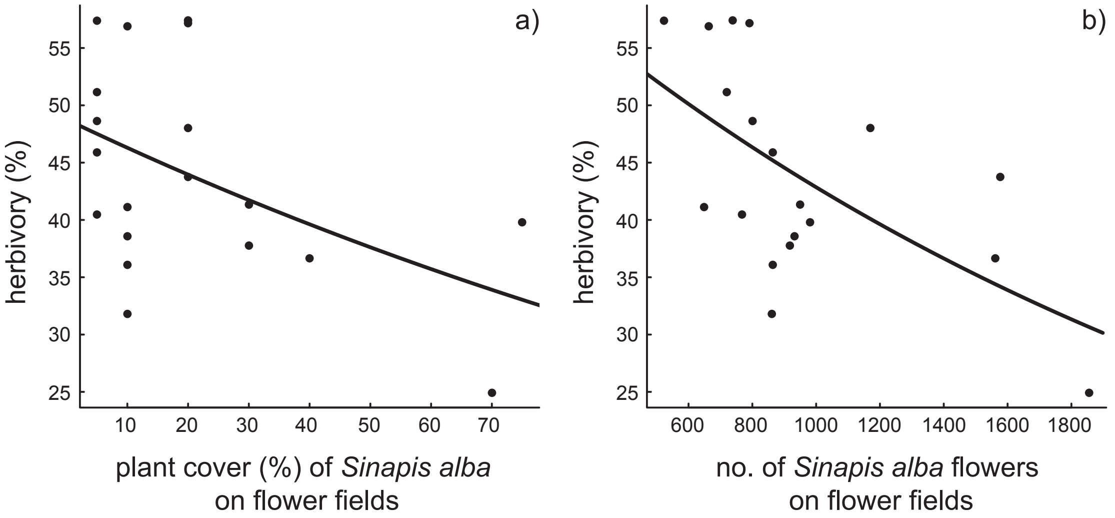

Fig. 1: The percentage of *Sinapis alba* plants damaged by *Meligethes aeneus* in flower fields decreases (a) with percentage plant cover of *Sinapis alba* plants (P = 0.038, n = 19), and (b) with number of *Sinapis alba* flowers on flower fields (P = 0.006, n = 19). The solid line represents the fitted model.

Herbivory was not related to any of the landscape parameters, but decreased with increasing number of *S. alba* flowers per plant and with increasing *S. alba* plant cover (Table 1, Fig. 1a,b). Host and parasitoid densities both increased with increasing *S. alba* plant cover and also with increasing numbers of *S. alba* flowers (Table 1), but did not respond to landscape parameters. Parasitoid densities were strongly related to host density (Table 1, Fig. 2a) as well as to plant infestation rates (= number of host larvae/number of flowers) (Table 1, Fig. 2b). In contrast, parasitism rates of *M. aeneus* larvae did not depend on

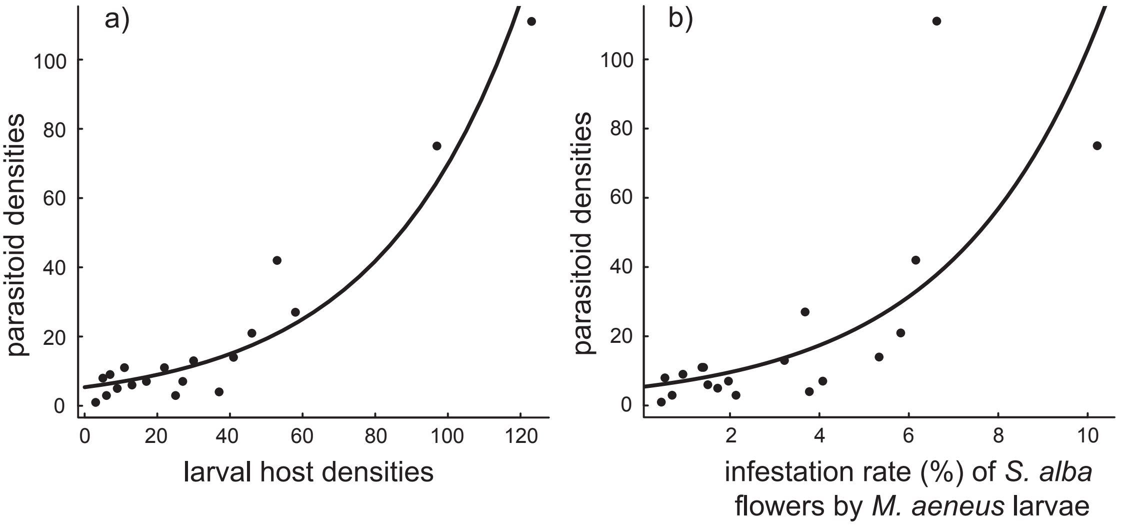

Fig. 2: Densities of specialized parasitoids *Tersilochus heterocerus* increase (a) with increasing larval host densities, and (b) with increasing infestation rate (%) of *Sinapis alba* flowers by *Meligethes aeneus* larvae. The solid line represents the fitted model; effects for both are significant ($P < 0.0001$; each $n = 19$).

host density or plant parameters, but were significantly affected by the proportion of arable land and also by the proportion of arable land including rape crop area of the landscape sectors (Table 1). Parasitism decreased as proportions of arable land and rape crop area increased and the related proportions of (semi-) natural habitats decreased (Fig. 3 a,b).

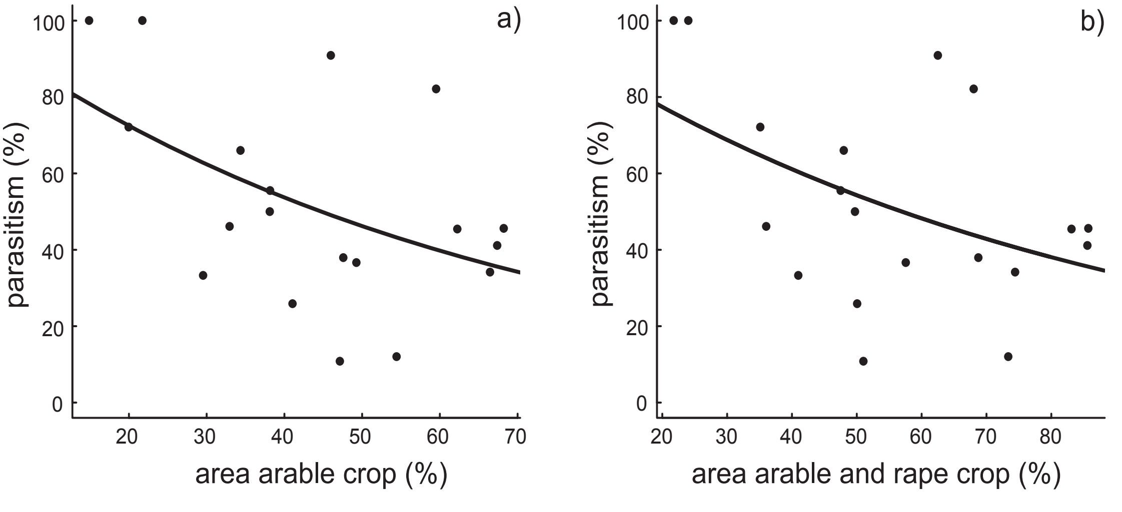

Fig. 3: Percent parasitism of *Meligethes aeneus* larvae in flower fields depends on (a) % arable crop area, and on (b) % arable and rape crop area in the landscape. The solid line represents the fitted model; effects for both are significant ($P < 0.05$; each $n = 19$).

Table 1: Results of generalized linear models for plant damage by *Meligethes aeneus* beetles, densities of host larvae and parasitoids (*Tersilochus heterocerus*) and parasitism of *M. aeneus* larvae by *T. heterocerus*, describing the effects of plant parameters and landscape parameters. NumDF = numerator degrees of freedom, DenDF = denumerator degrees of freedom.

	NumDF	DenDF	*F*-value	*P*-value
herbivory				
% plant cover of *Sinapis alba*	1	17	5.06	0.038
number of *Sinapis alba* flowers	1	17	9.93	0.006
host larvae				
% plant cover of *Sinapis alba*	1	18	7.16	0.015
number of *Sinapis alba* flowers	1	18	8.87	0.008
Tersilochus heterocerus				
% plant cover of *Sinapis alba*	1	18	6.64	0.019
number of *Sinapis alba* flowers	1	18	8.61	0.009
host larvae	1	18	45.83	< 0.0001
infestation rate	1	18	29.67	< 0.0001
parasitism				
arable land	1	17	7.08	0.017
arable land including rape crop	1	17	6.19	0.024

Discussion

In this study, we investigated the potential of sown flower fields to enhance the abundance of parasitoids thereby improving biological control of rape pollen beetles in nearby rape crop fields. We analyzed the impact of local and landscape parameters on herbivory of *S. alba* plants by rape pollen beetles on flower fields and on parasitism rates of *M. aeneus* larvae by its specialized parasitoid *T. heterocerus*. We found herbivory to be determined by the local host plant density, whereas parasitism rate was determined by the structural complexity on the landscape scale.

Densities of larval hosts were strongly related to plant cover and to the number of flowers per raceme indicating successful proliferating of rape pollen beetles on flower fields with a high percentage of *S. alba*. As numbers of parasitoids and numbers of host larvae were strongly correlated ($P = 0.0001$), we found the same relationship between parasitoid densities and plant cover and number of flowers per raceme. For both the hosts and the parasitoids, high plant cover and high numbers of flowers present more available resources

(Ekbom & Borg, 1996; Ferguson *et al*., 2006). This confirms our expectation that flower fields with a high percentage of *S. alba* plants are able to promote high parasitoid densities by ensuring their reproduction. On the other hand, herbivory by adult rape pollen beetles was negatively influenced by plant cover and by number of flowers per raceme and was even reduced on flower fields with high *S. alba* cover. This could be due to dilution effects and to less resource competition for more abundant host plants (Thies *et al*., 2008).

Densities of *T. heterocerus* were strongly related to their larval host densities, but there was no correlation between parasitism rate and larval host densities. Zaller *et al*. (2009) recently reported of an opposite finding, but studies in our study region (Thies *et al*., 2003, 2008), as well as studies from Switzerland (Büchi, 2002) and from Sweden (Billqvist & Ekbom, 2001) did not find any consistent relationship between larval host densities and parasitism rate. Ferguson *et al*. (2006) argue that at high host densities either parasitoids' foraging efficiency might be reduced or parasitoids' population densities might be too small for sufficient exploitation. The fact that we almost exclusively encountered *T. heterocerus* but hardly any *Phradis* spp. might be explained by *T. heterocerus* being generally more abundant in this region and being the predominant parasitoid of *M. aeneus* larvae (Kraus & Kromp, 2003; Thies *et al*., 2008).

As we expected, increasing parasitism of rape pollen beetle larvae was associated with a decreasing proportion of arable land in the surrounding of the study sites showing highest parasitism rates in complex landscapes. This is in line with other studies, which also found such a relationship (Thies and Tscharntke, 1999; Menalled *et al*., 2003; Schmidt *et al*., 2003; Thies *et al*., 2003; Roschewitz *et al*., 2005; Gardiner *et al*., 2009) and could be ascribed to the needs of adult parasitoids, which feed on nectar and pollen (Landis *et al*., 2000; Heimpel & Jervis, 2005; Lavandero *et al*., 2006; Fiedler *et al*., 2008). Jönsson & Anderson (2007) showed in a laboratory experiment that the proportion of starved parasitoids (*Phradis morionellus*) not responding to *M. aeneus* hosts-infested or non-infested rape was significantly higher compared to fed parasitoids, probably because of starved individuals being in food-seeking and not in host-seeking mode. Complex landscapes provide more (semi-) natural habitats, which offer alternative food, i.e. by higher supply of flowers, as well as overwintering sites and shelter (Steffan-Dewenter *et al*., 2001; Duelli & Obrist, 2003; Bianchi *et al*., 2006). Most of these habitats are undisturbed in terms of insecticide application and soil cultivation, which is very important for survival of parasitoids such as *T. heterocerus*, which hibernate in the soil and are thus very susceptible to soil disturbance (Nilsson, 2003; Ferguson *et al*., 2006; Williams, 2006).

Although *S. alba* is less preferred by *M. aeneus* than *Brassica* spp. (Ekbom & Borg, 1996; Hopkins *et al*., 1998; but Billqvist & Ekbom, 2001), we found a mean infestation rate of rape flowers by *M. aeneus* larvae of 14%, ranging from 2 to 45%. As the rape flowers on neighbouring rape crop fields were in the end of the flowering period, *S. alba* plants on flower fields appeared to be an attractive alternative for rape pollen beetles. Moreover, mean parasitism of second instar larvae by *T. heterocerus* was 52%, ranging from 10 to 100%, indicating that the flower fields were a suitable habitat for parasitoid reproduction. Model predictions show that the parasitism rate remains above 32 – 36% (Fig. 3a,b), which is considered to be the minimum threshold level of parasitism for successful biological control (Hawkins & Cornell, 1994). Nevertheless, parasitoid impact on *M. aeneus* becomes apparent in the following year as damage to rape plants is already done by adult pollen beetles and its larvae, before those are parasitized (Kraus & Kromp, 2002). Thus winter survival is crucial for biological control by these parasitoids. When parasitisation of rape pollen beetle larvae takes place within rape crop fields, the larvae drop to the soil, which will be ploughed/cultivated after harvest and mortality of parasitoids developing within the larvae could be very high (Nilsson, 2003). Parasitoids attacking *M. aeneus* larvae on *S. alba* plants on the flower fields would not be committed to soil disturbances, as flower fields are not allowed to be managed. Thus we assume successful overwintering rates of parasitoids in these sites. Büchi (2002) found significantly higher parasitism rates of *M. aeneus* larvae by *T. heterocerus* in rape crop fields with an adjacent wild flower strip than in fields adjacent to extensively managed meadows, and Klingenberg & Ulber (1994) stated that parasitism rates of up to 50% are likely to positively impact pest abundances in the long run (see also Hokkanen *et al*., 1988). This implies that flower fields including *S. alba* may provide a suitable habitat for rape pollen beetle parasitoids to build-up and maintain stable populations aside of rape crop fields. Here they are protected from enhanced mortality due to soil cultivation practices, and they may spill-over into rape crops in the following season (Büchi, 2002; Tscharntke *et al*., 2005; Rand *et al*., 2006). Thereby flower fields may exert positive impact in terms of biological control of *M. aeneus* in the next year. Rape crop rotation from year to year confronts parasitoids with a constantly changing environment, and the distances between rape fields in two subsequent years may be too large for host-finding by the parasitoids (Thies *et al*., 2008). Moreover, as parasitoids seem to perceive their environment at rather small spatial scales (Kruess, 2003; Thies *et al*., 2003, 2008; Zaller *et al*., 2009), they are assumed to be more strongly influenced by landscape and management change than their hosts. Flower fields offer constant and undisturbed habitats as they are implemented for about five years (ML Niedersachsen, 2010, NAU A6). During this period they provide a continuous supply of nectar and pollen and also host populations of rape pollen beetle larvae in *S. alba* plants. Therefore, landscapes interspersed with flower fields may contribute to a more stable environment promoting parasitoid populations and connecting rape crop fields over years (Cronin & Reeve, 2005; Zaller *et al.*, 2009).

As we found an almost significant trend of lower *M. aeneus* populations (adult beetles ~ plant cover $F_{1,18} = 4.32$, $P = 0.052$) and reduced herbivory on flower fields with a high cover of *S. alba,* we suggest that flower fields be sown with *S. alba,* not to promote *M. aeneus* populations, but to help parasitoids to build-up stable populations, which may provide control of rape pollen beetles in nearby rape crop fields.

Acknowledgements

We thank Eckhard Gottschalk and all farmers participating in the Partridge Conservation Project (www.rebhuhnschutzprojekt.de) for providing the sown flower habitats. Financial support came from the German Ministry of Research and Education (BMBF) and the German Science Foundation (DFG).

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Appendix

Appendix A1: List of plant species mixture of sown flower habitats for the grey partridge (*Perdix perdix*)

species	percent by seed weight	horticultural (h)/wildflower (w)
Linum usitatissimum L.	30	h
Helianthus annuus L.	10	h
Fagopyrum esculentum Moench	10	h
Lepidium sativum L.	6	h
Medicago sativa L.	5	h
Nigella sativa L.	5	h
Borago officinalis L.	5	h
Phacelia tanacetifolia Benth.	3	h
Raphanus sativus L.	3	h
Pisum sativum L.	3	h
Brassica oleracea L.	2	h
Sinapis alba L.	1	h
Foeniculum vulgare Mill.	1	h
Papaver rhoeas L.	5	w
Calendula arvensis L.	2.5	w
Leucanthemum vulgare Lam.	2	w
Isatis tinctoria L.	1	w
Pastinaca sativa L.	1	w
Carum carvi L.	1	w
Melilotus alba Medic.	0.5	w
Melilotus officinalis (L.) Pall..	0.5	w
Campanula rapunculoides L.	0.5	w
Hypericum perforatum L.	0.5	w
Cichorium intybus L.	0.5	w
Anthriscus sylvestris (L.) Hoffm.	0.5	w
Tanacetum vulgare L.	0.5	w

SUMMARY:

THE ROLE OF SOWN WILDFLOWER STRIPS FOR BIOLOGICAL CONTROL IN AGROECOSYSTEMS

Summary

Agriculture covers about 50% of the area of Germany. Representing the main land user, agro-ecosystems are major drivers of landscape structure, biodiversity and associated ecosystem services. The extension of monocultures and intensive use of chemicals led to simplified landscapes with often only small and fragmented remnants of refuge habitats and an associated decline of biodiversity. As beneficial insects provide ecosystem functions such as pollination and biological control, agriculture faces an important challenge to protect populations of beneficial insects to restore and maintain essential ecosystem services. This can be achieved by habitat manipulation, e.g. by the implementation of agri-environment schemes. Many beneficial organisms depend on flower resources such as pollen and nectar when they are in their adult stages, but need also further resources for reproduction. The aim of this study was to examine the effects of local habitat management with sowing flower habitats and of landscape composition on biological control of agricultural pests, which can cause severe crop damage.

In the first part of this thesis, we tested the effectiveness of sown flower habitats for natural enemy impact on cereal aphids in differently structured landscapes. In seven circular and non-overlapping landscape sectors (r = 1000 m) along a gradient of varying land-use intensity from structurally simple to complex, quantified as changing proportion of arable land (~30 – 100%), four winter wheat fields were selected. They were situated adjacent to different types of neighbouring semi-natural habitats: broad sown flower fields, narrow sown flower strips, naturally developed grassy field margin strips and wheat-wheat boundaries as a control.

In the first study, we experimentally excluded different groups of aphid natural enemies in winter wheat fields, to analyze how natural enemies and aphid population growth are influenced by habitat manipulation. As hypothesized, aphid densities decreased most when all natural enemy groups were present, with vegetation-dwelling predators such as syrphid fly larvae and parasitoids contributing most to aphid control. Aphid densities were reduced ca. five times by natural enemies and negatively related to vegetation-dwelling predator-prey ratio and parasitism rate. Adjacent to flower habitats lower aphid population growth was associated with enhanced predator-prey ratio and parasitism rate in the wheat fields. In contrast to our expectation, we did not detect any impact of the complexity of the surrounding landscape. A parallel study examined the impacts of the different wheat field neighbouring habitats and of landscape complexity especially on syrphid fly communities. Syrphid fly density and in particular, the density of aphidophagous species, was higher in sown flower strips and sown flower fields. In addition, species richness of aphidophagous syrphid flies within wheat fields adjacent to sown flower fields was also higher. In contrast to the first part of this study, species richness and abundance of syrphid flies in both sown flower habitats increased as the proportion of arable land in the surrounding landscape increased, suggesting concentration effects of syrphid flies on the most rewarding resources (= flower habitats) within structurally simple landscapes.

Based on the findings of these two studies and following the same study design, the third study concentrated on vegetation-dwelling aphid predators, i.e. syrphid fly larvae and chrysopid larvae, and parasitoids of cereal aphids, and their impact on aphid populations over a three year period. Both local and landscape factors significantly influenced aphids and natural enemies, with most effective suppression of aphids in wheat fields adjacent to both, narrow and broad sown flower habitats due to enhanced predator-prey ratios and parasitism rates, and with pronounced effects in complex landscapes. However, these effects were very susceptible to a high inter-annual variability, and were strongest in one year with low aphid densities.

The second part of this thesis dealt with the biological control of another agricultural pest, the rape pollen beetle *Meligethes aeneus*. Aim of this study was to investigate the potential of sown flower habitats to contribute to the biological control of *M. aeneus* in differently structured landscapes by enhancing reproduction of parasitoid populations. This was tested on 20 sown flower fields, each centred in a landscape sector along a gradient of different landscape complexities from structurally simple to structurally complex. Herbivory of *Sinapis alba* plants, sown with the seed mixture for the flower fields, by *M. aeneus* was not affected by the landscape structure. But – according to our hypothesis – parasitism of *M. aeneus* larvae, developing in *S. alba* inflorescences, increased with increasing percentage of (semi-) natural habitats in the landscape. Moreover, on the sown flower fields parasitoids are protected from enhanced mortality due to soil cultivation practices (ploughing) as occurs in rape crop fields. Hence, a high reproduction success of the parasitoid on the sown flower fields may translate into enhanced biological control through spillover in nearby rape crop fields.

We conclude that sown flower strips and sown flower fields offer constant and undisturbed habitats for natural enemies of agricultural pests, as they often exist for a couple of years, offering refuge, overwintering sites and food resources due to their rich pollen and nectar supply. The results of this study show that the sown flower habitats can contribute to the build-up and maintenance of natural enemy populations, which may provide biological control of cereal aphids and of rape pollen beetles in nearby crop fields across different landscape types.

Zusammenfassung

Die Landwirtschaft ist mit einem Flächenanteil von etwa 50% der Gesamtfläche Deutschlands der Hauptlandnutzer. Agrarökosysteme beeinflussen somit maßgeblich die Landschaftsstruktur, Biodiversität und die damit verbundenen Ökosystemleistungen. Die Zunahme von Monokulturen und der intensive Einsatz von Agrochemikalien hat zu einer strukturarmen, ausgeräumten Landschaft geführt, in der häufig nur noch kleine und fragmentierte Rückzugshabitate verblieben sind, und einem damit verbundenen Rückgang der Biodiversität. Da Nützlingsorganismen Ökosystemfunktionen wie Bestäubung von Pflanzen und biologische Schädlingsbekämpfung erfüllen, steht die Landwirtschaft vor der großen Herausforderung, die Nützlingspopulationen zu schützen, um diese äußerst wichtigen Ökosystemfunktionen wiederherzustellen und zu erhalten. Dies kann mit Hilfe von Habitat-Veränderungen erreicht werden, beispielsweise durch die Anwendung von Agrar-Umweltmaßnahmen. Viele Nützlingsorganismen sind im adulten Stadium auf das Nahrungsangebot von Blüten, wie Pollen und Nektar angewiesen, benötigen aber auch andere Ressourcen für die Fortpflanzung. Das Ziel dieser Arbeit war die Untersuchung lokaler Management-Effekte von angesäten Blühhabitaten und der Effekte der umgebenden Landschaftsstruktur auf die biologische Kontrolle von Agrarschädlingen, die ohne Kontrolle erhebliche Ernteschäden anrichten können.

Im ersten Teil dieser Arbeit haben wir die Effektivität von angesäten Blühhabitaten hinsichtlich ihres Einflusses auf die natürlichen Gegenspieler von Blattläusen in unterschiedlich strukturierten Landschaften untersucht. In sieben kreisrunden und sich nicht überlappenden Landschaftssektoren (r = 1000 m) wurden jeweils vier Winterweizen-Felder ausgewählt. Die Landschaftssektoren wurden aufgrund ihres Anteils an Ackerland im Umkreis von 1000 m um das jeweilige Weizenfeld charakterisiert, und deckten einen Gradienten von variierender Landnutzungsintensität von strukturreich (~30% Ackerland im Sektor) bis strukturarm (~100% Ackerland im Sektor) ab. An die Winterweizen-Felder grenzten verschiedene semi-naturelle Habitattypen: breite Blühflächen, schmale Blühstreifen, natürlich entwickelte Ackerrandstreifen und Weizen-Felder als Kontrolle.

In der ersten Studie haben wir ein Ausschluß-Experiment mit verschiedenen Gruppen natürlicher Gegenspieler von Blattläusen in den Winterweizen-Feldern durchgeführt, um zu untersuchen, wie sich die Habitat-Veränderung auf die natürlichen Gegenspieler und auf das Wachstum der Blattlaus-Populationen auswirkt. In Übereinstimmung mit unserer Hypothese gingen die Blattlaus-Dichten am stärksten zurück, wenn alle Gegenspieler-Gruppen vorhanden waren, wobei die in der oberen Vegetation lebenden Prädatoren wie Schwebfliegen-Larven und Parasitoide am meisten zur Kontrolle der Blattläuse beigetragen haben. Die Blattlaus-Dichten sind um ca. das Fünffache durch die natürlichen Gegenspieler reduziert worden und standen in einem negativen Zusammenhang zum Räuber-Beute-Verhältnis (der in der Vegetation lebenden Räuber) und zur Parasitierungsrate. In von Blühhabitaten benachbarten Feldern war ein verringertes Blattlaus-Populationswachstum korreliert mit einem erhöhten Räuber-Beute-Verhältnis und einer erhöhter Parasitierungsrate. Entgegen unserer Erwartung konnten wir jedoch keinen Einfluss der umgebenden Landschaftsstruktur feststellen. In einer parallel stattfindenden Studie wurde der Einfluss der unterschiedlichen, an die Winterweizen-Felder angrenzenden Habitate und der Landschaftsstruktur speziell auf Schwebfliegen-Gemeinschaften untersucht. Die Populationsdichte der Schwebfliegen, besonders die der aphidophagen Arten, war höher in Blühstreifen und Blühflächen. Außerdem war der Artenreichtum der aphidophagen Schwebfliegen innerhalb der Weizenfelder mit angrenzenden Blühflächen ebenfalls höher. Im Gegensatz zu den Ergebnissen der ersten Studie nahmen Artenreichtum und Abundanz der Schwebfliegen in beiden Blühhabitaten mit zunehmendem Ackeranteil in der umgebenden Landschaft zu, was einen Konzentrationseffekt nahe legt: die Schwebfliegen konzentrieren sich auf die lohnendsten Ressourcen (= Blühhabitate) in den strukturarmen Landschaften.

Auf Grundlage der Ergebnisse der beiden ersten Studien befasste sich die dritte Studie mit dem Einfluss von in der oberen Vegetation lebenden Blattlaus-Prädatoren, v. a. Schwebfliegen- und Florfliegen-Larven, und von Blattlaus-Parasitoiden auf Blattlaus-Populationen und umfasste einen Zeitraum von drei Jahren. Die Studie wurde nach dem gleichen Versuchs-Design wie die beiden vorher genannten Studien durchgeführt. Sowohl die Blattläuse als auch die natürlichen Gegenspieler wurden von den lokalen Faktoren und den Landschaftsfaktoren beeinflusst. Aufgrund von erhöhten Räuber-Beute-Verhältnissen und erhöhten Parasitierungsraten in Weizenfeldern, die benachbart zu sowohl schmalen als auch breiten Blühhabitaten lagen, war dort die Blattlauskontrolle am effektivsten. Diese Effekte waren zudem besonders in strukturreichen Landschaften ausgeprägt. Allerdings unterlagen alle Effekte einer hohen inter-annuellen Variabilität, und traten am stärksten in einem Jahr mit niedrigen Blattlausdichten in Erscheinung.

Den zweiten Teil dieser Arbeit bildet eine Studie zur biologischen Kontrolle eines weiteren Agrarschädlings, des Rapsglanzkäfers *Meligethes aeneus*. Im Fokus dieser Untersuchung stand die potentielle Bedeutung von Blühhabitaten in Landschaften unterschiedlicher Strukturdiversität für die biologische Schädlingskontrolle von *M. aeneus* durch die Förderung der Reproduktion von Parasitoiden-Populationen. Die Studie wurde auf 20 Blühflächen durchgeführt, die jeweils im Zentrum eines Landschaftssektors lagen. Auch in dieser Untersuchung deckten die Sektoren einen Gradienten unterschiedlicher Landschaftskomplexität von strukturarm bis strukturreich ab. Herbivorie durch *M. aeneus* an *Sinapis alba*-Pflanzen, eine auf den Blühhabitaten eingesäte Wirtspflanze von *M. aeneus*, wurde nicht von der umgebenden Landschaftsstruktur beeinflusst. Jedoch nahm – wie von uns angenommen – die Parasitierung von *M. aeneus*-Larven, die sich in den Blütenständen von *S. alba* entwickeln, mit zunehmenden Anteil an semi-naturellen Habitaten in der umgebenden Landschaft zu. Darüber hinaus sind die Parasitoide auf den Blühflächen vor einer erhöhten Mortalität geschützt, der sie sonst durch die Bodenbearbeitung (Pflügen) auf Rapsfeldern ausgesetzt sind. Somit kann sich ein großer Reproduktionserfolg der Parasitoiden auf den Blühflächen in eine erhöhte biologische Kontrolle der Rapsglanzkäfer durch „spillover" in nahe gelegene Rapsfelder übertragen.

Wir kommen zu dem Schluss, dass Blühstreifen und Blühflächen konstante und ungestörte Habitate für die natürlichen Gegenspieler von Agrarschädlingen darstellen, zumal sie häufig über einige Jahre hinweg Bestand haben, und dadurch längerfristig Rückzugs- sowie Überwinterungshabitate als auch alternative Nahrungsressourcen in Form eines sehr reichen Pollen- und Nektarangebots bieten. Die Ergebnisse dieser Arbeit zeigen, dass Blühhabitate zum Aufbau und zur Erhaltung der Populationen von natürlichen Gegenspielern beitragen können, die die biologische Kontrolle von Blattläusen und Rapsglanzkäfern in nahe gelegenen Raps- und Getreidefeldern sicherstellen.

ACKNOWLEDGEMENTS

I sincerely thank my supervisor Prof. Dr. Teja Tscharntke for his advice, guidance and support throughout the years and for very helpful and constructive feedback on the manuscripts of this thesis. I wish to acknowledge Prof. Dr. Stefan Vidal for co-reviewing my thesis and Prof. Dr. Johannes Isselstein for being part of my defence committee.

I like to express my thanks to Dr. Carsten Thies who developed the main idea of my thesis and the individual studies, and for his support and encouragement during all the times of my Ph.D.

I furthermore kindly thank Dr. Eckhard Gottschalk and Werner Beeke for organising the Partridge Protection Project and all the matters involved with it. Many thanks go to all the farmers participating in this project, for the provision of flower habitats and wheat fields and for the kind collaboration!

With Sebastian Hänke I had a funny field season and share one, hopefully soon two nice publications. He, Eike Horn and Matthias Erb were very helpful during fieldwork. Thank you very much!

For the statistical analyses I could rely on the very profound knowledge of Dr. Yann Clough and Dr. Christoph Scherber. Thank you both for your great help, your patience and spending your time.

I really want to thank my two roommates Birgit Meyer and Kristin Krewenka. They both have become very close and reliable friends! I am also very grateful to my friends and dear colleagues for their help, discussions, inspiration, support, and for having a great time with good friends in Göttingen, especially Stephanie Sobek, Dagmar Clough, Doreen Gabriel, Indra Roschewitz, Patrick Höhn, Jochen Fründ, Jutta Gilles and particularly Ines Vollhardt and Suse Schiele, definitely the most helpful persons around in the Agroecology group!

Finally I deeply thank my parents, Ulrike and Dieter, and my sister Sabine for their support, encouragement, trust and enthusiasm, and for being around at all good and difficult times! – And not to forget: without their financial support I would not have been able to do my Ph.D. work!

A very heartfelt thank goes to my partner Maximilian von Fragstein und Niemsdorff, who was very encouraging, caring and helping, especially in the last weeks finishing this work and for his help with the thesis layout!

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Scheid, B., Tscharntke, T. & Thies, C. (2006) Effects of flowering strips and landscape complexity on cereal aphids and their enemies. *Verhandlungen der Gesellschaft für Ökologie* **36**: 236.

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Scheid, B.E., Thies, C. & Tscharntke, T. Enhancing rape pollen beetle parasitism with sown flower habitats in complex landscapes. *Agricultural and Forest Entomology* (in revision).

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