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Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes

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Summary

Landscape context and habitat quality may have pronounced effects on the diversity of flower visiting insects. We investigated whether the effects of landscape context and habitat quality on flower visiting insects interact in agricultural landscapes in the Netherlands. Landscape context was expressed as the area of semi-natural habitats or the density of linear landscape features, and was quantified at spatial scales ranging from 250 to 2000 m. Habitat quality was determined as flower abundance. Species richness and abundance of hoverflies and bees were determined along 16 stream banks experiencing similar environmental conditions but situated in areas with contrasting landscape context. Only flower abundance and the area of semi-natural habitats within 500–1000 m were significantly related to species richness of hoverflies and bees and these factors had interacting effects on both species groups. Our results suggest that the regional area of semi-natural habitats had a positive effect on hoverfly species richness when flower abundance was relatively high, but not when flower abundance was low. Moreover, flower abundance had positive effects on hoverfly species richness only in areas with relatively many semi-natural habitats. Contrastingly, flower abundance had a more positive effect on bee species richness in landscapes with few semi-natural habitats compared to landscapes with more semi-natural habitats. Our results suggest that the importance of landscape context for the species richness of flower visiting insects depends upon the quality of the habitat patches.

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Zusammenfassung

Landschaftseinbindung und Habitatqualität könnten deutliche Auswirkungen auf die Diversität blütenbesuchender Insekten haben. Wir untersuchten, ob die Auswirkungen der Landschaftseinbindung und der Habitatqualität auf blütenbesuchende Insekten in Agrarlandschaften in den Niederlanden interagieren. Die Landschaftseinbindung wurde durch die Fläche der halbnatürlichen Habitate oder die Dichte linienhafter Landschaftsstrukturen ausgedrückt und auf räumlichen Skalen quantifiziert, die von 250 m bis 2000 m reichten. Die Habitatqualität wurde als Blütenabundanz bestimmt. Es wurde der Artenreichtum und die Abundanz von Schwebfliegen und Bienen entlang von Flussufern bestimmt, die gleiche Umweltbedingungen aufwiesen, sich aber in Gebieten unterschiedlicher Landschaftseinbindung befanden. Nur die Blütenabundanz und die Fläche halbnatürlicher Habitate innerhalb von 500–1000 m war signifikant mit dem Artenreichtum der Schwebfliegen und Bienen verbunden und die Faktoren hatten interagierende Auswirkungen auf beide Artengruppen. Unsere Ergebnisse weisen darauf hin, dass die regionale Fläche der halbnatürlichen Habitate einen positiven Effekt auf den Artenreichtum der Schwebfliegen hat, wenn die Blütenabundanz relativ hoch ist, jedoch nicht, wenn die Blütenabundanz gering ist. Darüber hinaus hatte die Blütenabundanz nur in Gebieten mit relativ vielen halbnatürlichen Habitaten positive Auswirkungen auf den Artenreichtum der Schwebfliegen. Im Gegensatz dazu hatte die Blütenabundanz in den Landschaften einen stärkeren positiven Effekt auf den Artenreichtum der Bienen, die im Vergleich zu Landschaften mit vielen halbnatürlichen Habitaten nur wenige halbnatürliche Habitate aufwiesen. Unsere Ergebnisse weisen darauf hin, dass die Bedeutung der Landschaftseinbindung für den Artenreichtum von blütenbesuchenden Insekten von der Qualität der Habitatflecken abhängt.

Introduction

Flower visiting insects provide important ecosystem services such as pollination (Kearns, Inouye, & Waser, 1998; Williams, 1995) and pest control (Kruess & Tscharntke, 1994). Honeybee numbers continue to decline due to infestations with *Varroa jacobsoni* mites and hybridization with Africanized honeybees. An increasing number of pesticides are prohibited because of more stringent environmental laws. Thus, the role of wild pollinators and natural enemies becomes increasingly important. However, many pollinating insect species are experiencing steep declines in both population densities and range (Buchmann & Nabhan, 1996; Williams, 1982). A large proportion of flower visiting insects are species that are colourful and conspicuous, aesthetically appealing even to the general public, and relatively easy to identify to the species level (e.g. bumblebees (Hymenoptera: Apidae, *Bombus* spp.), butterflies (Lepidoptera), hoverflies (Diptera: Syrphidae)). These considerations have resulted in a large body of research aiming to identify important factors that determine species richness and abundance of flower visiting insects, particularly in anthropogenic environments (Kleijn, Berendse, Smit, & Gilissen, 2001; Lagerlöf, Stark, & Svensson, 1992; Rands & Sotherton, 1986; Sparks & Parish, 1995; Steffan-Dewenter & Tscharntke, 1997; Steffny, Kratochwil, & Wolf, 1984; Wratten et al., 2003).

At the local scale, insect species richness is typically positively correlated with habitat quality. Habitat quality is usually measured as plant species richness (Banaszak, 1983; Kleijn et al., 2004; Steffan-Dewenter & Tscharntke, 2001) or the abundance of plants needed for food and reproduction (Moilanen & Hanski, 1998; Steffan-Dewenter & Tscharntke, 2001; Thomas et al., 2001). The majority of this kind of studies has been carried out in European agricultural landscapes. At the regional scale insect species richness and abundance is more often related to landscape context (i.e. quantity and distribution of specific habitats needed for foraging and reproduction, Dauber et al., 2003; Hanski, Pakkala, Kuussaari, & Guangchun, 1995; Steffan-Dewenter, Münzenberg, Buerger, Thies, & Tscharntke, 2002; Vandewoestijne, Martin, Liégeois, & Baguette, 2004; Weibull, Bengtsson, & Nohlgren, 2000). The surrounding quantity of habitats is usually positively related to insect species richness or abundance (Banaszak 1992; Krauss, Steffan-Dewenter, & Tscharntke, 2003), but these relationships may depend upon

the scale of investigation. Steffan-Dewenter et al. (2002) found that mobile species groups respond more positively to regional habitat quantity at larger spatial scales than less mobile species groups. Effects of different spatial configuration or isolation of habitat patches are not straight-forward and vary between studies and species groups (e.g. Krauss et al., 2003; Ricketts, Dailey, Ehrlich, & Fay, 2001; Steffan-Dewenter & Tscharntke, 1999; Thomas et al., 2001; Zschokke et al., 2000).

Various studies have examined the relative effects of habitat quality and landscape context on flower visiting insects (e.g. Collinge, Prudic, & Oliver, 2003; Moilanen & Hanski, 1998; Thomas et al., 2001) but, to our knowledge, none has directly examined whether the effects of habitat quality and landscape context on insects interact. For example, the density of host plants in habitats (e.g. an indication of habitat quality) may only be important when few other patches are available within dispersal distance of the individual (e.g. landscape context). Alternatively, the number and size of habitats may only be important when the density of host plants within each habitat is low.

We studied the effects of landscape context, habitat quality and their interaction on the species richness and abundance of bees and hoverflies. In our study area, an intensively farmed Dutch agricultural landscape, both grasslands and arable fields are generally unsuitable for foraging and reproduction of these species groups as they consist of crop monocultures. Two categories of potential habitats can be distinguished. First, semi-natural vegetation in areas that do not have an agronomic function and are relatively buffered from impacts of agricultural activities (i.e. woodlots, nature reserves, cemeteries; henceforth 'semi-natural habitats'). Second, semi-natural vegetation in linear landscape features that are heavily affected by agricultural activities (i.e. field boundaries, shelter belts, road-side verges, railway banks; henceforth 'linear landscape features'). Linear landscape features are more widespread and more uniformly distributed over the Dutch agricultural landscape than semi-natural habitats. On the other hand, they generally contain species-poor, dis-turbed vegetation (Kleijn & Verbeek, 2000) and it is unknown to what extent they are used for foraging or as nest or hibernation sites by flower visiting insects. Thus, for the landscape context we examined the effects of semi-natural habitats and linear landscape features on flower visiting insects separately.

Vegetation composition, and thus habitat quality, is strongly influenced by local environmental con-ditions and management (Van Strien, Van der Linden, Melman, & Noordervliet, 1991; Wassen, Peeters, & Venterink, 2003). To neutralize poten-tially confounding effects of these factors we used stream banks as standard habitats. In the study area, most stream banks have the same exposition and management, consist of the same soil type and are exposed to the same hydrological conditions, thus providing a relatively uniform substrate for vegetation development. We selected 16 streams that were similar in most respects but were located in parts of the landscape with contrasting areas of semi-natural habitats and lengths of linear land-scape features. We estimated flower abundance and sampled species richness and abundance of bees and hoverflies on the banks of these streams. We quantified linear landscape features and area of semi-natural habitats in the landscape surrounding each stream at spatial scales ranging from 250 to 2000 m. By relating insect variables to flower and landscape structural variables we addressed the following questions:

- Is there a relationship between flower abun-dance and species richness or abundance of bees and hoverflies?
- Is there a relationship between landscape con-text and species richness or abundance of bees and hoverflies?
- Are any relationships between landscape context and insects influenced by flower abundance (do the effects of habitat quality and quantity interact)?
- At what spatial scales are the above-mentioned relationships most accurately determined?

Methods

Study area and design

The study was conducted in 2002 in the central parts of the Netherlands (Fig. 1). The study sites were located on the western and eastern slopes of the *Veluwe*, a sandy ice-pushed ridge formed during the Saalian glaciation. Until approximately 1960, land-use in the area was extensive and small-scaled, mainly consisting of dairy farming. Fields were small, most field boundaries consisted of tree lines and shelter belts, and woodlots and heather fields were scattered abundantly throughout the area. In combination with the environmental gradient (hydrology, soil type) caused by the direct vicinity of the ice-pushed ridge this resulted in a diverse landscape that was once considered one of
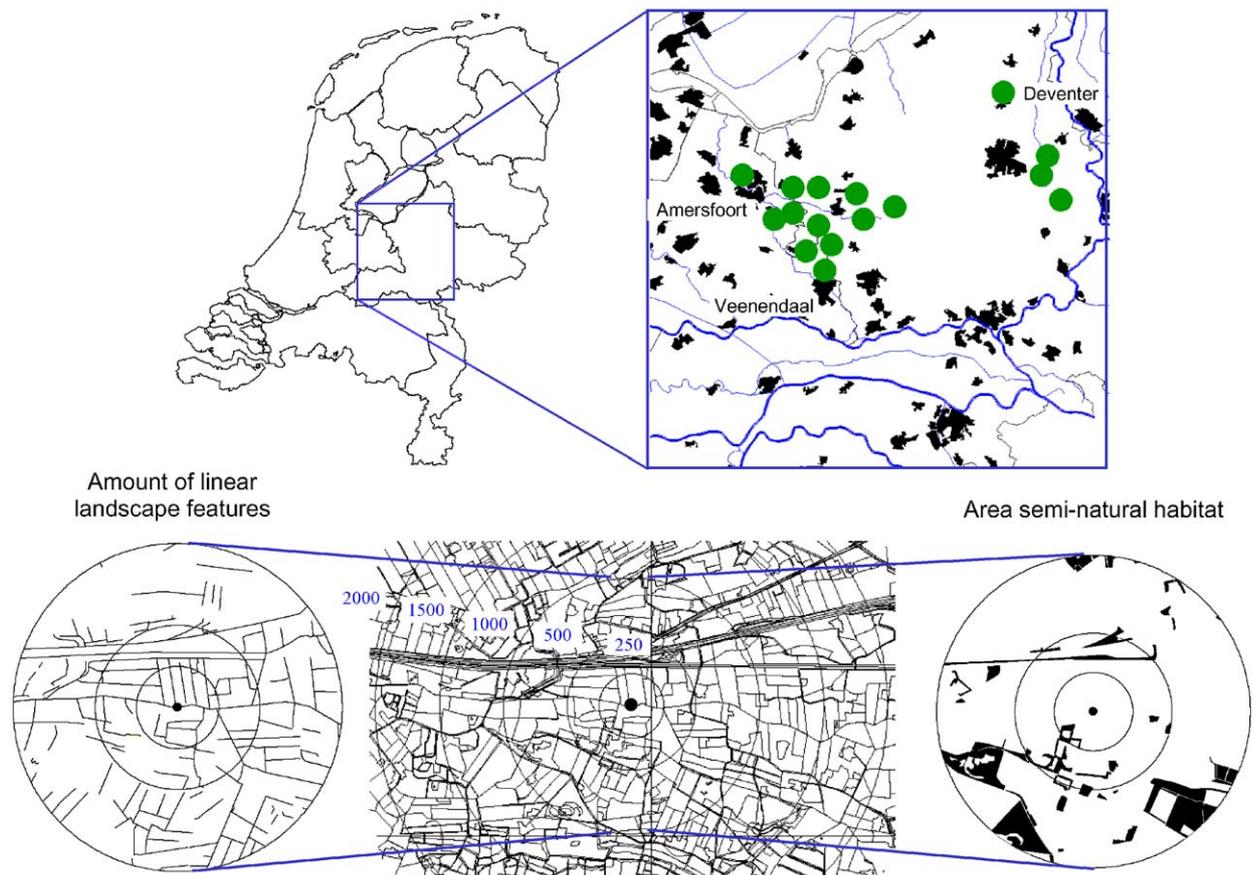
Figure 1. Design of the study with the locations of the 16 transects (top panels) and an example of one of the transects showing the concentric circles with increasing radii used to quantify the length of linear landscape features (left bottom panel) and the area of semi-natural habitats (right bottom panel).

the botanical hotspots in the Netherlands (Westhoff, Bakker, Van Leeuwen, & Van der Voo, 1970). Since then, agriculture has intensified and in some areas hardly any remnants of the old landscape have remained, resulting in an open, large-scaled landscape. Other areas have retained more of the original landscape features, resulting in structurally complex and simple landscapes in each other's direct vicinity.

Numerous streams fed by seepage water originate on the slopes and run in an east-westerly direction perpendicular to the orientation of the ice-pushed ridge. The soil of most streambeds consists of sand with a 15–50 cm thick humus-rich top-layer ('beekeerdgrond'). In the twentieth century, all streams were canalized, e.g. bends and meanders were removed and the banks were secured. The streams are therefore now basically straight, large ditches that carry off large quantities of water. The banks of the streams are managed by water boards or individual farmers with the aim to ensure sufficient water drainage. To this end the banks are usually mown 1–3 times a

year and cuttings are generally left on the banks. These streams, of which soil type, water table, vegetation management and exposition are fairly similar, run across areas in the landscape that are structurally very different. We therefore used stream banks as standard habitats to study the effects of landscape context and flower abundance on bees and hoverflies.

We selected twelve streams on the west slope and four streams on the east slope of the *Veluwe* and established a 750 m long and 2 m wide transect on the northern or north-western bank. The transects were positioned in parts of the landscape that varied independently in the area of semi-natural habitats and in average field size (and therefore the density of linear landscape features). The banks within transects all had grassy vegetation and areas with trees or shrubbery along the streams were avoided where possible. The centers of the different transects were at least 4 km apart. Dispersal distances of bees are generally below 2 km (Gathmann & Tscharntke 2002; Osborne et al., 1999; Walther-Hellwig & Frankl, 2000) so that different

transects can be considered as independent samples. Some hoverfly species have been observed to disperse over large distances (Sommaggio, 1999) but quantitative data on typical dispersal distances are lacking for virtually all species.

Sampling protocol

To ensure an even sampling effort over the various parts of the transects, each transect was divided into 30 25 × 2 m subplots. The insect groups were sampled by catching all bees and hoverflies observed in each subplot during 5 min. All specimens were killed quickly with ethyl acetate and brought to the lab for identification. Surveys took place between 10.00 and 17.00 h on sunny days with little wind. Bees and hoverflies were sampled three times during the season; the first period approximately covering the end of April and May, the second period covering June and the third period covering July and the first half of August. Immediately following an insect survey, flower abundance (the number of inflorescences of all forbs) was estimated by sight in each subplot. This is a rather simple method to determine the availability of food resources for flower visiting insects, but has been used before (Dramstad & Fry, 1995; Goulson & Darvill, 2004). Ultimately, the average number of inflorescences per transect was calculated (mean of 3 × 30 subplots) so that, despite the inaccuracy of the estimation method per subplot, a reliable estimate of the relative flower abundance per transect could be used for further analyses.

Determining landscape context

The area of semi-natural habitats and the length of linear landscape features was determined at several spatial scales using an approach similar to Ricketts et al. (2001) and Steffan-Dewenter et al. (2002). Both variables were quantified from digital maps (1:10.000, Topografische Dienst Emmen) in concentric circles with increasing radius (250, 500, 1000, 1500, 2000 m). Semi-natural habitats consisted of forests, heather, cemeteries, swamps and reed beds. In the study area, the large majority of linear landscape features that may be important to insects for foraging, resting or nesting (e.g. field boundaries, roadside verges, and railway banks) are bordered by ditches. We therefore used the total length of ditches as an estimate of the quantity of linear landscape features within the matrix of the agricultural landscape. Ditch length was simply estimated as the total length of all streams, large and small ditches, and seasonally dry ditches.

At the smallest scale (250 m radius) the data obtained from the digital maps were checked by mapping these areas manually in the field. We found a significant positive correlation between the total length of all linear landscape features measured manually in the field and the total ditch length obtained from the digital maps ($r = 0.56$, $P = 0.029$). Furthermore, the area of semi-natural habitats measured in the field and from the digital maps were positively correlated ($r = 0.86$, $P < 0.001$). For simplicity, only the data obtained from the digital maps will be used in the remainder of the paper.

Analysis

We calculated the 'number of inflorescences' (mean number of inflorescences of forbs per subplot and sampling round per transect) and the number of inflorescences of bee plants (based on Fussell & Corbet, 1992). For the latter category of plant species, we mainly selected plants frequently used by bumblebees, because 99% of the bees caught were bumblebees (see Results). Appendix A shows the plant species that were observed flowering at the time of the surveys, and therefore contributed to floral resources of one or both insect groups.

We determined the pooled species richness and abundance of bees and hoverflies over 30 subplots and three survey rounds in each transect. Honeybees were excluded from the analyses. Since 61% of the hoverfly individuals were from just four species (see Appendix B) which, in contrast to the other species, primarily feed on grass pollen, we examined the response of hoverfly abundance both with and without these 'grass species'. The comparison of species richness values between sites that differ considerably in abundance has been questioned on statistical grounds and rarefaction techniques have been proposed to correct for these differences (e.g. Gotelli & Colwell, 2001). We did not follow this approach as this would unlink our findings from important ecosystem processes such as competition, parasitism, pollination rate and pest control because all these processes depend on species richness and number of individuals per unit area and time, rather than on species richness per number of observed individuals.

We used multiple linear regression analysis to analyze whether insect species richness and abundance was significantly related to flower abundance, landscape context and their interaction. To avoid having to create and compare a large number

of statistical models with various numbers of explanatory variables as well as their interactions we analyzed the effects of length of linear landscape features and area of semi-natural habitats independently to evaluate their separate contributions. All analyses were carried out at all spatial scales after which the five models were compared based on R^2 and the statistical significance of (i) the model regressions and (ii) the regressions of the individual explanatory variables. Note that the analyses carried out at different spatial scales are not independent tests of the relationships but serve to determine at which spatial scale the best fit (based on explained variance, R^2, and statistical significance of the models) is achieved for each model describing a response variable (Van Langevelde, 2000). Two-factorial interactions usually indicate that the effect on the response variable of one factor differs at high and low levels of the second factor. We therefore explored the nature of significant interactions by analyzing the effect on the response variable of one factor, first, on a subset of transects with only high levels of the second factor and, second, on a subset of transects with only low levels of the second factor. All analyses were carried out using the statistical package GENSTAT (1993). In case of heteroscedasticity, data were ln-transformed prior to analysis. Throughout the paper means of untransformed data are given $\pm$ one standard error ($n = 16$).

Results

Characterization of study sites

We observed 40 species of hoverflies and five species of bees (Appendix B). All observed species are (very) common and the bees consisted almost exclusively of four bumblebee species. Only two individuals of the solitary bee *Halictus tumulorum* were observed (Appendix B). The vegetation of stream banks consisted mainly of nitrophilous ruderals and coarse grasses. On average, flower abundance was not particularly high but showed a wide range from virtually none present, to well over two inflorescences per square meter. The number of inflorescences of bee plants was approximately a quarter of the total number of inflorescences (Table 1). The total number of inflorescences and the number of inflorescences of bee plants were not significantly correlated ($r = 0.27$, $P = 0.32$).

The mean proportion of semi-natural habitats in the landscape increased with increasing investigated area, from 1.1% in a 250 m radius to 6.4% in a 2000 m radius. The maximum proportion of semi-natural habitats in the landscape increased from 5.5% to 17.6% over the same range. Minimum and maximum total ditch length varied threefold (Table 1). The area of semi-natural habitats and total ditch length were not correlated at any spatial scale.

Effects of flower abundance and landscape context on insects

There was no multi-colinearity between the number of inflorescences and either landscape variable at any spatial scale (variance inflation factors never exceeded 1.6).

Species richness of hoverflies was best described by a model containing the mean number of inflorescences in the transect, the area of semi-natural habitats within a radius of 500 m and the

Table 1. Species richness and abundance of bees and hoverflies, and number of inflorescences observed in transects along stream banks in 16 areas with contrasting landscape context

Variate	Species group	Mean $\pm$ se	Min	Max
Species richness	Bees	1.6 $\pm$ 0.30	0	4
	Hoverflies	15.5 $\pm$ 1.00	9	26
	Forb-visiting hoverflies	12.4 $\pm$ 1.00	5	23
Abundance	Bees	11.6 $\pm$ 4.07	0	62
	Hoverflies	126.1 $\pm$ 21.5	30	361
	Forb-visiting hoverflies	49.2 $\pm$ 6.26	15	97
Quantity	No. inflorescences (subplot, per 50 m^2)	53 $\pm$ 8.3	8	122
	No. inflorescences bees (subplot, per 50 m^2)	14 $\pm$ 3.8	1	53
	Semi-natural habitat in 1000 m radius (%)	5.3 $\pm$ 3.4	0.6	12.4
	Ditch length in 1000 m radius (km)	33.9 $\pm$ 9.8	17.3	49.1

Species richness and abundance of the insect groups is expressed per 7.5 h of sampling.

Table 2. The statistical characteristics of linear regression models describing the relationships between the species richness of hoverflies (number of species per 7.5 h sampling) and (a) floral resources and the area of semi-natural habitats and (b) floral resources and the length of linear landscape features at different spatial scales

(a) Area of semi-natural habitats					(b) Length of linear landscape features			
Radius (m)	Predictors	P-pred.	R^2-model	P-model	Predictors	P-pred.	R^2-model	P-model
250	No. flowers	0.006	40	0.027	No. flowers	0.006	41	0.024
	SN habitat	0.536			Ditch length	0.213		
	Interaction	0.221			Interaction	0.431		
500	No. flowers	<0.001	70	<0.001	No. flowers	0.009	32	0.058
	SN habitat	0.011			Ditch length	0.754		
	Interaction	0.020			Interaction	0.645		
1000	No. flowers	0.001	64	0.002	No. flowers	0.008	34	0.049
	SN habitat	0.049			Ditch length	0.757		
	Interaction	0.026			Interaction	0.452		
1500	No. flowers	0.002	55	0.005	No. flowers	0.008	34	0.045
	SN habitat	0.062			Ditch length	0.649		
	Interaction	0.127			Interaction	0.433		
2000	No. flowers	0.006	41	0.026	No. flowers	0.009	31	0.059
	SN habitat	0.239			Ditch length	0.733		
	Interaction	0.418			Interaction	0.711		

No. flowers: the mean number of inflorescences per subplot per survey round; SN habitat—the area of semi-natural habitats determined at a range of spatial scales.

interaction between the two variables (Table 2). The interaction was probably the result of the fact that hoverfly species richness was positively related to the area of semi-natural habitats in transects that contained relatively many inflorescences (>1 per m^2) but not in transects that contained few inflorescences (<1 per m^2; Fig. 2a). Moreover, the response of hoverflies to the quantity of floral resources was dependent on the surrounding landscape. Hoverfly species richness was only significantly related to the number of inflorescences in landscapes that consisted for more than 1% of semi-natural habitats (Fig. 2b). The model including the area of semi-natural habitats within a radius of 1000 m also significantly described hoverfly species richness but the fit of this model was lower (R^2: 70% and 64% at 500 and 1000 m radius respectively; Table 2). At the other spatial scales, area of semi-natural habitats did not significantly contribute to the fit of the model (Table 2). Ditch length or the interaction between ditch length and number of inflorescences were not significantly related to hoverfly species richness at any spatial scale (Table 2).

Hoverfly abundance was not significantly related to any of the predictor variables. However, when the four species feeding on grass pollen were excluded, models explaining a significant amount of the variation were found. Both the number of inflorescences and the area of semi-natural habitats within a radius of 1000 m contributed significantly to the model with the best fit (R^2: 71%, Table 3). When differences in the number of inflorescences between transects were accounted for, the area of semi-natural habitats had a pronounced positive effect on the abundance of forb-visiting hoverfly species (Fig. 3). Ditch length or the interaction between ditch length and number of inflorescences did not contribute significantly to the models describing hoverfly abundance at any of the investigated spatial scales (Table 3).

Bee species richness was best described by the same model that best described hoverfly species richness ($R^2 = 58\%$, Table 4). In this model the area of semi-natural habitats in a radius of 500 m did not contribute significantly to bee species richness, but the interaction between the number of inflorescences and area of semi-natural habitats within a radius of 500 m did. In contrast to the response of hoverflies, bees showed a more pronounced positive relationship to the number of inflorescences in transects in landscapes that had a low proportion of semi-natural habitats ($<1\%$) than in landscapes that contained more of this type of habitat ($>1\%$; Fig. 4). Ditch length did not contribute significantly to the fit of any model describing bee species richness (Table 4). Number of inflorescences of bee plants was positively related to bee abundance ($n = 16$, $F_{1,14} = 30.09$, $P<0.001$) but no landscape
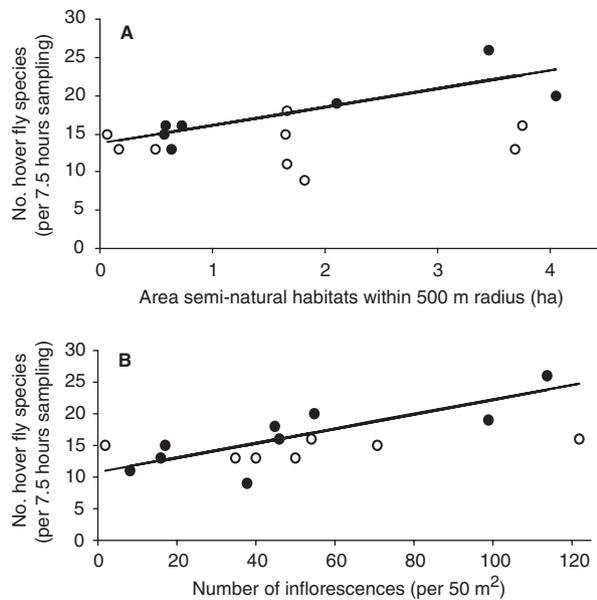
Figure 2. An illustration of the interacting effects of semi-natural habitats and floral resources on hoverfly species richness. (A) the relationship between the area of semi-natural habitat within a 500 m radius and the species richness of hover flies in transects with high floral resources (>1 per m^2, closed circles and line, species richness $= 13.70 + 2.40*$area of semi-natural habitats [500 m], $R^2 = 63\%$, $t_5 = 3.76$, $P = 0.02$) and in transects with low floral resources (< 1 per m^2, open circles, $t_7 = 0.22$, $P = 0.82$). (B) the relationship between the number of inflorescences and hoverfly species richness in transects with 'many' semi-natural habitats ($>1\%$ of total area in 500 m radius, closed circles and line, species richness $= 10.74 + 0.115*$number of inflorescences, $R^2 = 63\%$, $t_7 = 3.74$, $P = 0.007$) and in transects with few semi-natural habitats ($<1\%$, open circles, $t_5 = 1.86$, $P = 0.12$). Lines are drawn for significant relationships only.

context variable significantly contributed to models describing bee abundance, either alone or in interaction with the number of inflorescences (data not shown).

Discussion

Interactions between the effects of flower abundance and landscape context on insects

Habitat quality and landscape context have interacting effects on hoverfly species richness. We observed a positive effect of area of semi-natural habitats on hoverfly species richness only when flower abundance was higher than a minimum level (Fig. 2a). Furthermore, a positive relationship

between flower abundance and hoverfly species richness was found only in areas with relatively many semi-natural habitats. These results suggest that the quantity of surrounding semi-natural habitats is clearly important to hoverflies, but does not explain hoverfly species richness by itself. Semi-natural habitats also need to be of sufficient quality to have positive effects. Similarly, habitat quality is not straightforwardly related to hoverfly species richness but seems to only have positive effects on species richness when the landscape is past a threshold of a minimum amount of semi-natural habitats. To our knowledge this is the first time this has been demonstrated experimentally for flower visiting insects.

An alternative explanation for the observed interaction is that the effects of semi-natural habitats, although existing, were not detected in transects with low flower abundance because these transects were simply not visited by hoverflies for lack of food rewards. However, as transects with high flower abundance, but few semi-natural habitats were not visited by many hoverfly species either (Fig. 2b), we consider this explanation unlikely. The lack of a positive relationship between flower abundance and species richness of hoverflies in landscapes with few semi-natural habitats may be due to isolation effects (Steffan-Dewenter & Tscharntke, 1999) or to the low carrying capacity of landscapes with few semi-natural habitats.

Flower abundance and the area of semi-natural habitats also had interacting effects on bee species richness. In contrast to the response of the hoverflies, bee species richness showed a stronger positive response to flower abundance in areas with little semi-natural habitats than in areas with more semi-natural habitats (Fig. 4). Unlike hoverflies, bumblebees (which comprised 99% of the total number of bee individuals) are social insects with their colony located at a fixed place in the landscape. Individual workers are known to actively search for resource-rich patches and, once found, to return to these patches on successive foraging trips (Bhattacharya, Primack, & Gerwein, 2003; Heinrich, 1976; Osborne et al., 1999). In areas with few resource-rich patches this may result in a more pronounced concentration of bumblebees in these patches than in areas with many resources scattered throughout the landscape.

Similar to Steffan-Dewenter et al. (2002) and Westphal, Steffan-Dewenter, & Tscharntke (2003) we did not find a straightforward relationship between landscape context and species richness or abundance of bumblebees. Westphal et al.

Table 3. The statistical characteristics of linear regression models describing the relationships between the abundance of hoverflies (number of individuals per 7.5 h sampling; excluding four 'grass species' see Appendix B) and (a) floral resources and the area of semi-natural habitats and (b) floral resources and the length of linear landscape features. For abbreviations see Table 2

| (a) Area of semi-natural habitats					(b) Length of linear landscape features			
Radius (m)	Predictors	P-pred.	R^2-model	P-model	Predictors	P-pred.	R^2-model	P-model
250	No. flowers	<0.001	56	0.004	No. flowers	<0.001	53	0.007
	SN habitat	0.341			Ditch length	0.489		
	Interaction	0.323			Interaction	0.471		
500	No. flowers	0.001	52	0.008	No. flowers	0.001	51	0.008
	SN habitat	0.449			Ditch length	0.502		
	Interaction	0.694			Interaction	0.703		
1000	No. flowers	<0.001	71	<0.001	No. flowers	<0.001	56	0.010
	SN habitat	0.022			Ditch length	0.224		
	Interaction	0.176			Interaction	0.528		
1500	No. flowers	<0.001	61	0.002	No. flowers	<0.001	59	0.003
	SN habitat	0.149			Ditch length	0.221		
	Interaction	0.254			Interaction	0.306		
2000	No. flowers	<0.001	63	0.002	No. flowers	<0.001	57	0.004
	SN habitat	0.185			Ditch length	0.359		
	Interaction	0.135			Interaction	0.265		
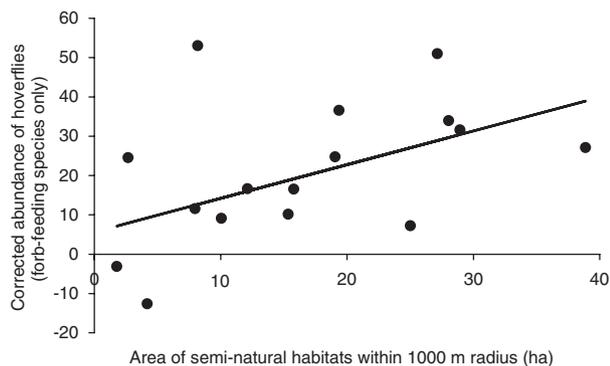
Figure 3. The relationship between the abundance of hoverflies and the area of semi-natural habitats within a 1000 m radius after hoverfly abundance has been corrected for differences between transects in the number of inflorescences. Correction based on the relation: Number of individuals = 5.64+0.553∗number of inflorescences+0.856∗area of semi-natural habitats within a 1000 m radius ($R^2 = 68$, $F_{2,13} = 17.26$, $P<0.001$). Only the 37 hoverfly species that feed on pollen of forbs are considered (see Appendix B).

(2003) found a strong positive relationship between the regional area of the mass flowering crop oil seed rape and the abundance of bumblebees. This relationship cannot explain the lack of response of bees to landscape context in our study as no mass-flowering crops were grown in the study area. Many semi-natural habitats in the study area were forests, a type of habitat not particularly favoured by most bumblebee species for foraging or nesting (Svensson, Lagerlöf, & Svensson, 2000). On the other hand, forest edges are generally suitable nesting habitats (Kells & Goulson, 2003; Sladen, 1912; Svensson et al., 2000) and, due to the fragmented and patchy nature of most semi-natural habitats in the study area (Fig. 1), this biotope was plentifully available. The lack of responsiveness may have been due to the low numbers of observed bees. Currently, Dutch agricultural landscapes host very few bee species (Kleijn et al., 2001). Banaszak (1992) suggested that at least 25% of agricultural landscapes should consist of refuge habitats in order to support a diverse bee fauna. In this study, which, for Dutch standards, was carried out in a small-scaled and diverse agricultural landscape, the combined proportion of semi-natural habitats and linear landscape features was approximately 8% (Table 1, average width of linear landscape features based on manual mapping: 2.53 m). Currently, a target level of 5% semi-natural habitats is proposed for farms in the Netherlands in order to increase their ecological

Table 4. The statistical characteristics of linear regression models describing the relationships between the species richness of bees (number of species per 7.5 h sampling) and (a) floral resources and the area of semi-natural habitats and (b) floral resources and the length of linear landscape features. For abbreviations see Table 2

| (a) Area of semi-natural habitats					(b) Length of linear landscape features			
Radius (m)	Predictors	P-pred.	R^2-model	P-model	Predictors	P-pred.	R^2-model	P-model
250	No. flowers	0.004	40	0.028	No. flowers	0.004	42	0.022
	SN habitat	0.729			Ditch length	0.285		
	Interaction	0.448			Interaction	0.846		
500	No. flowers	0.001	58	0.003	No. flowers	0.002	50	0.010
	SN habitat	0.712			Ditch length	0.141		
	Interaction	0.029			Interaction	0.427		
1000	No. flowers	0.003	49	0.011	No. flowers	0.001	56	0.004
	SN habitat	0.769			Ditch length	0.356		
	Interaction	0.114			Interaction	0.052		
1500	No. flowers	0.002	50	0.010	No. flowers	0.002	54	0.006
	SN habitat	0.770			Ditch length	0.587		
	Interaction	0.103			Interaction	0.058		
2000	No. flowers	0.003	45	0.017	No. flowers	0.002	50	0.010
	SN habitat	0.786			Ditch length	0.961		
	Interaction	0.207			Interaction	0.095		
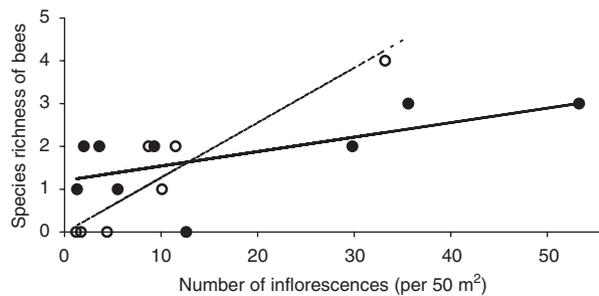
Figure 4. An illustration of the interacting effects of semi-natural habitats and floral resources on bee species richness. The relationship between the number of inflorescences of bee plants and bee species richness in transects with 'many' semi-natural habitats ($>$1% of total area within 500 m radius, closed circles and solid line, species richness = 1.20+0.034*number of inflores-cences, $R^2 = 32\%$, $t_7 = 2.19$, $P = 0.062$) and in transects with few semi-natural habitats ($<$1%, open circles and dashed line, species richness = $-0.01+0.128$*number of inflorescences, $R^2 = 86\%$, $t_5 = 6.08$, $P = 0.002$).

sustainability (e.g. Manhoudt, Van de Ven, Udo de Haes, & De Snoo, 2002). Our findings suggest that, unless extensive areas of semi-natural habitats are located in the direct vicinity of farms, this level is insufficient to sustain a diverse fauna of flower visiting insects, particularly if the vegetation is of low quality.

At what spatial scale do bees and hoverflies optimally respond to landscape context?

Our results suggest that hoverflies and to a lesser extent (bumble)bees are optimally related to landscape context in radii of 500–1000 m (Tables 2–4). As far as we know, this is the first time that hoverfly species richness and abundance is related quantitatively to the landscape context at a range of spatial scales. The relatively low dispersability of hoverflies ($\leqslant$1000 m) suggested by our results is perhaps surprising. In contrast to bees, hoverflies are not spatially restricted to a single nest site and may therefore disperse widely across the land-scape.

The larval stages of a number of the less frequently observed species (*Myatropa florea*, *Pipiza noctiluca*, *Scaeva* spp., *Xylota segnis*) occur on trees or in rotting wood (NJN, 1998; Sommaggio, 1999). This may explain the positive correlation between hoverfly species richness and area of semi-natural habitats at a small spatial scale (500 m, Fig. 2a). However, the positive relationship between the abundance of forb-visiting hoverflies and the area of semi-natural habitats within a radius of 1000 m suggests that even the common species are dependent on semi-natural habitats at some stage

during their life-cycle. The larvae of most of the common hoverfly species live in dung, ditch water, rotting vegetation or plant parts of common herbs (NJN, 1998). These were all plentifully available outside semi-natural habitats. Possibly, semi-natural habitats were the most important areas supplying pollen and nectar in the study area, however, an exact elucidation of the mechanism underlying the observed relationships needs additional experimental investigations.

Conclusions

The quality of the agricultural landscape for flower visiting insects seems to be determined by both quantity and quality of semi-natural habitat patches, at least for the common species of hoverflies and bees observed in this study. Currently, conservation initiatives place much emphasis on the conservation and restoration of linear landscape features on farms such as hedgerows, field edges, field margin strips and conservation headlands (Banaszak, 1992; Kleijn, Joenje, Le Coeur, & Marshall, 1998; Rands & Sotherton, 1986). Often, such efforts are subsidized through agri-environment schemes (Kleijn & Sutherland, 2003). Our results suggest that when the quality of these landscape elements is low, as was the case in the study area, these elements are of little value to flower visiting insects. In such areas, conservation and restoration of semi-natural habitats not directly related to modern agriculture may be a more effective means of conserving flower-visiting insects. Whether these relationships also hold in areas where linear landscape features still offer a rich and continuous food supply is uncertain and should be subject of further study.

Furthermore, for hoverflies conservation initiatives on farms, such as agri-environment schemes, should be implemented in areas with a high proportion of semi-natural habitats (see also Duelli & Obrist, 2003). Only in such areas may substantial positive effects be expected of improvements in local habitat quality. For bumblebees, no such straightforward recommendations can be given. The more positive response of this species group in areas with few semi-natural habitats may simply have been the result of a foraging response and does not necessarily indicate higher densities of colonies. Research aimed to identify factors that influence nest sites (bees) and larval food and overwintering sites (hoverflies) may therefore be necessary to be able to better explain the observed responses of both species groups to habitat quality and landscape context.

Appendix A

For plant species observed in 16 transects along stream banks see Table A1).

Table A1. Plant species observed in 16 transects along stream banks in the central parts of The Netherlands

Achillea millefolium[a]	*Equisetum palustre*	*Nasturtium microphyllum*[a]	*Taraxacum officinalis*[a,b]
Achillea ptarmica[a]	*Erodium cicutarium*	*Oxalis fontana*[a]	*Trifolium pratense*[a,b]
Aegopodium podagraria[a]	*Eupatorium cannabinum*[a,b]	*Phalaris arundinacea*	*Trifolium repens*[a,b]
Agrostis capillaris	*Festuca arundinacea*	*Phleum pratensis*	*Triticum aestivum*
Agrostis stolonifera	*Festuca rubra*	*Ph rag mites austral is*	*Typha latifolia*
Ajuga reptans[a,b]	*Filipendula ulmaria*[a,b]	*Pinus sylvestris*	*Urtica dioica*
Alisma plantago-aquatica[a]	*Galeopsis tetrahit*[a,b]	*Plantago lanceolata*[a]	*Valeriana officinalis*[a,b]
Allium vineale	*Galium aparine*[a]	*Plantago major*	*Veronica arvensis*[a]
Alnus glutinosa	*Galium palustre*[a]	*Poa annua*	*Veronica catenata*[a]
Alopecurus geniculatus	*Geranium molle*[a]	*Poa pratensis*	*Veronica chamaedris*[a]
Alopecurus pratensis	*Geranium robertianum*[a]	*Poa trivialis*	*Veronica hederifolia*[a]
Anemone nemorosa	*Glechoma hederacea*[a,b]	*Polygonum amphibium*[a]	*Veronica serpyllifolia*[a]
Angelica sylvestris[a,b]	*Glyceria fluitans*	*Polygonum aviculare*	*Vicia cracca*[a,b]
Anthoxanthum odoratum	*Glyceria maxima*	*Polygonum hydropiper*	*Vicia sepium*[a,b]
Anthriscus sylvestris[a]	*Gnaphalium uliginosum*	*Polygonum persicaria*[a]	*Viola arvensis*[a,b]

Table A1. (*continued***)**

Arabidopsis thaliana	*Heracleum sphondylium*[a]	*Potentilla anserina*
Arrhenatherum elatius	*Hieracium umbellatum*[a]	*Potentilla reptans*
Artemisia vulgaris	*Holcus lanatus*	*Prunus avium*
Athyrium filix-femina	*Holcus mollis*	*Quercus robur*
Atriplex prostrata	*Humulus lupulus*	*Ranunculis acris*[a]
Bellis perennis	*Hypericum dubium*	*Ranunculus bulbosus*
Berula erecta[a]	*Hypericum perforatum*	*Ranunculus ficaria*[a]
Bidens tripartita	*Hypochaeris radicata*[a]	*Ranunculus repens*[a]
Brassica napus[a,b]	*Iris pseudacoris*[a,b]	*Ranunculus sardous*
Bromus hordeaceus	*Juncus articulatus*	*Ranunculus sceleratus*[a]
Calystegia sepium[a]	*Juncus effusus*	*Rorippa amphibia*[a]
Capsella bursa-pastoris[a]	*Lamium album*[a,b]	*Rorippa palustris*[a]
Cardamine amara	*Lamium purpureum*[a,b]	*Rubus fruticosus*[a,b]
Cardamine hirsuta[a]	*Lapsana communis*[a]	*Rumex acetosa*
Cardamine pratensis[a]	*Lathyris pratensis*[a,b]	*Rumex acetosella*[a]
Carduus crispus	*Leontodon autumnalis*	*Rumex crispus*
Carex remota	*Linaria vulgaris*[a,b]	*Rumex hydrolapathum*
Carex rostrata	*Lolium multiflorum*	*Rumex obtusifolius*
Cerastium fontanum[a]	*Lolium perenne*	*Salix sp.*
Cerastium glomeratum	*Lotus uliginosus*[a,b]	*Scirpus sylvaticus*
Cerastium semidecandrum[a]	*Luzula campestris*	*Scrophularia nodosa*
Cirsium arvense[a,b]	*Lychnis flos-cuculi*[a,b]	*Sedum telephium*
Cirsium palustre	*Lycopus europaeus*[a,b]	*Senecio vulgaris*[a,b]
Cirsium vulgare	*Lysimachia nummularia*[a]	*Silene dioica*[a,b]
Convolvulus arvensis[a]	*Lysimachia punctata*[a]	*Sisymbrium officinale*[a]
Crepis biennis[a]	*Lythrum salicaria*[a,b]	*Solanum dulcamara*[a]
Crepis capillaris[a]	*Matricaria discoidea*[a]	*Solanum nigrum*[a]
Dactylis glomerata	*Matricaria maritima*[a]	*Sparganium erectum*
Deschampsia cespitosa	*Matricaria recutita*[a]	*Stachys palustris*[a,b]
Dipsacus fullonum	*Medicago lupulina*[a,b]	*Stellaria graminea*[a]
Eleocharis palustris	*Mentha aquatica*[a,b]	*Stellaria holostea*
Elymus repens	*Myosotis arvensis*[a]	*Stellaria media*[a]
Epilobium hirsutum[a]	*Myosotis laxa*[a]	*Symphytum officinale*[a,b]
Equisetum arvense	*Myosotis palustrus*	*Tanacetum vulgare*[a]

[a] All forbs observed flowering and related to species richness and abundance of hover flies.
[b] All plant species visited by bees observed flowering and related to the species richness and abundance of bees.

Appendix B

For the abundance (*n*) and frequencies of hoverfly and bee species see Table A2.

Table A2. The abundance (*n*) and frequencies (*f*: number of transects a species was found in) of hoverfly and bee species in 16 transects along banks of streams in the central parts of The Netherlands

Hover flies	*n*	(*f*)	Hover flies	*n*	(*f*)	Bees	*n*	(*f*)
Anasimyia lineata	4	(1)	*Melanostoma scalare*	5	(4)	*Bombus hortorum*	17	(3)
Cheilosia albitarsis	8	**(4)**	*Myatropa florea*	29	(5)	*Bombus pascuorum*	117	(12)
Cheilosia pagana	8	(5)	*Neoascia podagrica*	5	(4)	*Bombus pratorum*	16	(2)
Chrysogaster hirtella	76	(8)	*Neoascia tenur*	1	(1)	*Bombus terrestris/lucorum*	33	(6)
Chrysogaster nuda	3	(1)	*Parhelophilus versicolor*	2	(1)	*Halictus tumulorum*	2	(2)
Chrysogaster viduata	7	(3)	*Pipiza noctiluca*	1	(1)			
Episyrphus balteatus	108	(14)	*Platycheirus albimanus*	4	(3)			
Eristalis abusivus	9	(5)	*Platycheirus angustatus*[a]	30	(8)			
Eristalis arbustorum	50	(13)	*Platycheirus clypeatus*[a]	358	(16)			

Table A2. (*continued*)

Hover flies	*n*	(*f*)	Hover flies	*n*	(*f*)	Bees	*n*	(*f*)
Eristalis horticola	8	**(4)**	*Platycheirus peltatus*	1	(1)			
Eristalis intricarius	2	(2)	*Platycheirus scambus*[a]	31	(10)			
Eristalis nemorum	45	(11)	*Pyrophaena granditarsa*	32	(2)			
Eristalis pertinax	14	(6)	*Rhingia campestris*	108	(8)			
Eristalis tenax	40	(12)	*Scaeva pyrastri*	1	(1)			
Eristalinus sepulchralis	5	**(4)**	*Scaeva selenitica*	2	(1)			
Eupeodes corollae	53	(12)	*Sphaerophoria scripta*	25	(9)			
Helophilus hybridus	4	(3)	*Syritta pipiens*	37	(12)			
Helophilus pendulus	28	(8)	*Syrphus ribesi*	13	(8)			
Helophilus trivittatus	36	(13)	*Syrphus vitripennis*	7	(5)			
Lejogaster metallina	5	(2)	*Xylota segnis*	1	(1)			
Melanostoma mellinum[a]	811	(16)						

[a]Species feeding mainly on grass pollen.

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