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Landscape configuration of crops and hedgerows drives local syrphid fly abundance

Running title: Landscape configuration effects on hoverflies

Sebastian Haenke^{1*}, Anikó Kovács-Hostyánszki^{1,2}, Jochen Fründ¹, Péter Batáry¹, Birgit Jauker³, Teja Tschamtké¹ and Andrea Holzschuh^{1,4}

¹Department of Crop Sciences, Agroecology, Georg-August University, Grisebachstr. 6, D-37077 Göttingen; ²MTA ÖK Ecosystem Services Research Group, Alkotmány út 2-4, H-2163 Vácraót, Hungary; ³Justus Liebig University, Department of Animal Ecology, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany; ⁴University of Würzburg, Department of Animal Ecology and Tropical Biology, Am Hubland, 97074 Würzburg, Germany

*Corresponding author: Sebastian Haenke, Grisebachstr. 6, D-37077, Göttingen, Tel.: +49-177-4651195, E-mail address: shaenke@gwdg.de

Summary

1. Human-dominated landscapes are characterized by a mosaic of natural and managed ecosystems, affecting arthropod communities on different spatial scales. Effective landscape management for functionally important organisms suffers from little understanding of

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organism spillover between semi-natural habitats and adjacent crops, and of how it is affected by the surrounding landscape.

2. We examined syrphid abundance (Diptera: Syrphidae) in three types of linear semi-natural habitats, differing in connectedness to annual crops and forest (forest edges (n=12), forest-connected hedges (n=11) and isolated hedges (n=12)), as well as in the adjacent oilseed rape or winter wheat fields (i.e. altogether n= 70 sites in 35 landscapes). The landscape circles with 1-km radius around the study sites differed in the proportion of oilseed rape (ranging from 0 to 35% oilseed rape) enabling us to test landscape-scale effects of oilseed rape.

3. Aphidophagous syrphids were more abundant in forest-connected hedgerows than in forest edges (with isolated hedges being intermediate), and more abundant in crop fields adjacent to hedgerows than adjacent to forest edges, indicating spillover from semi-natural habitats to the adjacent crop fields. Aphidophagous syrphid abundance was higher in semi-natural habitats adjacent to oilseed rape fields than adjacent to wheat fields if the proportion of oilseed rape in the landscape was low (indicating local concentration).

4. *Synthesis and applications.* This study highlights the potential of hedgerows to enhance the abundances of beneficial syrphids and their spillover to adjacent crop fields, especially when they are connected to forests. We provide evidence that this local exchange is moderated by the extent of mass-flowering crops in the surrounding landscapes due to local concentration. Therefore, measurements for the improvement of local biological functioning should be evaluated by simultaneously investigating local and regional aspects of crop configurations to allow for region-specific management recommendations. Increasing the total amount of hedgerows in the agricultural matrix under moderate landscape-scale proportions of mass-flowering crops may serve best for the conservation of biodiversity and augmentation of important ecosystem services such as biological control and pollination in landscapes dominated by agricultural cultivations.

Key words: *agri-environmental management, dilution, floral resources, habitat connectivity, habitat fragmentation, hoverflies, oilseed rape, wheat*

Introduction

Human-dominated landscapes are mosaics of cultivated areas interspersed by semi-natural habitats with changing degrees of connectedness, affecting trophic interactions and the spillover across the crop–non-crop interface (Kremen, Williams & Thorp 2002; Marshall & Moonen 2002; Tschardtke *et al.* 2005; Rand, Tylianakis & Tschardtke 2006). Configuration and composition of agricultural landscapes have an impact on biodiversity and associated ecosystem services such as pollination and biological pest control (Tews *et al.* 2004; Holzschuh *et al.* 2007; Fahrig *et al.* 2011; Holzschuh *et al.* 2011).

Landscape-wide conservation of natural habitats has been shown to mitigate the negative effects of agricultural intensification (Altieri 1995; Burel & Baudry 1995) and maintain local functionally important species pools (Loreau, Mouquet & Gonzalez 2003). Improving landscape heterogeneity and connectivity can facilitate recolonisation of disturbed habitats, counterbalancing locally degraded ecosystem functioning (Fahrig 1997; Elmqvist *et al.* 2003). Woody landscape elements such as scattered forest patches and hedgerows are often the only remaining refuges for wildlife in agricultural landscapes (Forman & Baudry 1984). Non-crop habitats can provide natural enemies and pollinating insects with resources such as alternative prey or nectar and pollen resources, shelter from adverse weather conditions or hibernating sites. Spillover of beneficial insect groups from semi-natural habitats to adjacent crops has been reported for many insect groups such as ground beetles (Carabidae), lacewings (Chrysopidae) or syrphids (Syrphidae) (Booij, Nijs & Noorlander 1995; Long *et al.* 1998; Bianchi, Booij & Tschardtke 2006; Haenke *et al.* 2009). However, only little is known about the importance of species movements between semi-natural

habitats and crops, including bi-directional spillover between crop and non-crop habitats (Rand, Tylianakis & Tscharntke 2006; Blitzer *et al.* 2012).

One of the most recent challenges for biodiversity conservation in European agricultural landscapes is the increased area of oilseed rape *Brassica napus* L. planted mainly for bio-fuel production. Oilseed rape, a highly rewarding food resource, attracts insect groups providing both services such as biological control of aphid pests (e.g. syrphid flies) or pollination (e.g. bees) and disservices such as sap-feeding, herbivory and dissemination of diseases (e.g. cabbage aphids, pollen beetles, stem weevils) (Ferguson *et al.* 2003; Pontoppidan *et al.* 2003; Westphal, Steffan-Dewenter & Tscharntke 2009; Jauker *et al.* 2012). Although densities of important pollinators such as bumblebees (*Bombus* spp.) and cavity-nesting bees and wasps have been shown to increase with high amounts of oilseed rape at the landscape scale (Westphal, Steffan-Dewenter & Tscharntke 2003; Diekötter *et al.* 2013), negative effects such as increased competition between crop and wild plants for pollinators have also been found recently (Holzschuh *et al.* 2011).

Syrphids are of particular importance in intensively used agricultural landscapes by maintaining two important ecosystem services, biocontrol and pollination. Species differentially utilize crop and non-crop habitats, depending on traits such as dispersal abilities or larval and adult food requirements. Highly mobile and generalist syrphids can profit from mass-flowering crops (e.g. oilseed rape and field beans) as highly rewarding nectar and protein resources, needed for adult feeding and egg development (Jauker & Wolters 2008). Additionally, aphidophagous syrphid larvae can profit from high densities of cereal aphids (e.g. *Metopolophium dirhodum* L., *Rhopalosiphum padi* L., *Sitobion avenae* L.) temporarily occurring in cereals such as wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) (Schmidt *et al.* 2003).

In this study, we compared the abundance of aphidophagous and non-aphidophagous syrphids among three linear semi-natural habitat types (forest edges, forest-connected hedges and isolated hedges) and among two crop types (oilseed rape and wheat) adjacent to these habitats, along a gradient of oilseed rape proportion in the surrounding landscapes. To the best of our knowledge, the effect of landscape context on local spillover between crop and non-crop habitats has not yet been analysed.

We tested the following hypotheses: (i) abundance of syrphids differs among linear woody habitats, and these differences are mirrored in adjacent crop fields due to spillover from the semi-natural habitats. (ii) abundance of syrphids is higher in the flower-rich oilseed rape than in wheat fields, and this difference between crop types also affects syrphid spillover from crop fields to adjacent semi-natural habitats. (iii) spillover from oilseed rape fields is more pronounced in landscapes with low proportions of oilseed rape, because of landscape-scale dilution of syrphids in landscapes with high proportions of oilseed rape (see Fig. 1).

Materials and methods

Study area and study design

The study was conducted in the vicinity of the city of Göttingen (51.5°N, 9.9°E) in southern Lower Saxony, Germany, in 2009. A map of the study sites is available in Kovács-Hostyánszki *et al.* 2013. The area is dominated by intensive agriculture (*ca.* 75%) with cereal and oilseed rape fields (2–5 ha average field size), interspersed by fragments of semi-natural habitats such as forests, hedgerows and grasslands (Steffan-Dewenter *et al.* 2002). Forest edges and hedges are usually managed by pruning (every 8–15 years). Forest edges are linear structures like hedges, but dominated by deciduous tree species such as the common beech *Fagus sylvatica* L.. Hedges in this study are linear landscape elements that are connected to

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forest edges (forest-connected hedgerows; spreading perpendicularly from the forest edge into the agricultural matrix) or isolated (isolated hedgerows; completely surrounded by crop fields). Example photos for examination of local configuration of forest, hedgerows and crop fields are available in Appendix S1 in Supporting Information. The dominant shrub species in hedges are blackthorn *Prunus spinosa* L., hawthorn *Crataegus* spec. L. and hip *Rosa canina* L.. Limitations in the availability of suitable study sites did not allow selection of hedgerows and forest edges of equal orientation. Furthermore, due to lack of suitable linear semi-natural habitats it was not possible to find study sites in a wider spectrum than 0 to 35 % of landscape-wide oilseed rape proportions. However, spatial orientation across semi-natural habitat types was randomly mixed across, whereas, if possible, sampling was mainly carried out at south-west orientated sides of hedgerows and forest edges. We compared syrphid abundance in three types of linear semi-natural habitats (semi-natural habitat = SNH), which differed in connectedness to annual crops and forest: forest edges bordering crop fields on one long side (forest edge, n=12), hedgerows connected to forest on one narrow side and reaching perpendicularly into a matrix of crop fields (forest-connected hedge, n=11) and isolated hedgerows completely surrounded by crop fields (isolated hedge, n=12), with a minimum distance of 300 m to the next forest. With respect to syrphid movements, this represents gradients of expected organism exchange between forest edges or hedgerows (over-wintering habitat, Hondelmann & Poehling 2007) and crop fields (foraging and ovipositioning habitat, Meyer, Jauker & Steffan-Dewenter 2009). Influx of syrphids from forest to linear woody habitats should be highest in forest edges (where one long side borders forest), intermediate in connected hedges (where only one narrow side borders forest), and lowest in isolated hedges (with no forest nearby). Accordingly, the influx from forest to crop fields should be highest via forest edges, intermediate via connected hedges, and lowest via isolated hedges. Influx from crop fields to woody habitats should be highest in isolated

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hedges, which have the highest relative cover of crop fields in the surrounding area, intermediate to connected hedges bordering crop fields on both long sides and lowest in forest edges.

Additionally syrphid abundance was analysed in conventionally managed crop fields (oilseed rape and winter wheat) adjacent to the above-mentioned habitat types. To the best of our knowledge, crop management did not differ between fields with different adjacent habitat type. Half of the replicates of each habitat type (n=6) was located adjacent to oilseed rape fields, whereas the other half was located adjacent to wheat fields (n=6). In the course of this study one study site of forest-connected hedgerow next to wheat had to be excluded, because the farmer withdrew permission to sample in his field (reducing this category to n=5). Study sites had a minimum distance of 300 metres to each other in order to minimize spatial autocorrelation (Steffan-Dewenter & Tschardt 1999). Study sites were selected along a gradient of the proportion area of oilseed rape (OSR %) within 1-km radius around sites. In a comparison of multiple radii of landscape sectors (0.5–4 km), Haenke *et al.* (2009) showed that aphidophagous syrphids respond to environmental changes in structural landscape complexity at rather small landscape scales (0.5–1 km). Calculations were based on digital thematic maps (ATKIS DTK 50) complemented by ground checking of crops in the study season (ArcGIS Desktop 10.0).

Sampling of syrphid flies

Adult syrphids were sampled along 200-m long transects by sweep netting (i) in vegetation structure of forest edges and hedgerows (three-step method, one sweep per footstep; 1st sweep near the ground, followed by 2nd sweep in medium height, and 3rd sweep in maximum reachable height of forest edges and hedgerows) and (ii) in the adjacent winter wheat and oilseed rape fields, located parallel to the forest edges and hedgerows at distances of 6 m

from the field boundary one sweep per footstep). Sampling was carried out in both semi-natural habitat and adjacent crops two times during oilseed rape flowering in the first half of May (once per week) and two times during wheat milk-ripening in the first half of June (once per week). Sampling was done under comparable weather conditions and time of day. Data were pooled for oilseed rape flowering (May) and for winter wheat milk-ripening period (June). All invertebrates were placed in 3- L plastic bags, killed with diethyl ether, cooled, and then taken to the laboratory. Syrphids were separated from all other arthropod taxa and identified, where possible, to species level using identification keys (van Veen 2004). Syrphid species were separated into two trophic groups according to their larval feeding type: aphidophagous feeding type and non-aphidophagous feeding type including saprophagous, detritivorous, bacteriophagous, phytophagous and fungivorous species (a list of syrphid species is available in Table S1).

Statistical analyses

Abundance of syrphids (aphidophagous and non-aphidophagous separately) was analysed using linear mixed models (LMM) with site as random factor to control for the lack of temporal independence between the data from the two sampling dates per site. We performed two separate analyses (i) for semi-natural habitats (data collected from forest edges, forest-connected and isolated hedgerows) and (ii) for crop fields (data collected from oilseed rape and wheat fields). Models for abundance in semi-natural habitats included the following explanatory variables: (i) OSR % in the surrounding landscape at 1-km radius, (ii) habitat type (forest edges, forest-connected and isolated hedgerows), (iii) adjacent crop type (oilseed rape vs. wheat) and (iv) sampling date (during oilseed rape flowering vs. wheat milk-ripening). Models for abundance in crop fields included the following explanatory variables: (i) OSR % in the surrounding landscape at 1 km radius, (ii) adjacent habitat type (forest

edges, forest-connected and isolated hedgerows), (iii) crop type (oilseed rape vs. wheat) and (iv) sampling date (during oilseed rape flowering vs. wheat milk-ripening). Model assumptions were checked by examining the Gaussian distribution of the residuals in normal quantile-quantile plots. Data on abundance of syrphids were log-transformed to compensate for the skewness of the data in order to achieve normally distributed residuals. Up to three-fold interactions were tested in the models. All non-significant main effects and interactions were excluded from the models using a backward selection procedure. In a second step, we tested model simplifications with maximum likelihood tests in order to gain minimum adequate models. All calculations were done using “nlme”, R package version 3.1-109 (R Development Core Team 2012). Differences between types of semi-natural habitat (main effect) were further analysed using Tukey HSD post-hoc tests implemented in “multcomp”, R package version 1.2-18 (Hothorn, Bretz & Westfall, 2008; R Development Core Team, 2012) (R Development Core Team 2012). Means and standard errors are given in the text. *Pseudo* R^2 (percent of variation explained) as goodness-of-fit-measure for linear mixed models were calculated, using function lmmR2W of “lmmfit”, R package version 1.0.

Species richness of aphidophagous and non-aphidophagous syrphids was highly correlated with their corresponding abundance in semi-natural habitats (aphidophagous species richness: Spearman $\rho=0.9$, $P<0.001$; non-aphidophagous species richness: $\rho=0.9$, $P<0.001$) and in crops (aphidophagous species richness: $\rho=0.9$, $P<0.001$; non-aphidophagous species richness: $\rho=0.9$, $P<0.001$). Therefore, we included abundance as covariate in the species richness models. The largest part of variance in species-richness models was explained by the variance in syrphid abundance. Results of species-richness analyses are presented in the supplementary material (Table S2; Fig. S1–S 2).

Results

A total of 47 syrphid species with 526 individuals was collected during the two sampling periods. Syrphids predominantly occurred in semi-natural habitats (321) compared to crop fields (205 individuals). The syrphid community was dominated by aphidophagous species (30) and individuals (445). Absolute number per syrphid species is given in Table S1 in Supporting Information.

Aphidophagous syrphids

Abundance of aphidophagous syrphids in semi-natural habitat was higher in forest-connected hedgerows than in forest edges, with isolated hedges being intermediate (Table 1; Fig. 2). Adjacent oilseed rape fields enhanced aphidophagous syrphid abundance in the adjacent SNH compared to SNH adjacent to wheat, but this effect was modified by the total amount of oilseed rape in the landscape (interaction adjacent crop type \times OSR %; Table 1). Thus, at increasing proportions of oilseed rape in the surrounding landscape, abundance of aphidophagous syrphids increased in SNH next to winter wheat and decreased in SNH next to oilseed rape fields (Fig. 3). The abundance of aphidophagous syrphids during wheat milk-ripening (date 2) was more than twice as high as during oilseed rape flowering (date 1) (means \pm SE: 5.5 ± 1.0 vs. 2.1 ± 0.4).

Abundance of aphidophagous syrphids in crop fields was affected by the type of adjacent SNH, with higher numbers in crop fields next to forest-connected and isolated hedgerows than to forest edges (Table 1; Fig. 2). Here, crop type had a weak effect on aphidophagous abundance, which tended to be higher in oilseed rape than in wheat fields (Table 1; Fig. 2).

Non-aphidophagous syrphids

There was only a weak effect of SNH type on non-aphidophagous syrphid abundance, which tended to be lowest in isolated hedges (Table 1, Fig. 4). Other factors did not affect this functional group in semi-natural habitats (Table 1). In crop fields, non-aphidophagous abundance was higher in oilseed rape than in wheat fields (Table 1; Fig.4). Abundance of this group declined in crop fields next to forest edges, and was higher during oilseed rape flowering (date 1) than during wheat milk-ripening (date 2). Temporal change was less apparent or even positive in fields next to hedges when located next to forest edges (interaction: adjacent habitat type \times date; Table 1; Fig.4).

Discussion

In this study we compared the influence of three linear semi-natural habitat types (SNH; forest edges vs. forest-connected hedgerows vs. isolated hedgerows) and two cropping systems (wheat vs. oilseed rape fields = OSR) on the abundance of two functional groups of syrphids (aphidophagous and non-aphidophagous). Furthermore, we compared the influence of the SNH types on syrphid abundance in adjacent crop habitats and vice versa, and the effects of varying proportions of mass-flowering OSR at the landscape scale (OSR %).

Aphidophagous syrphid abundance was higher in forest-connected hedgerows than in forest edges with isolated hedges showing intermediate abundance. This pattern was mirrored by the adjacent crop fields, where abundance was highest adjacent to forest-connected hedgerows and lowest adjacent to forest edges. These similar patterns in SNH and adjacent crop fields appear to be a result of spillover from SNH to nearby crop fields. Thereby syrphids may predominantly use crop fields as oviposition sites and adult feeding (pollen and nectar resources), whereas nearby SNH may be more permanently used as resting sites, shelter from predator pressure or disturbance and as alternative food resources (Sutherland,

Sullivan & Poppy 2001a; Scalerio, Iannotta & Brandmayr 2007). Furthermore, our results suggest that the relationship of syrphid abundance in semi-natural habitats is modified by the amount of OSR at the landscape scale. Thereby large-scale syrphid movements being mediated by high amounts of oilseed rape at the landscape scale may strongly influence the extent of local spillover from crop fields to nearby SNH.

Abundance of both aphidophagous and non-aphidophagous syrphids was higher in oilseed rape than in wheat fields, confirming the general idea that functionally important insect guilds can profit from mass-flowering crops that provide huge amounts of pollen and nectar resources (Jauker *et al.* 2012). Aphidophagous syrphids appeared to profit from oilseed rape even after the main flowering period, possibly due to late-season aphid infestations (Brown *et al.* 1999). While the role of wild bees and managed honeybees for crop pollination is comprehensively documented (Corbet, Williams & Osborne 1991; Delaplane & Mayer 2000), recently also syrphids have been shown to be potentially efficient pollinators of oilseed rape (Jauker & Wolters 2008; Bommarco, Marini & Vaissière 2012). Syrphid fly communities were dominated by the aphidophagous larval feeding type, a pattern that is typical in highly intensified land-use systems (Frank 1999; Sadeghi & Gilbert 2000; Haenke *et al.* 2009, Meyer, Jauker & Steffan-Dewenter 2009).

Aphidophagous syrphid flies

Aphidophagous syrphids were strongly affected by the type of SNH, with higher abundance in forest-connected hedgerows compared to forest edges. Movements of syrphids in the agricultural matrix appear to be influenced by both the connectedness of semi-natural habitat and the crop cover in the surrounding landscape. The connectedness of SNH is highest for forest edges, intermediate for forest-connected hedgerows and lowest in isolated hedgerows, while surrounding crop-cover is lowest for forest edges and highest for isolated hedgerows.

Although aphidophagous syrphids often use forest edges as overwintering habitats (Hondelmann & Poehling 2007), they find their larval prey mainly in arable fields (Meyer, Jauker & Steffan-Dewenter 2009). Jauker *et al.* (2009) showed increasing aphidophagous syrphid abundance with increasing distance from SNH. The relative cover of crop fields is higher around hedgerows than around forest edges and this may facilitate syrphid movements across the crop–non-crop interface due to better access to feeding sites in crop fields. In turn, this could have increased the attractiveness of hedgerows – compared to forest edges – as resting sites or places for alternative food resources. Additionally, the high abundances of aphidophagous syrphids in forest-connected hedgerows provide evidence that high connectivity of forest edges and linear non-crop habitats facilitates syrphid dispersal from hibernation sites in forest patches into the agricultural matrix. Habitat connectivity and fragmentation are supposed to affect species movements according to species-specific traits such as dispersal ability, reproduction frequency, or breadth of feeding niches (Öckinger *et al.* 2010). Thus increasing the total amount of hedgerows and connectivity can help to mitigate the negative effects of agricultural intensification such as species loss and loss of related ecosystem functions like biological control and pollination.

After main oilseed rape flowering, aphidophagous syrphid abundance increased in SNH. This temporal pattern suggests that SNH become increasingly attractive during the season and may serve as refugia providing alternative reproduction sites and sites for adult feeding. Nevertheless also phenology and development of annual syrphid fly populations may contribute to increased syrphid abundance in SNH. Additionally, this study suggests that mass-flowering OSR can have positive effects on the abundance of aphidophagous syrphids in nearby SNH, with increased abundance in SNH next to OSR fields compared to wheat fields. This finding resembles patterns found for bumblebees, which exhibit strongly increased visitation rates of flowering wild plants in SNH adjacent to mass-flowering field

bean fields (Hanley *et al.* 2011). A novel finding of our study is that the landscape-scale amount of mass-flowering crops, i.e. of OSR, apparently modifies spillover processes between non-crop and crop habitats. Aphidophagous syrphid abundance was higher in SNH adjacent to OSR fields than adjacent to wheat fields only if the proportion of oilseed rape in the landscape was low. This positive effect of adjacent oilseed rape decreased with increasing proportion of oilseed rape in the landscape. This interesting pattern is obviously a result of differing OSR availabilities at the landscape scale, resulting in specific effects on abundance depending on local crop systems. Excellent flight abilities may allow aphidophagous syrphids to use remote, but highly attractive OSR fields in landscapes with low OSR proportions. This may lead to increased local concentration of syrphids in nearby SNH (Sutherland, Sullivan & Poppy 2001b) due to spillover from crop fields to adjacent SNH. Contrastingly, in landscapes with high OSR proportions, only low abundance of syrphids was recorded in SNH. This finding suggests that at high OSR proportions, local abundance in SNH and OSR fields is depressed due to landscape-wide dilution of syrphids among extensively available oilseed rape fields. Landscape-scale effects such as dilution of functionally important insect guilds are poorly understood, but may often lead to negative effects on maintaining important ecosystem services such as pollination and biological control in crops used, and also in conservation sites (Tschardt *et al.* 2012, Kovács-Hostyánszki *et al.* 2013). Holzschuh *et al.* (2011) showed that increasing amounts of oilseed rape at the landscape scale can lead to an increased competition for pollinators between crops and endangered wild plants. Such negative effects on wild plant reproduction may also occur in the SNH investigated in this study, potentially affecting different taxa such as overwintering farmland birds and small mammals, which depend on fruit bearing shrubs in forest edges and hedgerows (Siriwardena, Calbrade & Vickery 2008). Moderate proportions of mass-flowering crops may serve best for the demand to increase densities of beneficial

arthropods, whereas habitat management schemes should take into account the varying influence of mass-flowering crops in relation to local crop systems.

In contrast to the situation in SNH, a landscape-scale effect of OSR on local aphidophagous syrphid abundance within crop fields was not found. This may indicate that crop fields compared to SNH are only temporarily used habitats for adult feeding and oviposition, resulting in a high variability and low abundance, thereby explaining only marginally increased aphidophagous abundance in OSR compared to wheat fields.

Non-aphidophagous syrphids

In contrast to the results for aphidophagous syrphids, non-aphidophagous larval feeding types were only weakly affected by SNH type. Non-aphidophagous abundance was higher in OSR fields with higher abundance next to forest edges during the OSR flowering period.

Non-aphidophagous syrphids showed a tendency of higher abundance in forest edges compared to isolated hedgerows. Compared to aphidophagous syrphids these smaller differences among SNH may be a result of relatively low numbers of observed non-aphidophagous individuals. Nevertheless, differences in reproduction strategy of non-aphidophagous syrphids may have caused lesser preference of non-aphidophagous syrphids for the SNH compared in this study. While aphidophagous flies can find suitable aphid species for larval feeding in crop fields as well as in hedgerows and forest edges, most of the non-aphidophagous syrphid individuals found in this study belong to species dependent on relatively moist larval habitats such as wet decaying plant material or water bodies (e.g. *Eristalis spec.* and *Syrirta pipiens*) (van Veen 2004), which are scarce in the investigated SNH. However, non-aphidophagous abundance was increased in oilseed rape fields providing huge amounts of pollen and nectar resources, thereby suggesting large-scale foraging behaviour of this syrphid fly group. Non-aphidophagous syrphid abundance was highest in

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forest edges adjacent crop fields during oilseed-rape flowering. This temporal pattern may be explained by an increased overwintering success of non-aphidophagous syrphids in forest edges compared to openland habitats such as hedgerows, whereas later in the year, migration to sites suitable for oviposition may become increasingly important. Thus non-aphidophagous syrphids, although apparently benefiting from mass-flowering crops such as oilseed rape, appear to be less adapted to intensively used agricultural landscape than generalist aphidophagous syrphids, possibly due to a higher heterogeneity of larval habitat requirements.

Conclusion

Biodiversity in highly intensified land-use systems is of crucial importance for both, maintaining important ecosystem services and improving resilience against spatial and temporal changes in landscape composition (Bengtsson *et al.* 2003). We show how linear landscape elements such as hedgerows attract beneficial aphidophagous syrphid flies, with a potentially positive effect on biological control in highly intensified land-use systems. Thus environmental schemes should aim to increase the amount of connected hedgerows, as these habitats appear to also increase the abundance of aphidophagous syrphids in nearby crop fields. Furthermore, we provide evidence that high amounts of oilseed rape at the landscape scale lead to landscape-scale dilution of aphidophagous syrphids and also affect movements of these functionally important insects across the crop–non-crop interface. Hence, future environmental schemes should take landscape-scale effects of mass-flowering crops into account, with moderate proportions potentially serving best for augmentation and sustainment of locally important ecosystem services.

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Table 1: Linear mixed models (LMM) relating aphidophagous and non-aphidophagous syrphid abundance to four predictive factors. Table shows results for syrphids within semi-natural habitats and within crop fields. In semi-natural habitats we tested for (i) landscape scale proportion of oilseed rape OSR %, (ii) habitat type (forest edge vs. connected hedge vs. isolated hedge), (iii) adjacent crop type (oilseed rape vs. winter wheat) and (iv) date (during oilseed rape flowering vs. winter wheat milk-ripening). In crop fields we tested for (i) OSR %, (ii) adjacent habitat type, (iii) crop type and (iv) date. F-, P- and *Pseudo R*²-values (i.e. % variation explained) are given. Significant effects are shown in bold. Brackets indicate marginal significance

| | Semi-natural habitat | F | P | % variation explained | Crop | F | P | % variation explained |
|-------------------|----------------------|-------------|--------------|-----------------------|-----------------------|------------|--------------|-----------------------|
| SYRPHID ABUNDANCE | | | | | | | | |
| Aphidophagous | OSR % | 0.0 | 0.962 | 0.1 | adjacent habitat type | 8.0 | 0.002 | 18.6 |
| | habitat type | 6.8 | 0.004 | 13.5 | crop type | 3.9 | (0.059) | 6.0 |
| | adjacent crop type | 8.3 | 0.008 | 8.1 | | | | |
| | date | 11.4 | 0.002 | 12.7 | | | | |
| | OSR % × | 4.7 | 0.038 | 4.7 | | | | |

| | | | | | | | | |
|-------------------|--------------------|-----|---------|-----|------------------------------|------------|--------------|-------------|
| Non-aphidophagous | adjacent crop type | 3.1 | (0.061) | 8.4 | adjacent habitat type | 0.4 | 0.647 | 1.1 |
| | habitat type | | | | crop type | 4.4 | 0.044 | 5.9 |
| | | | | | date | 1.0 | 0.321 | 1.3 |
| | | | | | adjacent habitat type × date | 4.0 | 0.029 | 10.3 |

Figure legends

Figure 1: Hypothesized syrphid fly densities (continuous arrows) and local spillover as the crop–non-crop interface (dashed arrows) in situations of high (a) vs. low (b) proportions of oilseed rape at the landscape scale.

(a) In oilseed rape (1), low local syrphid density because of dilution effects across large areas of mass-flowering crops and low local spillover. In winter wheat (2), high local syrphid density in landscapes with high proportions of OSR (concentration due to high aphid abundance in wheat), accompanied by high local spillover between the crop–non-crop interface.

(b) In oilseed rape (3), high local syrphid density in landscapes with low proportions of OSR (concentration to highly rewarding pollen and nectar availability of OSR), accompanied by high local spillover between the crop–non-crop interface. In winter wheat (4), low local syrphid density in landscapes with low proportions of OSR (dilution among wheat fields) accompanied by low local spillover between the crop–noncrop interface.

Figure 2: Abundance of aphidophagous syrphid flies in semi-natural habitats (in SNH) adjacent to wheat and oilseed rape fields (first row of graphs; Forest = forest edges, Conn. =

forest-connected hedges, Isol. = isolated hedges) and in crop fields (in crop) adjacent to semi-natural habitats (second row of graphs) at Date 1 (first column; during oilseed rape flowering) and at Date 2 (second column; during winter wheat milk-ripening). Means and standard errors (on the log-scale) are shown. Number labels on the y-axis are back-transformed.

Figure 3:

Aphidophagous syrphid fly abundance in semi-natural habitats (SNH) next to (i) oilseed rape fields (solid line) and (ii) wheat fields (dashed line) in relation to proportion of oilseed rape in the surrounding landscape (1-km radius). Lines show linear mixed model (LMM) predictions.

Figure 4: Abundance of non- aphidophagous syrphid flies in semi-natural habitats (in SNH) adjacent to wheat and oilseed rape fields (first row of graphs; Forest = forest edges, Conn. = forest-connected hedges, Isol. = isolated hedges) and in crop fields (in crop) adjacent to semi-natural habitats (second row of graphs) at Date 1 (first column; during oilseed rape flowering) and at Date 2 (second column; during winter wheat milk-ripening). Means and standard errors (on the log-scale) are shown. Number labels on the y-axis are back-transformed.

Figure 1:

Crop-noncrop spillover of syrphid flies

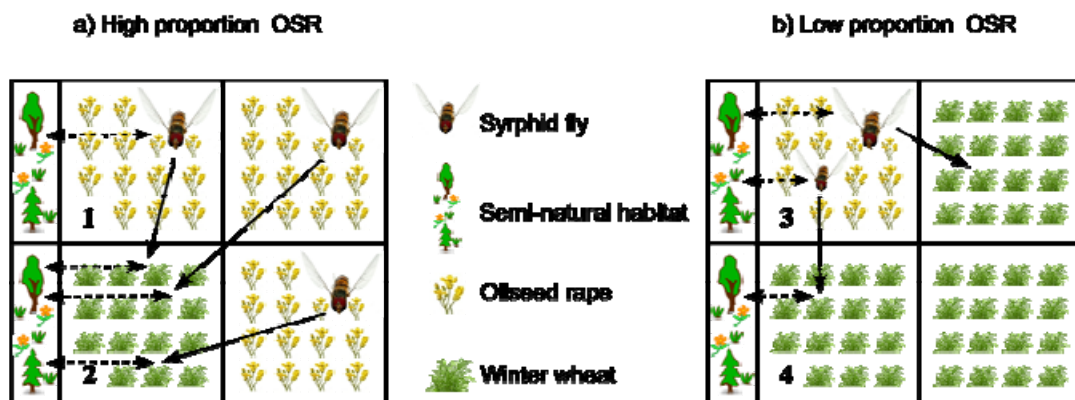


Figure 2:

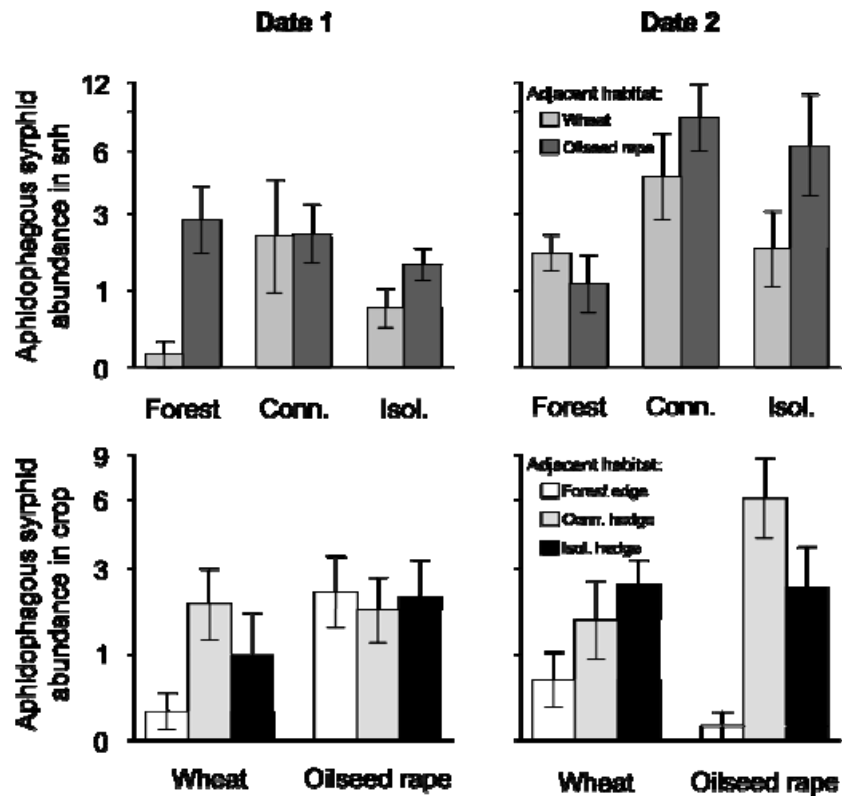


Figure 3:

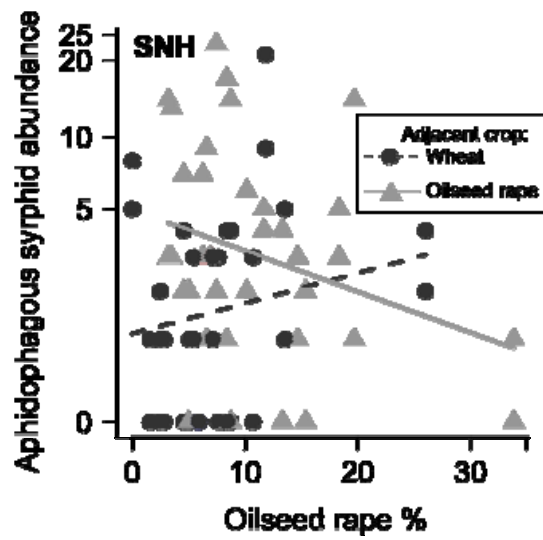
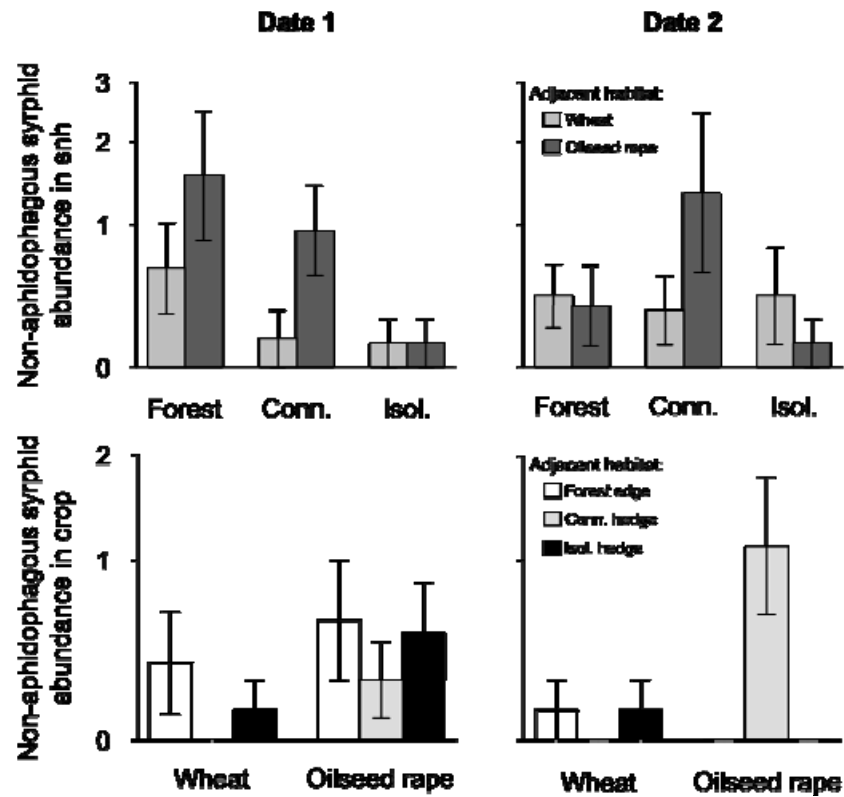


Figure 4:



Supporting Information

Additional supporting information can be found in the online version of this article.

Appendix S1. Example photos for examination of local configuration of forest, hedgerows and crop fields

Table S1. Syrphid numbers in semi-natural habitats and crop fields

Table S2. Results of aphidophagous and non-aphidophagous syrphid species analyses

Fig. S1. Aphidophagous syrphid species in semi-natural habitats and crop fields separated by date of sampling

Fig. S2. Non-aphidophagous syrphid species in semi-natural habitats separated by date of sampling.