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The importance of landscape and spatial structure for hymenopteran-based food webs in an agro-ecosystem

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Summary

1. Understanding the environmental factors that structure biodiversity and food webs among communities is central to assess and mitigate the impact of landscape changes.

2. Wildflower strips are ecological compensation areas established in farmland to increase pollination services and biological control of crop pests and to conserve insect diversity. They are arranged in networks in order to favour high species richness and abundance of the fauna.

3. We describe results from experimental wildflower strips in a fragmented agricultural landscape, comparing the importance of landscape, of spatial arrangement and of vegetation on the diversity and abundance of trap-nesting bees, wasps and their enemies, and the structure of their food webs.

4. The proportion of forest cover close to the wildflower strips and the landscape heterogeneity stood out as the most influential landscape elements, resulting in a more complex trap-nest community with higher abundance and richness of hosts, and with more links between species in the food webs and a higher diversity of interactions. We disentangled the underlying mechanisms for variation in these quantitative food web metrics.

5. We conclude that in order to increase the diversity and abundance of pollinators and biological control agents and to favour a potentially stable community of cavity-nesting hymenoptera in wildflower strips, more investment is needed in the conservation and establishment of forest habitats within agro-ecosystems, as a reservoir of beneficial insect populations.

Key-words: biological control agents, ecological compensation areas, ecosystem services, landscape ecology, parasitism, pollinators, quantitative food webs, trap nest, wildflower strip

Introduction

Intensification of agriculture in the 20th century has been accompanied by a drastic loss of biodiversity (Robinson & Sutherland 2002). Agricultural land use and conservation have traditionally been viewed as incompatible, but a cultivated landscape can be heterogeneous and provide many suitable habitats (Tscharntke *et al.* 2007). The identification of environmental factors that structure biodiversity among communities is central to the assessment of the impact of landscape changes (Jeanneret, Schupbach & Luka 2003) and the planning of conservation strategies. The proportion, quality and spatial arrangement of semi-natural habitats and overall habitat heterogeneity in the surroundings are thought to play major roles (Duelli 1997; Hendrickx *et al.* 2007; Fahrig *et al.* 2011; Gagic *et al.* 2011; Schüepp *et al.* 2011). Currently, however, there is limited knowledge of how these environmental factors also affect the functioning of entire food webs in agro-ecosystems (Albrecht *et al.* 2007).

The importance of conserving a high diversity of mutualistic and antagonistic interactions has been the subject of many studies (e.g. Thebault & Loreau 2006; Tylianakis, Tscharntke & Lewis 2007; Ings *et al.* 2009), especially because ecosystem services associated with species interactions such as pollination and biological control are of particular interest for human welfare (Balvanera *et al.* 2006; Cardinale *et al.* 2012). For example, the loss of

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interactions is predicted to threaten ecosystem stability and functioning, and like community composition, this also seems to be influenced by the spatial arrangement of habitat patches (Holt 1996) and landscape heterogeneity (Gagic *et al.* 2011). Locally, high compartmentalization in food webs is predicted to reduce the risk of species extinctions and increase food web persistence (Stouffer & Bascompte 2011), and spatial effects are likely to influence this characteristic. However, although there is a solid body of research on how spatial structure is related to the stability of metacommunity food webs (McCann 2000; Pillai, Gonzalez & Loreau 2011), few generalizations exist about the consequences of spatial structure on food web architecture. Rooney, McCann & Moore (2008) proposed general hypotheses about how food web structure is related to spatial scale at the landscape level, but they do not easily apply to the arthropod-based systems studied here.

In Europe, agri-environmental schemes have been introduced to restore agricultural landscapes and enhance biodiversity. As a result, networks of ecological compensation areas have been created in farmland, including hedges, field margins and wildflower strips (Marshall & Moonen 2002). In Switzerland, wildflower strips are made up of a recommended plant mixture containing 24 herbaceous species sown inside fields or along their edges and are maintained for 6 years (Nentwig 2000). The species mixture was elaborated in order to benefit a maximal number of functional groups of animals, for ecosystem services (Haaland, Naisbit & Bersier 2011).

Different arthropod trophic groups respond differently to landscape changes (Jeanneret, Schupbach & Luka 2003; Klein, Steffan-Dewenter & Tscharntke 2004; Attwood *et al.* 2008), and the diversity of these groups can affect rates of ecosystem processes such as pollination (Garibaldi *et al.* 2011) and biological control (Thies *et al.* 2011), or the parasitism of beneficial parasitoids (Tylianakis, Tscharntke & Klein 2006). Trap-nesting bee and wasp communities are relevant indicators of ecological changes, due to their participation in all three types of interaction (Tscharntke, Gathmann & Steffan-Dewenter 1998). Like most species living in agro-ecosystems, they depend on complementary resources in different habitats (Klein, Steffan-Dewenter & Tscharntke 2004) for food (Ebeling *et al.* 2012) or nesting sites (Gathmann & Tscharntke 2002; Steffan-Dewenter & Leschke 2003; Sobek *et al.* 2009) and thus are sensitive to landscape heterogeneity (Fahrig *et al.* 2011) and the isolation of habitat patches (Holzschuh, Steffan-Dewenter & Tscharntke 2009; Krewenka *et al.* 2011; Schüepp *et al.* 2011).

In recent literature, trap-nest communities are usually split into three groups: bees, wasps and higher trophic enemies (predators and parasitoids; Schüepp *et al.* 2011; Ebeling *et al.* 2012). However, while cavity-nesting wasps can act as biological control agents by collecting herbivorous arthropods (including phloem-sucking aphids (Aphididae), as well as larvae of smaller moths (microlepidoptera), leaf beetles (Chrysomelidae) and weevils (Curculionidae) (Tscharntke, Gathmann & Steffan-Dewenter 1998)), other wasp species feed on spiders (Araneae), which can themselves represent important biological control agents (Schmidt-Entling & Dobeli 2009). Thus, the wasps can usefully be separated into three trophic guilds, as predators of aphids, other herbivores, or spiders, to account for the ecological role of their prey.

Our trap-nest data set derives from a temperate agro-ecosystem, reporting species richness, abundances and interaction frequencies between insect hosts and their enemies, and giving abundance estimations of the prey of trap-nesting wasps. We constructed food webs with quantitative trophic links and collected measures of local vegetation and landscape characteristics, to address the following questions:

1 What is the relative importance of vegetation characteristics, spatial arrangement and landscape composition to understand the structure of trap-nesting communities?
2 To which habitat characteristics (plant species richness, plant biomass, habitat isolation, landscape heterogeneity and the cover of different landscape components) do bees, aphid-, other herbivore- and spider-predating wasps, and their enemies respond?
3 To what extent is food web structure (generality, vulnerability, link density, interaction diversity and compartment diversity) influenced by these habitat characteristics?

Materials and methods

FIELD MANIPULATIONS

This study was carried out as part of a larger project to assess the importance of biodiversity for the functioning of agricultural compensation zones, by manipulating the number of plant species and trophic levels in experimental wildflower strips (Bruggisser *et al.* 2012; Fabian *et al.* 2012). In spring 2007, twelve wildflower strips (hereafter strips) were sown in field margins around Grandcour, 10 km south of Lake Neuchatel in north-west Switzerland at an altitude of 479 m (coordinates: 46° 52′ N 06° 56′ E). The region (4 × 4 km) is characterized by a mosaic of arable fields (intensive agriculture), grasslands and forests, and the average distance between our strips was 1·6 ± 0·8 km. The strips each covered 864 m^2 and were either flat or slightly sloped. Within each strip, plant species diversity treatments (2, 6, 12 or 20 species) were repeated in four subplots in three blocks, with fencing treatments for other experiments as explained in the study by Fabian *et al.* (2012); a fourth block contained the complete 24 species wildflower mixture (Fig. S1, Supporting information).

VEGETATION AND LANDSCAPE DESCRIPTORS

Vegetation characteristics

In the 14 subplots per strip (Fig. S1, Supporting information), the percentage cover of each plant species was determined in autumn 2008 using the Braun–Blanquet method (1964). The

vegetation in each strip was characterized by the total plant species richness and by the average plant biomass (measured as leaf area index in each subplot) as a measure of productivity (see Fabian *et al*. 2012 for details).

Spatial arrangement of experimental wildflower strips

Strips were established to obtain a gradient of isolation from each other (minimum and maximum distances to the nearest strip were 118 and 777 m, respectively; see Table S1, Supporting information). The spatial distribution of the strips (Fig. S2, Supporting information) was characterized by the X and Y coordinates (in m) of the central point of each strip, relative to the centre of the study region. To capture more complex spatial structuring, we added the terms X^2, Y^2 and XY in the analyses (Borcard, Legendre & Drapeau 1992). Note that centring the coordinates removes the correlation between X and X^2, and between Y and Y^2 (Legendre & Legendre 1998).

Landscape composition, heterogeneity and habitat isolation

The landscape was categorized on the basis of official topographical maps (Bundes Amt Für Umwelt BAFU 2008; 1:5000) using ArcView GIS (version 3.3) and verified on field inspections in 2007 and 2008. For each strip, the surrounding landscape composition was characterized in a circle of radius 500 m (Gathmann & Tscharntke 2002). Correlations of landscape composition with trap-nest community richness and abundance were stronger at this radius than at smaller radii (100, 200, 300 and 400 m; see supplementary methods), while larger radii would have resulted in too great an overlap between the surroundings of the different strips. Percentage cover was measured for six landscape elements: (i) agricultural fields; (ii) extensive meadows (no fertilization, late mowing), gardens, orchards and hedges; (iii) forest; (iv) wildflower strips; (v) water bodies and (vi) urban areas (roads and houses). Further details are given in Fig. S2 and Table S1 (Supporting information). The exponential of Shannon diversity (exp (H')) was calculated as a measure of landscape heterogeneity, with $H' = -\sum p_i \log(p_i)$, and p_i the proportion of each landscape category. Isolation was measured as the edge-to-edge shortest distance from a strip to the nearest wildflower strip (distance to wildflower strip in m). The distance from the strip to the nearest forest edge (distance to forest) was also measured, but due to its strong correlation with forest cover (Pearson's product-moment correlation, $r = -0{\cdot}74$, d.f. = 8, $P = 0{\cdot}014$) and the correlations among landscape measures (Table S4, Supporting information), we used only forest cover in the surroundings (%) in the analyses. Forest stands were managed mixed forests of similar height (~25 m) dominated by spruce (*Picea abies*) and beech (*Fagus sylvatica*).

TRAP NESTS

Community composition

Trap nests enabled us to study species richness, abundance and quantitative interactions of above-ground nesting hymenopterans and their natural enemies under standardized nesting conditions (Tscharntke, Gathmann & Steffan-Dewenter 1998). The nests consisted of 170–180 internodes of common reed *Phragmites australis* (length 20 cm), placed in plastic pipes (20 cm long, 10 cm diameter). The internal diameter of the reeds ranged from 2 to 8 mm. Each reed-filled plastic pipe was fixed on a wooden pole (1·5 m long) and protected by a 30 × 30 cm wooden roof (Fig. S3, Supporting information). Fourteen trap nests were positioned in each strip (Fig. S1, Supporting information) from mid-April until October 2008. After collection, they were stored at 4°C for at least 7 weeks to simulate winter. Some nests were destroyed while in place, including nearly all of those in two strips that were dismantled by a heron; thus, in total 136 trap nests from 10 strips were analysed.

In spring 2009, all reed internodes containing brood cells were opened and counts made of the number of cells and the occurrence of (clepto-) parasites, parasitoids and predators (hereafter called 'enemies') attacking the nest makers (hereafter called 'hosts'). Reeds were stored separately in glass tubes to collect emerging adult bees, wasps and their enemies for identification. If no adult emerged, features of the nest and larval food were used to identify the genus or (sub) family using the identification key of Gathmann & Tscharntke (1999). Empty brood cells of eumenid wasps were assumed to belong to the bivoltine *Ancistrocerus nigricornis*, because it was the only species for which offspring of the first generation emerged before trap collection (Krewenka *et al*. 2011). Species richness and abundance (number of brood cells) in each wildflower strip were recorded for the entire trap-nest community and separately for the following groups: pollen- and nectar-collecting bees (Apidae), aphid-predating wasps (Sphecidae of the genera *Passaloecus*, *Pemphredon* and *Psenulus*), other herbivore-predating wasps (Eumenidae and Sphecidae, feeding on Chrysomelidae, Curculionidae, Caelifera and microlepidoptera larvae), spider-predating wasps (Pompilidae and Sphecidae of the genus *Trypoxylon*) and enemies (see Tables S2 and S3, Supporting information). Note that the abundance of enemies was measured as the number of parasitized brood cells, and not the total number of emerging individual enemies.

Food web metrics

Quantitative host–enemy interaction food webs were constructed for each strip, and five food web metrics were calculated following Bersier, Banašek-Richter & Cattin (2002; for formulae see Supplementary Methods) using the bipartite package (Dormann *et al*. 2009). *Vulnerability* is the weighted mean effective number of enemies per host species, and *generality* is the weighted mean effective number of hosts per enemy species. *Link density* is the weighted mean effective number of links per species, and *interaction diversity* is the Shannon diversity of interactions, which takes both the number and the evenness of interactions into account (Tylianakis, Tscharntke & Lewis 2007). *Compartment diversity* is a measure of the size homogeneity of compartments (subsets of a web that are not connected with other subsets). These metrics are often used as measures of food web complexity.

AVAILABILITY OF ARTHROPOD PREY

To estimate arthropod abundance, 14 vacuum samples were taken in each wildflower strip using a D-vac foliage hoover type SH 85C (Stihl, Dieburg, Germany). Measures were taken in May 2008, between 10:00 and 16:00 on dry and sunny days. This period covers both the peak in flight activity of early and abundant species (*Trypoxylon* and the bivoltine *Ancistrocerus nigricornis*)

and the start of the peak of late species (*Ancistrocerus gazella* and *Passaloecus borealis*; Bellmann 1995). In the middle of each subplot, the vegetation and ground in an area of 1 m^2 were vacuumed for two minutes. Collected arthropods were stored in ethanol and grouped into orders. The average aphid and spider abundances per strip were used as estimates of food availability for aphid- and spider-predating wasps, respectively (Table S1, Supporting information). Average abundances of Lepidoptera, Psocoptera, Coleoptera larvae and Caelifera were summed per strip and used as estimates of 'herbivore' availability for other herbivore-predating wasps. In the analyses treating all wasps, the average abundances of all six prey groups were summed and included as 'arthropods'.

STATISTICAL ANALYSES

All statistical analyses were conducted in R 2.12.1 (R Development Core Team 2012). The species richness and abundance (number of brood cells) of bees, wasps and enemies were log-transformed to meet the assumptions of constant error variance and normality of errors (Sokal & Rohlf 1995). Explanatory variables were standardized to zero mean and unit variance using the function *scale*. Correlations between the vegetation and landscape variables were tested using a Pearson correlation matrix. Several of the landscape elements were strongly correlated with landscape heterogeneity (Table S4, Supporting information), so they were excluded from the analyses.

Variance partitioning of the trap-nest community with respect to landscape and vegetation characteristics

In order to compare the explanatory power of the three sets of environmental descriptors (vegetation composition, landscape composition and spatial arrangement) for the trap-nest community data, we used a variance partitioning method (Hofer, Bersier & Borcard 2000), using the function *varpart* in vegan (Oksanen *et al.* 2011). This application uses partial redundancy analysis (RDA) with the community matrix as dependent variable and the sets of environmental descriptors as independent variables (Blanchet, Legendre & Borcard 2008). The analysis was applied for the entire community and for seven subsets: all host species, bees, wasps, aphid-, other herbivore- and spider-predating wasps, and all enemy species. To reduce the asymmetry of the heavily skewed abundance data, they were log-transformed according to Anderson, Ellingsen & McArdle (2006). The rationale of variance partitioning can be simply understood using the example of a single response variable in a linear framework: to measure the effect of one independent variable, one firstly regresses the data with all other variables (the variables to be excluded) and extracts the residuals, which are then regressed with the variable of interest. Adjusted R square values (R^2_{adj}) can be used to represent the percentage variance in the data explained by each independent variable (Peres-Neto *et al.* 2006); note that R^2_{adj} can be negative, which must be interpreted as an absence of explanatory power. In our case, the response variable was multidimensional (observations – i.e. strips – can be seen as points in an n-dimensional space whose axes are the abundances of the n species) and we consequently used ordination approaches. Ordinations define a new system of axes where the variability of the data is expressed on few informative dimensions. RDA is a method of so-called constrained ordination, where the new axes are linear combinations of explanatory variables – in essence, it is a multiple regression for multidimensional data.

We have 10 observations (strips), so first summarized each set of environmental descriptors as a single composite variable to avoid over-fitting. This yielded a single explanatory variable for each environmental set and thus avoided giving greater weight to sets of variables with more descriptors. To achieve this, we again relied on ordinations and extracted the coordinates of the strips on the first ordination axis. For the vegetation composition, we conducted a correspondence analysis (CA) on the log-transformed cover of the 30 most abundant plant species (the first axis explained 20% of the variation in cover) and used principal component analyses (PCA) for the six square-root-transformed landscape composition parameters and for the five spatial arrangement parameters of the strips (the first axes explained 65% and 53% of the variation, respectively). PCA is the standard method of dimension reduction; CA is a method of choice for abundance data, which typically includes many zeros, because shared absence of species is considered non-informative. Extensive explanations of these multivariate methods can be found in Legendre and Legendre (1998).

The RDA provided estimates of the percentage of variance due exclusively and in common to the three groups of descriptors. To test significance of the exclusive fractions, we applied a test with 9999 permutations using the function ANOVA. To further inspect the relationship between the trap-nest communities and individual variables, we performed a canonical correspondence analysis (CCA) for each full set of environmental descriptors. CCA is a method of constrained ordination customarily applied to test the effects of environmental variables on abundance data of communities; we used the function *cca* in vegan. We further applied the function *ordistep* with stepwise backward elimination of the least significant variables, to identify the descriptors that best explained the variation in trap-nest communities.

Habitat characteristics affecting species richness, abundances and food web metrics

The effects of local vegetation (species richness and biomass), of landscape (percentage of forest cover and landscape heterogeneity) and of spatial arrangement (distance to the nearest wildflower strip) were modelled on the response variables species richness and abundance, for the entire community and for each functional group separately. For the analyses of aphid-, of other herbivore-, of spider-predating and of all wasps, one variable that represents prey availability was added to the model. It was obtained from the D-vac sampling data and was composed of the abundance of aphids, of other herbivores, of spiders and of all these three groups, respectively. For enemy richness and abundance, the host species richness and abundance, respectively, served as a sixth variable, again expressing prey availability. To account for the possible dependence of the functional groups on their prey, the prey availability was always retained in all models.

First, we compared the AICs of the full generalized least squares (gls) models for each response variable with and without spatial autocorrelation structure in the residuals, based on the coordinates of the centre of each strip. We used five different spatial correlation structures following Zuur *et al.* (2009, Chapter 7·2). The AIC of the simplest gls model without spatial correlation was always lowest, indicating that spatial autocorrelation is weak in our data (results not shown). However, this procedure

does not account for the statistical dependence of the strips for which the surrounding landscapes overlap (see Fig. S2, Supporting information). Consequently, we analysed the data using gls models with a correlation structure induced by the pairwise proportional overlap between the experimental strips. Proportional overlap c_{ij} between strips i and j is the ratio of the shared area divided by the total area covered by both 500 m landscape radii. Our model is given by $y = X\beta + \varepsilon$ with y the vector of the response variable, X the matrix of explanatory variables (the first column contains 1 for the intercept), β the vector of parameters and ε the vector of residuals. In our case, we consider $\varepsilon \sim N(0,\Sigma)$ with

$$\Sigma = \delta^2 \begin{pmatrix} 1 & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & 1 \end{pmatrix} + \lambda\delta^2 \begin{pmatrix} 0 & \dots & c_{ij} \\ \vdots & \ddots & \vdots \\ c_{ij} & \dots & 0 \end{pmatrix}. \qquad \text{eqn 1}$$

The parameter λ determines the strength of the correlation structure induced by the overlap in landscape and δ^2 denotes the variance. To estimate the P-value of λ, we performed log-likelihood ratio tests between models with and without the correlation structure. The code for the models is available upon request to the corresponding author.

To avoid over-fitting, we chose among models with one and two explanatory variables only (when appropriate, prey availability was included as a third variable not subjected to selection). We ran the 16 possible models (the first contains the intercept only, or when appropriate, the intercept and prey availability) and chose the one with the lowest AIC, provided the difference in AIC was larger than 2 relative to the best model with fewer variables; otherwise, we chose that with fewer variables.

Assumptions of normality of residuals were tested with Q–Q plots and Shapiro–Wilk tests. With correlation structure, the residuals must be 'decorrelated' (in other words, made identically and independently normally distributed) before checking for normality. This is achieved by the following transformation: $\tilde{r} = L^T r$, with r and $\tilde{r}$ the vector of residuals and of transformed residuals, respectively; L^T is the transpose of the lower triangular matrix, L, from Cholesky decomposition of Σ^{-1}, the inverse of the matrix Σ (L^T can be thought of as the square root of the matrix Σ^{-1}; see Houseman, Ryan & Coull 2004).

The same procedure and explanatory variables (vegetation, landscape and spatial arrangement) were used to analyse the quantitative food web metrics: vulnerability, generality, link density, interaction diversity and compartment diversity. To account for the possible dependence of these metrics on species richness (Banašek-Richter *et al.* 2009; Dormann *et al.* 2009), the latter was always included in the models. As a control, we repeated the analyses with host abundance included in the place of species richness, but do not present the results as they were very similar; moreover, host abundance was not significant except for compartment diversity (see Table 3 for comparison).

Results

In total, 136 trap nests were collected with 17 243 brood cells of 38 hymenopteran host species (Table S2, Supporting information), which used 17·2% of all provided reeds. Thirteen species of bees were identified in 11 980 cells, with *Osmia bicornis* L. (Megachilidae, code 11 in Table S2, Supporting information) the most abundant. Twenty-five species of wasps were identified in 4716 brood cells, including mason wasps (Eumenidae), digger wasps (Sphecidae) and spider wasps (Pompilidae). Records were dominated by the spider-predating *Trypoxylon figulus* L. (code 45) and the caterpillar-predating *Ancistrocerus nigricornis* Curtis (code 23). Enemies from 40 taxa (not all identified to the species level) were recorded, in the orders Hymenoptera (clepto-parasites and parasitoids), Diptera (parasites), Coleoptera (predators) and Acari (parasites). Nine taxa were specialized on wasps, ten on bees, seven attacked both bees and wasps, and 14 attacked undetermined species (Table S3, Supporting information). Mortality due to enemies, that is, the number of parasitized cells divided by the total number of cells, was 19·7% for bee and 17·1% for wasp hosts. The most abundant generalist was *Mellitobia acasta* Walk. (Chalcidoidea: Eulophidae, code 66 in Table S3, Supporting information), a gregarious pupal parasitoid found attacking 596 brood cells of 23 species.

VARIANCE PARTITIONING OF THE TRAP-NEST COMMUNITY

The three sets of descriptors together explained 17% and 15% of the total variation in the community composition of hosts and enemies, respectively. The variance partitioning revealed that landscape composition was the most important descriptor for the trap-nesting hosts and for their enemies, explaining exclusively 17% and 11% of the variation, respectively (Table 1). Neither the spatial arrangement of the wildflower strips nor the plant composition explained a significant fraction of the variation in hosts and enemies. After applying backward elimination of the landscape composition variables, the CCA analyses (Fig. S4, Supporting information) identified forest cover as the most significant element for hosts ($F = 1{\cdot}8$, $P = 0{\cdot}003$) and for enemies ($F = 2{\cdot}0$, $P = 0{\cdot}005$).

TRAP-NEST COMMUNITY STRUCTURE

Landscape variables were by far the most important in explaining community richness and abundance (Table 2). Forest cover had a positive effect on the species richness of hosts in general, on wasp and aphid-predating wasp richness and on the total abundance of brood cells. Landscape heterogeneity had a positive effect on total species richness in the trap nests, on the species richness of bees and of aphid-predating wasps, and a negative effect on the abundance of other herbivore-predating wasps. An effect of spatial arrangement was detected only for the abundance of wasps, which was negatively affected by the distance to the closest wildflower strip. Vegetation variables were significant only in three instances: plant richness had a positive effect on host richness, whereas plant biomass negatively affected the species richness of other herbivore-predating wasps and the abundance of

Table 1. Partitioning of the variation in community composition explained by plant composition, wildflower strip spatial arrangement and landscape composition

Response variable	Total variation (SS)	Unexplained variation%	Total variance (including shared variances) explained by			Variance explained exclusively by		
			Plants A	Landscape B	Spatial arrangement C	Plants a	Landscape b	Spatial arrangement c
All species	1841	83	0·03	0·13	0·02	0·00	0·15*	−0·01
All hosts	1314	83	0·01	0·14	0·00	0·01	0·17**	0·00
Bee hosts	632	83	−0·04	0·16	−0·04	0·04	0·20*	0·02
Wasp hosts	682	82	0·06	0·12	0·04	−0·02	0·13*	−0·02
Aphid predators	238	75	0·11	0·13	0·08	0·01	0·15†	−0·01
Other herbivore predators	536	79	0·08	0·12	0·05	0·00	0·16*	−0·01
Spider predators	123	91	0·00	0·13	0·02	−0·08	0·08	−0·05
Enemies	513	85	0·06	0·09	0·05	−0·01	0·11†	−0·03

Uppercase: A, B, C are the variances explained by each set, including the shared variance. Lowercase: a, b, c are the variances explained exclusively by each set. The adjusted R^2 values are given. $^{**}P < 0{\cdot}01$, $^{*}P < 0{\cdot}05$, $^{\dagger}P < 0{\cdot}1$.

Table 2. Parameter estimates and their significance from the best-fitting generalized linear models relating species richness and abundance of the trap-nest community to descriptors of vegetation, landscape and spatial arrangement, and of prey availability for higher trophic levels. Bold values $P < 0.05$

	Prey availability		Vegetation				Landscape				Spatial		
			Species richness		Biomass		Forest cover		Heterogeneity		Distance to wildflower strip		λ
	β	P	β	P	β	P	β	P	β	P	β	P	P-value
Species richness													
Total community	NA	NA	-	-	-	-	-	-	**0·17**	**0·002**	-	-	**0·032**
All hosts	NA	NA	**0·08**	**< 0·001**	-	-	**0·15**	**0·005**	-	-	-	-	**< 0·001**
Bees	NA	NA	-	-	-	-	-	-	**0·25**	**< 0·001**	-	-	**< 0·001**
Wasps	**0·13**	**0·042**	-	-	-	-	**0·21**	**0·005**	-	-	-	-	**< 0·001**
Aphid predators	**0·32**	**0·001**	-	-	-	-	**0·20**	**0·020**	**0·22**	**0·002**	-	-	**< 0·001**
Other herbivore predators	**0·32**	**0·011**	-	-	**−0·27**	**0·025**	-	-	-	-	-	-	**0·035**
Spider predators	0·03	0·378	-	-	-	-	-	-	-	-	-	-	0·056
Enemies	**0·09**	**0·008**	-	-	-	-	-	-	-	-	-	-	**< 0·001**
Abundance													
Number of brood cells	NA	NA	-	-	-	-	**0·18**	**0·005**	-	-	-	-	**< 0·001**
Bee cells	NA	NA	-	-	-	-	-	-	0·45	0·120	-	-	**< 0·001**
Wasp cells	0·04	0·364	-	-	-	-	-	-	-	-	**−0·38**	**0·011**	**< 0·001**
Aphid predators	0·02	0·382	-	-	-	-	0·41	0·16	-	-	-	-	**0·032**
Other herbivore predators	0·18	0·089	-	-	-	-	-	-	**−0·43**	**< 0·001**	-	-	**< 0·001**
Spider predators	−0·12	0·340	-	-	**−0·12**	**0·001**	-	-	-	-	-	-	**< 0·001**
Enemies	**0·61**	**< 0·001**	-	-	-	-	-	-	-	-	-	-	**0·010**

The prey availability for the analyses of wasps and their subgroups is the abundance of their corresponding prey groups; prey availability for species richness of enemies is the number of host species; prey availability for abundance of enemies is the number of brood cells. A dash indicates parameters that were not included in the set of best-fitting models and thus were not estimated. Prey availability variables were always included in the models, except those indicated by NA (not applicable).

spider-predating wasps. Prey availability had a significant effect in most cases on the richness of the various functional groups, but not on their abundance, with the exception of the enemies, whose abundance was positively correlated with host abundance. Including the correlation structure to account for the statistical dependence of strips always yielded significantly better models, with the exception of the species richness of spider-predating wasps (for which $P = 0{\cdot}056$).

FOOD WEB STRUCTURE

Landscape variables were again by far the most important in explaining the quantitative food web metrics. The

proportion of forest in the surroundings positively affected vulnerability, generality, link density and interaction diversity (Table 3). Landscape heterogeneity had a negative effect on vulnerability and a positive effect on interaction diversity. An effect of spatial arrangement was detected for generality and link density, both negatively affected by the distance to the closest wildflower strip. Vegetation variables were significant only for compartment diversity, which was positively affected by plant species richness and biomass.

The importance of forest cover for the food web structure can be seen when comparing the pooled quantitative food web for the five strips with lowest forest cover in the surroundings (0–1·6%) with that for the five with highest forest cover (6·2–17%) (Fig. 1). A higher diversity of hosts and enemies and higher link density are the hallmarks of food webs with greater forest cover in the surroundings.

It is interesting to further explore the results of Table 3 in terms of the effects on the proportions of generalist vs. specialist species and the changes in the shapes of distributions of interaction frequencies. For each of the five dependent variables, we discuss only the explanatory variable with the strongest effect. Increasing vulnerability and generality with forest cover might occur through three non-exclusive mechanisms: (i) a decreased proportion of 'specialists' (i.e. hosts that only ever have one enemy species or enemies that have only one host) in sites with greater forest cover nearby; (ii) a greater diversity of interactions by the 'generalists' in such sites (i.e. more enemies for each 'generalist' host and more hosts for each 'generalist' enemy); and (iii) a more equitable distribution of enemies or of hosts, which can be measured by interaction evenness. For vulnerability, we found that all three mechanisms play a role: in strips with greater forest cover in the surroundings, (i) there tended to be fewer 'specialist' hosts ($r = -0{\cdot}63$, d.f. = 8, $P = 0{\cdot}053$; Fig. S5a, Supporting information); (ii) 'generalist' host species were usually attacked by more enemies (14 of 17 species had a positive relationship between the effective number of enemies and forest cover; binomial test $P = 0{\cdot}013$; Fig. S5b, Supporting information) and (iii) the interaction evenness of hosts increased with greater forest cover ($r = 0{\cdot}75$, d.f. = 8, $P = 0{\cdot}012$; Fig. S6, Supporting information). In contrast, for generality, forest cover in the surroundings did not affect the proportion of specialists ($r = 0{\cdot}03$, d.f. = 8, $P = 0{\cdot}93$; Fig. S7a, Supporting information), and there was no overall trend for the number of hosts per 'generalist' enemy to increase with forest cover (7 of 16 species had positive relationships; binomial test $P = 0{\cdot}80$; Fig. S7b, Supporting information). However, the overall positive effect of forest cover on generality seems to result from the fact that the enemies with the greatest numbers of hosts did show an increase in the number of hosts with increasing forest cover (positive values on the y axis in Fig. S7b, Supporting information), and the interaction evenness of enemies also increased with greater forest cover (gls model controlling for host abundance, forest cover $\beta = 0{\cdot}01$, $P = 0{\cdot}045$; Fig. S6, Supporting information).

The link density can be expressed as the arithmetic mean of vulnerability and generality, so we do not discuss further the effect of forest cover on this variable. We note, however, the negative relationship between link density and community species richness (i.e. the 'size' of the food webs), which contrasts with a strong positive relationship for the qualitative link density (slope = 0·52, $P = 0{\cdot}002$, not shown). This indicates that species-rich systems have very uneven distributions in interaction frequency at the species level compared with species-poor systems (Banašek-Richter *et al*. 2009). Interaction diversity considers frequency distributions globally for the food web matrix (and not for each species individually as does link density). The significant positive relationship with forest cover is due to a greater number of trophic interactions in strips with high forest cover ($r = 0{\cdot}65$, d.f. = 8, $P = 0{\cdot}042$) and not to a change in evenness of the interactions at the food web level ($r = 0{\cdot}17$, d.f. = 8, $P = 0{\cdot}63$;

Table 3. Parameter estimates and their significance from the best-fitting generalized linear models relating food web metrics to descriptors of community species richness, vegetation, landscape and spatial arrangement. Bold values $P < 0.05$

			Vegetation				Landscape				Spatial		
	Community species richness		Species richness		Biomass		Forest cover		Heterogeneity		Distance to wildflower strip		λ
Food web metric	β	P	β	P	β	P	β	P	β	P	β	P	P-value
Vulnerability	0·23	0·056	-	-	-	-	**0·50**	**< 0·001**	**−0·41**	**0·001**	-	-	**< 0·001**
Generality	**−0·58**	**0·001**	-	-	-	-	**0·92**	**< 0·001**	-	-	**−0·34**	**0·009**	**< 0·001**
Link density	**−0·38**	**< 0·001**	-	-	-	-	**0·71**	**< 0·001**	-	-	**−0·20**	**0·011**	**< 0·001**
Interaction diversity	−0·11	0·220	-	-	-	-	**0·09**	**< 0·001**	**0·08**	**0·032**	-	-	**< 0·001**
Compartment diversity	**−1·10**	**0·004**	**1·70**	**0·001**	**1·06**	**0·006**	-	-	-	-	-	-	**< 0·001**

Community species richness was included in all models. A dash indicates parameters that were not included in the set of best-fitting models and thus were not estimated.

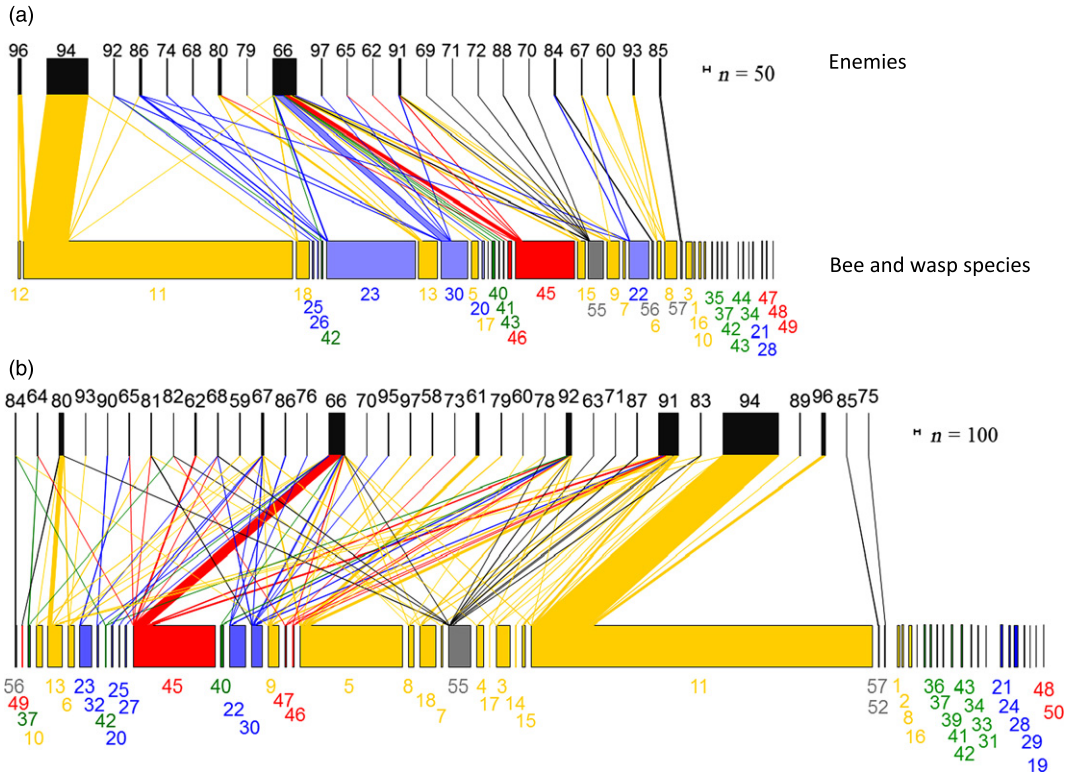


Fig. 1. Quantitative host–enemy food webs from five wildflower strips with (a) low forest cover (0–1·6%; total number of trap nests = 66) and (b) high forest cover (6·2–17%; total number of trap nests = 70) in a 500 m radius. Note that the scale of the upper panel is double that of the lower. Width of bars represents host and enemy abundance and width of links number of interactions. Species richness: (a) 41 hosts and 23 enemies; (b) 53 hosts and 34 enemies. Host functional groups: bees (yellow), aphid-predating wasps (green), other herbivore-predating wasps (blue), spider-predating wasps (red) and undetermined groups (grey). Upper bars represent enemy abundance (black). Species codes are given in Tables S2 and S3 (Supporting information). Hosts and enemies are ordered to minimize the overlap of interactions.

Fig. S8, Supporting information). The positive effect of plant species richness on compartment diversity might simply be a consequence of an increased proportion of enemy species with only one host ($r = 0{\cdot}65$, d.f. = 8, $P = 0{\cdot}039$; Fig. S9, Supporting information) and hosts with only one enemy species ($r = 0{\cdot}68$, d.f. = 8, $P = 0{\cdot}030$), making it more likely that the web is split into compartments.

Discussion

In our system, landscape composition played a greater role than either vegetation characteristics within the strips or spatial arrangement in determining the composition of the trap-nest community. Furthermore, species richness and abundances were most strongly affected by the landscape composition (forest cover and landscape heterogeneity) in the surroundings, followed by the vegetation (plant species richness and biomass) and the spatial arrangement of the wildflower strips (distance to the nearest wildflower strip). Our results also show that the foremost influence on community functioning, as measured by the quantitative food web structure, was the landscape in the surroundings, followed by the spatial arrangement and the vegetation in the strips. Interestingly, the strongest effect on most quantitative food web measures (vulnerability, generality, link density and interaction diversity) was due to the forest cover in the surroundings, and this effect was apparent even after accounting for the effects on species richness or host abundance.

The affiliation of cavity-nesting wasps to forest and woody habitat in agricultural landscapes has been demonstrated in other systems (Holzschuh, Steffan-Dewenter & Tscharntke 2009; Schüepp *et al.* 2011). Forests are thought to provide dead-wood nesting sites with cavities made by wood-boring insects, which are otherwise not present in primarily cleared or simple habitats (Sobek *et al.* 2009). Hence, forests house source populations of wild bees and wasps, which spill over into adjacent agricultural habitats, potentially enhancing pollination and biocontrol (Tscharntke, Rand & Bianchi 2005). We found that the presence of woody habitats not only enhanced community diversity, but also strongly affected food web complexity.

The differences in food web structure mediated by forest cover were not merely a consequence of differences in community composition, but also in behaviour. Mechanisms behind the positive effect of forest cover on quantitative vulnerability and generality included (i) the presence of fewer hosts with a single enemy species; (ii) a

greater diversity of interactions by generalist hosts; (iii) a greater effective number of hosts for the highly generalist enemies and (iv) a higher interaction evenness of both hosts and enemies. The mechanism driving the positive effect of forest cover on quantitative interaction diversity was due to a higher number of interactions. To our knowledge, this is the first study to disentangle the underlying causes of variation in the quantitative food web measurements.

In theory, highly diverse communities with higher connectance (link density/species richness) are more persistent in a metacommunity setting (Gravel *et al*. 2011); thus, our study underlines the importance of forest cover for the diversity of natural pollinators and biological control agents and for the maintenance of intact and persistent food webs in agro-ecosystems.

Similarly, when comparing the importance of vegetation characteristics, landscape composition and the spatial arrangement of wildflower strips for the composition of the trap-nest community, we found that the landscape components surrounding the strips were by far the most important descriptors. A large fraction of the variation remained unexplained, which may result from the setting of our study: strips can be considered as islands of favourable habitat in a hostile matrix of agricultural land, and the establishment of particular species may be strongly affected by stochastic events. Our variance partitioning analyses showed that forest cover was the only variable showing significant effects within this high level of variability. Thus, we think that wildflower strips should not be viewed as a network of patches of a single habitat type with their inhabitants behaving as a self-supporting metacommunity (Leibold *et al*. 2004), but rather as elements of a heterogeneous landscape that bridge agricultural and late succession habitats.

The tree species richness, canopy height and age of forests are important parameters determining the species richness and abundance of cavity-nesting communities (Sobek *et al*. 2009). In our study, these parameters were very similar for all strips, but for a better understanding of the importance of forest patches for ecosystem services in agricultural land, future studies should consider these characteristics. Furthermore, identification of the pollen collected by solitary bees and the origin of prey collected by wasps might provide further insights into the importance of wildflower and forest patches in agro-ecosystems.

Availability of resources may increase if the landscape matrix surrounding a focal patch includes other suitable habitat types. In our system, high landscape heterogeneity promoted the species richness of trap-nest communities in general and specifically the richness of bees and aphid-predating wasps. However, landscape heterogeneity was strongly correlated with the cover of several habitat types, and in particular was negatively correlated with the cover of agricultural fields ($r = -0{\cdot}98$, $P < 0{\cdot}001$), so it is possible that some taxa are responding to the presence of particular habitats, rather than to heterogeneity itself. For instance, in contrast to all other taxa, we found that herbivore-predating mason wasps (Eumenidae) were less abundant when the surroundings were more heterogeneous, a result in line with the findings of Steffan-Dewenter (2003). These wasps may forage mainly in agricultural fields and thus be limited by the cover of cultivated habitat. They were abundant in our wildflower strips, and studies on their role in biological control, including the foraging distances that they cover, would be promising avenues for future research. Our study highlights the importance of distinguishing between different wasp trophic guilds for the evaluation of the contribution of agricultural compensation zones to biocontrol. Furthermore, the species richness of these guilds was strongly affected by the abundance of their prey, which underlines the importance of including prey availability in statistical models.

Radmacher & Strohm (2010) found that *Osmia bicornis*, the most abundant species in our study, maximizes its foraging rate by temporally and locally specialized foraging behaviour within the agricultural landscape. In early season, they mainly visited oak (*Quercus* sp.) and maple (*Acer* sp.) trees, whereas in late season, they used poppy (*Papaver* sp.) and buttercup (*Ranunculus* sp.) with only traces from other plant families. This use of multiple food sources and habitats might underlie the positive correlation between bee diversity and landscape heterogeneity in our study.

Holt (1996) predicted strong effects of habitat isolation and spatial structure on food web topology. We found negative effects of isolation (distance to the next strip) not only on the abundance of wasps, but also on the generality and link density of the food webs. By accounting for the spatial overlap in the surrounding landscape between the experimental wildflower strips, we always achieved a better fit of the models compared with the simple model lacking spatial autocorrelation, and this was in contrast to the results with classical spatial autocorrelation approaches (Zuur *et al*. 2009). We thus present a new method to incorporate a correlation matrix into linear models for applied use in future landscape ecology research.

The abundance and diversity of trap-nesting bees and wasps were high in our study (mean of 126·8 brood cells per standardized trap nest), compared with research in forest patches (Sobek *et al*. 2009; 27·4 brood cells), grasslands (Albrecht *et al*. 2007; Schüepp *et al*. 2011; Ebeling *et al*. 2012; with 170·5, 70·5 and 90·3 brood cells, respectively) and agricultural areas (Holzschuh, Steffan-Dewenter & Tscharntke 2010; 61·3 brood cells). Thus, managed wildflower strips appear to provide favourable habitat with access to food resources for pollinators and biological control agents. The species richness of plants in the wildflower strips positively affected the total species richness of the trap-nesting community and the compartment diversity of their food webs. Theory suggests that higher levels of compartment diversity should increase the stability of food webs (McCann 2000; Stouffer & Bascompte 2011), which emphasizes the need to promote

plant diversity within agricultural landscapes. However, in contrast to other studies reporting a positive relation between bee species richness and plant species richness (Albrecht *et al.* 2007 with 9–18 naturally occurring plant species; Ebeling *et al.* 2012 with 1–16 sown species), we did not detect an effect of vegetation on bees. This may be because plant species richness only limits the richness of pollinators when it is very low, whereas it was relatively high (30–50 species) in all strips in our study.

In line with other studies, the diversity and abundance of the highest trophic level, the enemies, were strongly positively affected by the species richness and abundance of hosts, but not by vegetation and landscape characteristics (Steffan-Dewenter 2003; Albrecht *et al.* 2007).

CAVEATS OF OUR STUDY

We could only sample ten wildflower strips, and thus, small sample size surely limits the statistical power of our analyses, but in our opinion, this is counterbalanced by the high sampling effort for each strip (on average 1700 individuals collected per strip). Consequently, most effects were strong and consistent across analyses.

Another caveat is that some hosts and enemies could not be determined to species level, which may have biased some of the food web metrics. We tried to minimize this by identifying these individuals as far as possible, by delimiting morphospecies, and by using information on nest and food remains to assign them to a trophic group. The proportion of individuals not determined to the species level was 11·1%, within the range of other studies (e.g. Albrecht *et al.* 2007 and Schüepp *et al.* 2011, with 2·8% and 27·4% respectively); typically, these were individuals that did not complete development or were heavily damaged by their enemies.

Conclusion

Wildflower strips are intended to provide pollinators and biological control agents with sufficient pollen and herbivore prey to maintain high abundances and species richness close to agricultural fields. We found that communities in the strips strongly respond to the presence of forest habitats, with effects on species richness, abundance and food web complexity. In order to ensure long-term sustainability of wild bee and wasp communities and consequently their ecosystem services as pollinators and biological control agents, we conclude that it is not only necessary to maintain and restore a dense network of flower-rich habitat patches in agricultural landscapes, but also to conserve a diverse landscape mosaic that includes forest areas.

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Data accessibility

Data are publicly accessible at Dryad Digital Repository doi:10.5061/dryad.ck842 (Fabian *et al.* 2013).

Author contributions

PK, LFB, YF and OB designed and AA, OB, NS and YF established the experiment; YF and RPR performed the analysis and YF wrote the first draft; and REN, YF, PK and LFB revised the manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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Fig. S5. Potential explanations for the relationship between forest cover and vulnerability.

Fig. S6. Potential explanations for the relationship between forest cover and generality/vulnerability: the average interaction evenness of all hosts and enemies in each strip as a function of forest cover.

Fig. S7. Potential explanations for the relationship between forest cover and generality.

Fig. S8. Potential explanations for the relationship between forest cover and interaction diversity: a) the total interaction evenness for each food web as a function of forest cover, and b) the total number of interactions of each food web as a function of forest cover.

Fig. S9. A potential explanation for the relationship between plant species richness and compartmentalisation: the proportion of "specialist" hosts with only one enemy and of specialist enemies with only one host both increase significantly with plant species richness.

APPENDIX

1. Supplementary Methods

1.1. Mantel tests

We performed simple Mantel tests to determine the area over which landscape composition best explained the abundance of bees, wasps and enemies. We used Bray-Curtis dissimilarities for the percentage cover of the seven landscape categories at a distance of 100, 200, 300, 400 and 500 m and the abundance of the trap-nest community members, and performed 10,000 permutations (Goslee & Urban 2007).

In accordance with Gathmann and Tscharntke (2002), measurements at a radius of 500 m best explained species abundances in the trap nests (r = 0.37, P = 0.02).

1.2. Food web metrics

Quantitative, weighted measures of link density, generality, vulnerability, interaction diversity and compartment diversity based on Shannon's entropy were calculated following Bersier *et al.* (2002), Tylianakis *et al.* (2007) and Dormann *et al.* (2008). Quantitative metrics are weighted to incorporate the total inflow and outflow (based on frequency of interactions) of individuals per species. Diversity of hosts ($H_{N,k}$) and diversity of consumers ($H_{P,k}$), were calculated for each species k as:

$$H_{\mathrm{N},k} = -\sum_{i=1}^{s} \frac{b_{ik}}{b_{\bullet k}} \log_2 \frac{b_{ik}}{b_{\bullet k}} \qquad H_{\mathrm{P},k} = -\sum_{j=1}^{s} \frac{b_{kj}}{b_{k\bullet}} \log_2 \frac{b_{kj}}{b_{k\bullet}}$$

The sum of column $b_{\bullet k}$ is the number of individuals attacked by taxon k and the sum of row $b_{k\bullet}$ is the number of individuals attacking taxon k. The frequency of interactions from taxon i to taxon k, and from taxon k to taxon j, is represented as b_{ik} and b_{kj}, respectively.

The "reciprocals" of the diversities ($n_{N,k}$ - effective number of hosts and $n_{P,k}$ - effective number of consumers) give the theoretical number of species interacting in equal proportion that would yield the same value of H:

$$n_{\mathrm{N},k} = \begin{cases} 2^{H_{\mathrm{N},k}} \\ 0 \qquad \text{if } b_{\bullet k} = 0 \end{cases} \qquad n_{\mathrm{P},k} = \begin{cases} 2^{H_{\mathrm{P},k}} \\ 0 \qquad \text{if } b_{k\bullet} = 0. \end{cases}$$

Generality (G_q), the weighted average effective number of host species per consumer, and **vulnerability** (V_q), the weighted average effective number of consumer species per host, were calculated as:

$$G_q = \sum_{k=1}^{s} \frac{b_{\bullet k}}{b_{\bullet\bullet}} n_{\mathrm{N},k} \qquad V_q = \sum_{k=1}^{s} \frac{b_{k\bullet}}{b_{\bullet\bullet}} n_{\mathrm{P},k}$$

where $b_{\bullet\bullet}$ is the total number of attacked individuals.

Link density (LD_q) is the number of links per species, calculated as the arithmetic mean of generality and vulnerability:

$$LD_q = \frac{1}{2}\left(\sum_{k=1}^{s} \frac{b_{k\bullet}}{b_{\bullet\bullet}} 2^{H_{\mathrm{P},k}} + \sum_{k=1}^{s} \frac{b_{\bullet k}}{b_{\bullet\bullet}} 2^{H_{\mathrm{N},k}} \right).$$

Interaction Diversity (ID_q) was calculated as:

$$ID_q = -\sum_{i=1}^{s}\sum_{j=1}^{s} p_{ij} \ln\left(p_{ij}\right)$$

where p_{ij} is the number of cells of host i attacked by enemy j, divided by the grand sum of the number of attacked cells. It uses Shannon's diversity index with links rather than individuals as the basis of measurement.

Compartment diversity (CD_q) was calculated as:

$$CD_q = \exp\left(-\sum_{i=1}^{n} p_i \ln\left(p_i\right) \right)$$

where p_i is the fraction of all species in the ith of n compartments. The number of compartments in a web is defined as the number of sub webs with no link to any other sub web (Tylianakis, Tscharntke & Lewis 2007).

2. **Supplementary Tables**

Table S1. Means ± standard errors, minimum and maximum values of each variable across the 10 strips.

	Mean ± SE	Min	Max
Species richness			
total community	40.8 ± 3.1	29	54
all hosts	26.6 ± 1.7	19	35
bees	9.9 ± 0.9	5	15
wasps	14.7 ± 1.4	9	22
aphid predators	4.3 ± 0.7	2	8
other herbivore predators	6.5 ± 0.7	4	10
spider predators	3.1 ± 0.3	2	4
enemies	12.7 ± 1.3	8	19
Abundance (number of cells)			
average number of brood cells per trap	124.7 ± 16.8	29.1	193.3
bee cells	86.2 ± 13.9	7.5	144.1
wasp cells	34.8 ± 6.4	16.0	70.1
aphid predators	2.5 ± 0.7	0.2	7.4
other herbivore predators	18.0 ± 4.3	6.0	54.6
spider predators	13.9 ± 5.3	0.9	44.2
cells parasitized	23.1 ± 17.4	4.3	58.4
Food web metrics			
vulnerability	1.7 ± 0.2	1.2	3.2
generality	2.3 ± 0.2	1.2	3.9
link density	2.0 ± 0.2	1.2	2.9
interaction diversity	2.1 ± 0.2	1.5	2.8
compartment diversity	2.6 ± 0.5	1.0	6.3
Average abundance in D-vac samples			
arthropods	103.1 ± 10.1	63.7	175.0
aphids	48.3 ± 7.5	28.7	103.6
other herbivores	10.1 ± 1.5	3.1	16.2
spiders	42.4 ± 6.6	15.3	86.9
Vegetation measurements			
Plant species richness	39.6 ± 2.1	30	50
Plant biomass (g/m^2)	522.9 ± 28.6	379.6	686.2
Landscape cover (%)			
Agricultural fields	75.0 ± 3.1	58.4	90.5
Forest	6.3 ± 2.1	0.0	17.0
Orchards, hedges, extensive meadows	9.7 ± 2.1	2.8	19.6
Wildflower strips	0.6 ± 0.2	0.0	1.7
Water bodies	0.2 ± 0.1	0.0	1.3
Roads and houses	8.0 ± 1.2	3.6	16.3
Landscape heterogeneity	2.4 ± 0.2	1.5	3.6
Distance to closest wildflower strip (m)	291.0 ± 72.2	118	777
Distance to closest forest (m)	291.4 ± 87.4	20	861

Table S2. Trap-nesting host Hymenoptera in the 10 experimental wildflower strips. Species codes are used in Fig. 1. Larval food: p/n = pollen and nectar; a = aphids; h = other herbivores; s = spiders. The species groups used in the analyses are defined as follows: "bees" = Apidae; "wasps" = Eumenidae, Sphecidae, Pompilidae; the three subgroups for wasps (aphid-, other herbivore- and spider-predating wasps) are defined according to their larval food.

Nesting species	# brood cells	Larval food	Code	Nesting species	# brood cells	Larval food	Code
Apidae				**Sphecidae**			
Hylaeus communis	58	p/n	1	*Ectemius continuus*	1	h	31
H. difformis	7	p/n	2	*Isodontia mexicana*	31	h	32
Hylaeus sp.	301	p/n	3	*Nitela* sp.	5	h	33
Chelostoma florisomne	124	p/n	4	Sphecidae sp.	27	h	34
Heriades truncorum	1819	p/n	5	*Passaloecus borealis*	73	a	35
Megachile centuncularis	138	p/n	6	*P. gracilis*	62	a	36
M. ericetorum	53	p/n	7	*P. insignis*	43	a	37
M. versicolor	219	p/n	8	*P. corniger*	11	a	38
Megachile sp.	250	p/n	9	*P. vandeli*	3	a	39
Osmia adunca	119	p/n	10	*Passaloecus* sp.	83	a	40
O. bicornis	7980	p/n	11	*Pemphredon lugubris*	20	a	41
O. brevicornis	21	p/n	12	*Pemphredon* sp.	20	a	42
O. caerulescens	362	p/n	13	*Psenulus pallipes*	22	a	43
O. gallarum	4	p/n	14	*Psenulus* sp.	2	a	44
O. caerulescens/gallarum	87	p/n	15	*Trypoxylon figulus*	1823	s	45
O. cornuta	12	p/n	16	*Trypoxylon* sp.	73	s	46
Osmia sp.	13	p/n	17	**Pompilidae**			
Apidae sp.	413	p/n	18	*Agenioides cinctellus*	27	s	47
Eumenidae				*Auplopus carbonarius*	9	s	48
Alastor atrops	1	h	19	*Dipogon subintermedius*	5	s	50
Allodynerus rossii	55	h	20	*Dipogon* sp.	6	s	49
Ancistrocerus antillope	61	h	21	**Others**			
A. gazella	498	h	22	Symphyta sp.	6	-	52
A. nigricornis	1253	h	23	undetermined hosts	512	-	55
A. parietinus	11	h	24	Host Braconidae 1	12	-	56
Ancistrocerus sp.	16	h	25	Host Braconidae 2	17	-	57
Euodynerus notatus	5	h	26				
Gymnomerus laevipes	34	h	27				
Microdynerus timidus	74	h	28				
Symmorphus gracilis	18	h	29				
Eumenidae sp.	344	h	30				
Total number of brood cells					17 243		

Table S3. Higher trophic level ("enemy") species in the 10 experimental wildflower strips. Species codes are used in Fig. 1. Host group: B = bees; W = wasps; G = bees and wasps; O = enemies of undetermined hosts. *Morphospecies.

Enemy species	# Cells attacked	Host group	Code
Hymenoptera			
Apidae			
Coelioxys inermis	4	B	59
C. mandibularis	4	B	60
C. inermis/mandibularis	3	B	58
Stelis breviscula	61	B	61
Chrysididae			
Chrysis cyanea	22	G	62
C. ignita	3	O	63
Omalus auratus	5	W	64
Chrysididae sp.	7	W	65
Eulophidae			
Mellitobia acasta	596	G	66
Ichneumonidae			
Ephialtes manifestator	45	G	67
Ichneumonidae spp. 1-5*	17	O	68-72
Cryptinae sp.	1	W	73
Lissonota sp.	2	W	74
Tryphoninae sp.	1	O	75
Campopleginae sp.	1	W	76
Ophion sp.	5	O	77
Gasteruptiidae			
Gasteruption assectator	2	B	78
Sapygidae			
Sapyga decemguttata	16	B	79
S. quinquepunctata	127	G	80
Sapygidae sp.	7	G	81
Pteromalidae			
Pteromalidae sp.	3	W	82
Toryminae			
Monodontomerus obsoletus	15	B	83
Braconidae			
Braconidae spp. 1-6*	77	O	84-89
Isodontia parasites	3	W	90
Coleoptera			
Trichodes alvearius	407	G	91
Megatoma undata	108	G	92
Diptera			
Anthrax anthrax	13	B	93
Cacoxenus indagator	1544	B	94
Diptera larvae	2	W	95
Acari			
Chaetodactylus osmiae	106	B	96
undetermined			
Species 1	1	W	97
Total	3208		

Table S4. Correlations among variables. Cell entries are Pearson's correlation coefficient, n=10. ***P<0.001, **P<0.01, *P<0.05, †P<0.1

		Cover (%)							Distance (m) to next		Vegetation	
		forest	extensive meadows	gardens, hedges & orchards	wildflower strips	roads & houses	water bodies	landscape hetero-geneity	wildflower strip	forest	species richness	bio-mass
Cover (%)	agricultural fields	-0.61 †	-0.80 **	-0.78 *	-0.07	-0.12	0.29	-0.98 ***	0.20	0.81 **	-0.23	-0.07
	forest		0.12	0.12	0.11	-0.43	0.14	0.56	-0.19	-0.74 *	0.02	-0.25
	extensive meadows			0.92 ***	0.08	0.16	-0.25	0.86 ***	-0.26	-0.51	0.18	0.29
	gardens, hedges & orchards				0.28	0.07	-0.40	0.86 ***	-0.52	-0.46	0.02	0.42
	wildflower strips					-0.44	-0.39	0.17	-0.72 *	0.22	-0.67 *	0.40
	roads & houses						-0.47	0.01	0.65 †	0.06	0.51	-0.06
	water bodies							-0.27	0.12	-0.10	-0.12	-0.36
	landscape heterogen-eity								-0.33	-0.75 *	0.17	0.11
Distance (m) to next	wildflower strip									0.03	0.60 †	-0.57
	forest										-0.17	0.04
Vege-tation	species richness											-0.57

3 Supplementary Figures

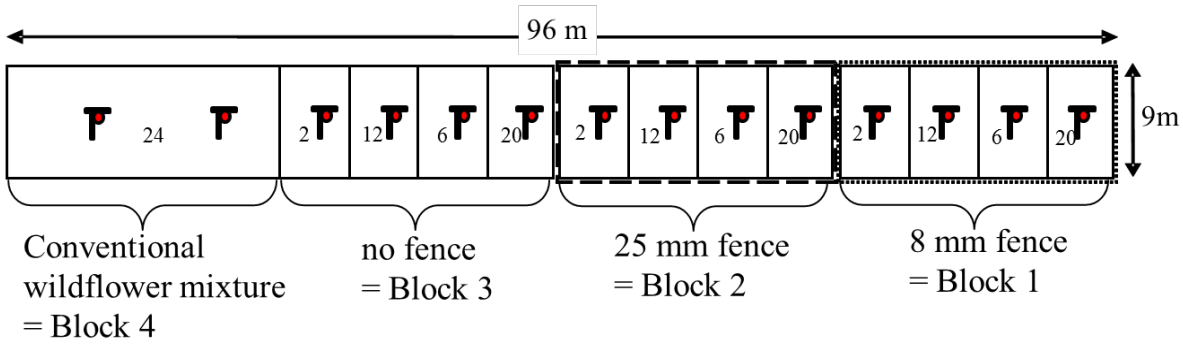


Fig. S1. Arrangement of the 14 trap-nests (red circles) within subplots in the experimental wildflower strips. Numbers indicate sown plant species richness. Strips were divided into four blocks of equal size: 1. fence with 8 mm mesh (dotted-line), 2. fence with 25 mm mesh (dashed-line), 3. no fence, and 4. conventional wildflower mixture without fence. Note that fencing had no effect on the trap-nest community, and the effects of the plant diversity treatments are discussed elsewhere (Fabian 2013).

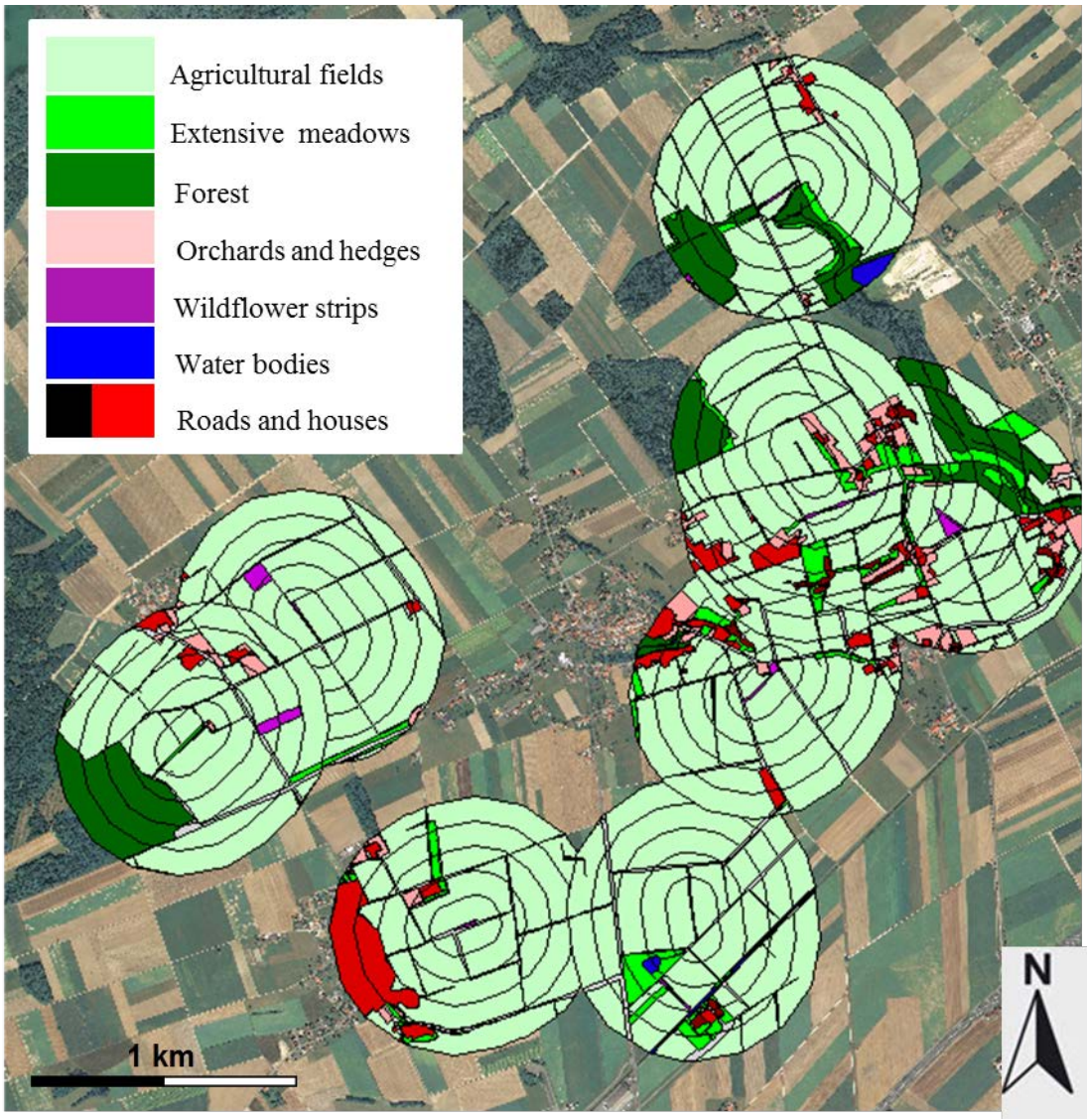
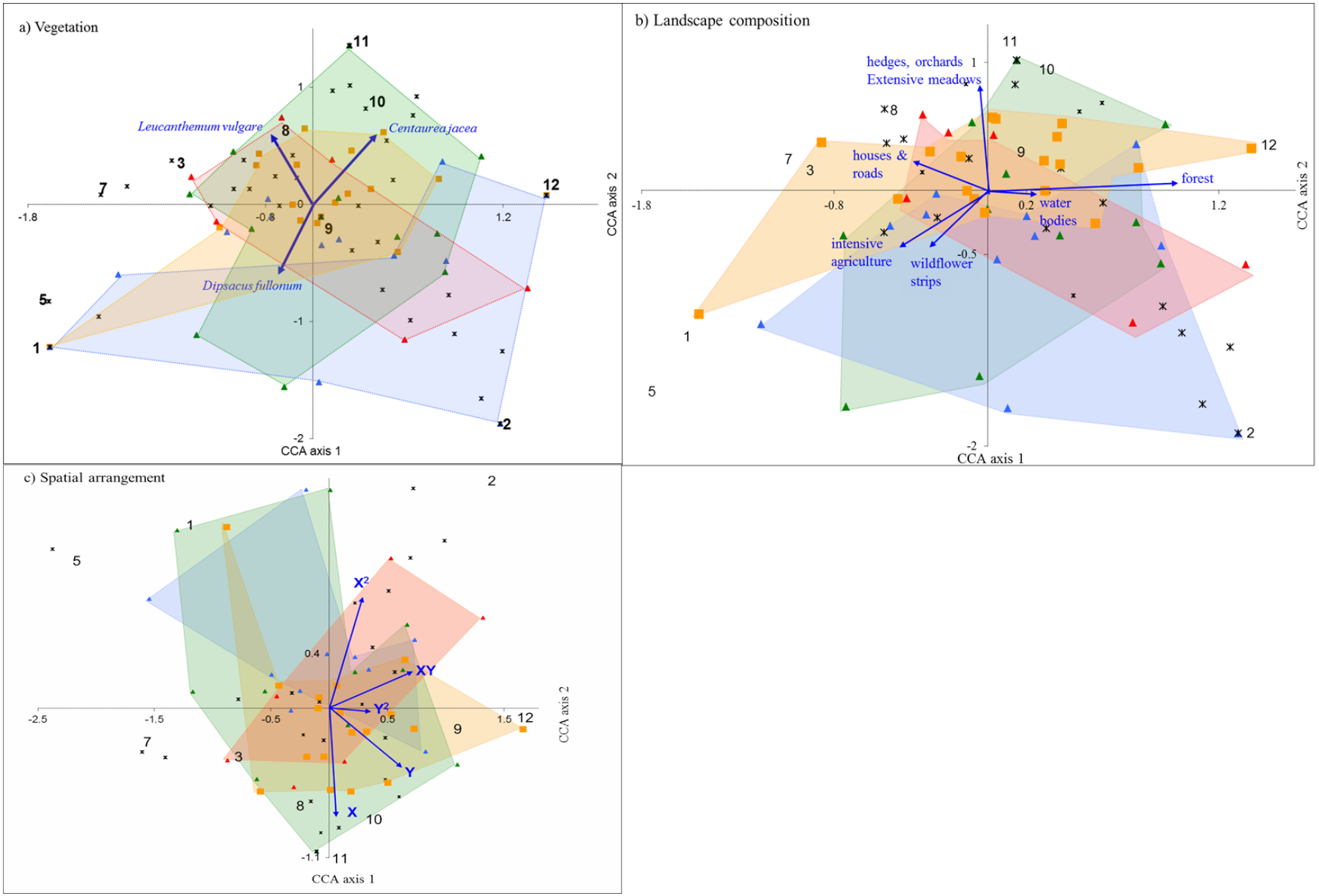


Fig. S2. Aerial photo of the study area. The 10 experimental wildflower strips are surrounded by ellipsoids of 500 m radius in which land use was measured. The colours depict landscape composition.

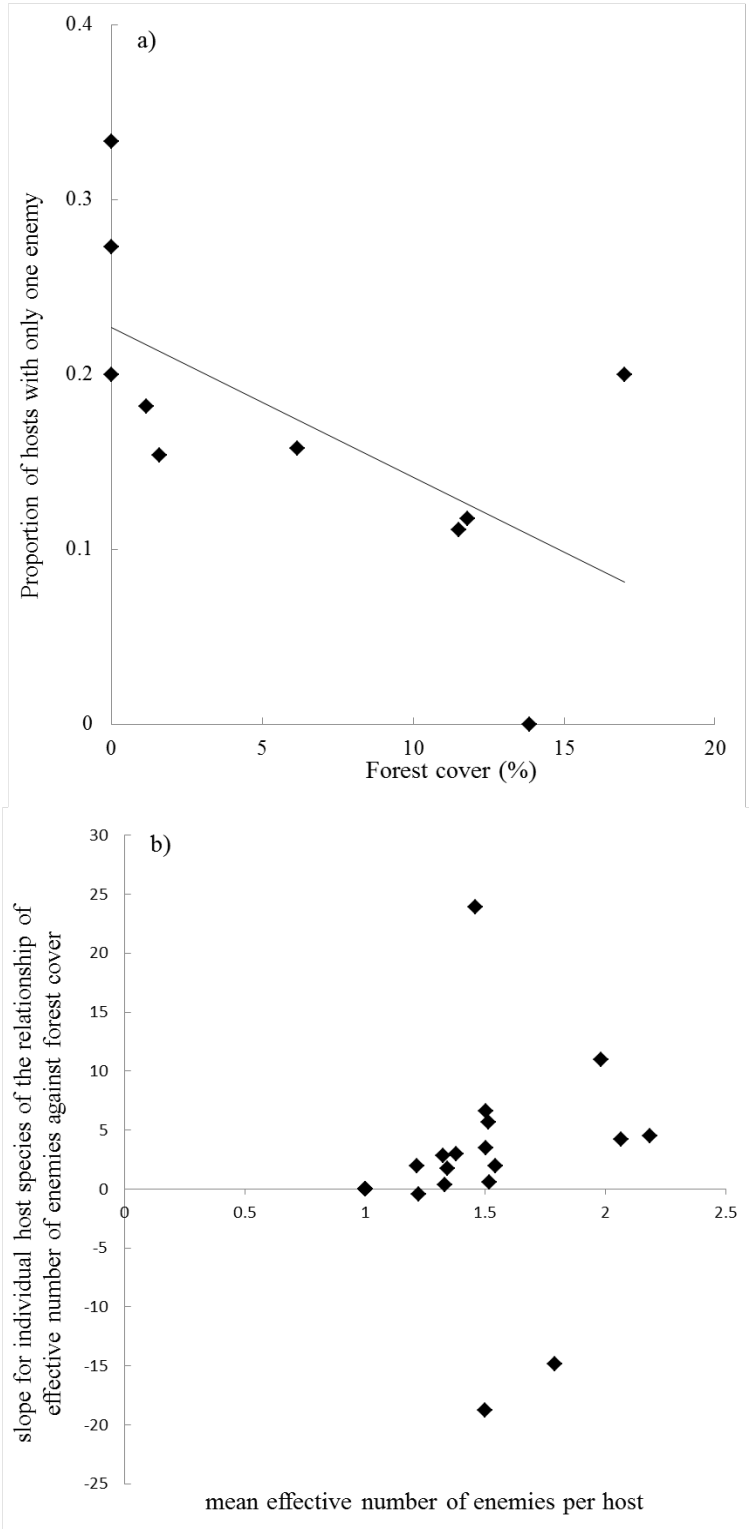


Fig. S3. Trap nests for solitary bees and wasps. Photographs show a single trap and its placement in a wildflower strip in an agricultural landscape. Photographs by N. Sandau


a) Vegetation
Leucanthemum vulgare
Centaurea jacea
Dipsacus fullonum
CCA axis 1
CCA axis 2
b) Landscape composition
hedges, orchards
Extensive meadows
houses &
roads
forest
water
bodies
intensive
agriculture
wildflower
strips
CCA axis 1
CCA axis 2
c) Spatial arrangement
X²
XY
Y²
Y
X
CCA axis 1
CCA axis 2

786

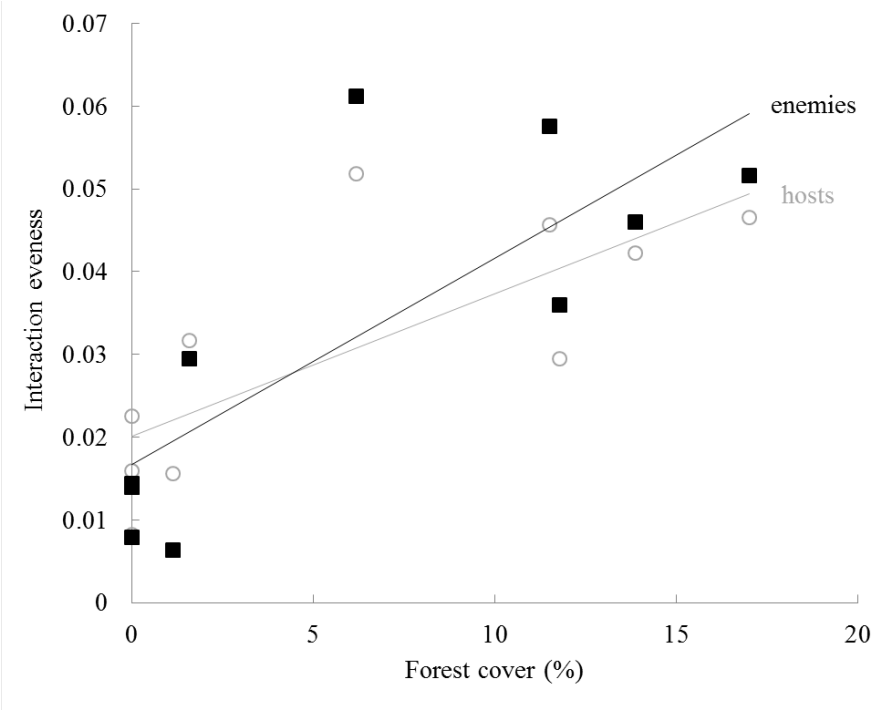
Fig. S4. Relationship between the three sets of environmental descriptors and the trap-nest community in canonical correspondence analyses. The host functional groups are shown as coloured areas: bees = orange squares, aphid predators = green triangles, other herbivore predators = blue triangles, spider predators = red triangles; enemies are shown with black stars. Only the most important among the 30 most abundant plant species are shown. Black numbers indicate the identity of the wildflower strips.



790

791 **Fig. S5.** Potential explanations for the relationship between forest cover and vulnerability.
792 The relationship between a) the proportion of hosts that have only a single enemy and forest
793 cover, and b) values of the slopes for individual host species in the effective number of
794 enemies regressed against forest cover and their mean effective number of enemies over all 10

795 strips. It shows that most host species interact with more enemies in strips with greater forest
796 cover.



797

798 **Fig. S6.** Potential explanations for the relationship between forest cover and
799 generality/vulnerability: the average interaction evenness of all hosts (grey circles) and
800 enemies (black squares) in each strip as a function of forest cover. Evenness for a given host
801 is measured as the ratio of the Shannon index for the frequencies of interactions with its
802 enemies, over the maximum value of this index (the log of its number of enemies). Evenness
803 for enemies is measured similarly, but based on interactions with hosts. Values given here are
804 averages for each food web.

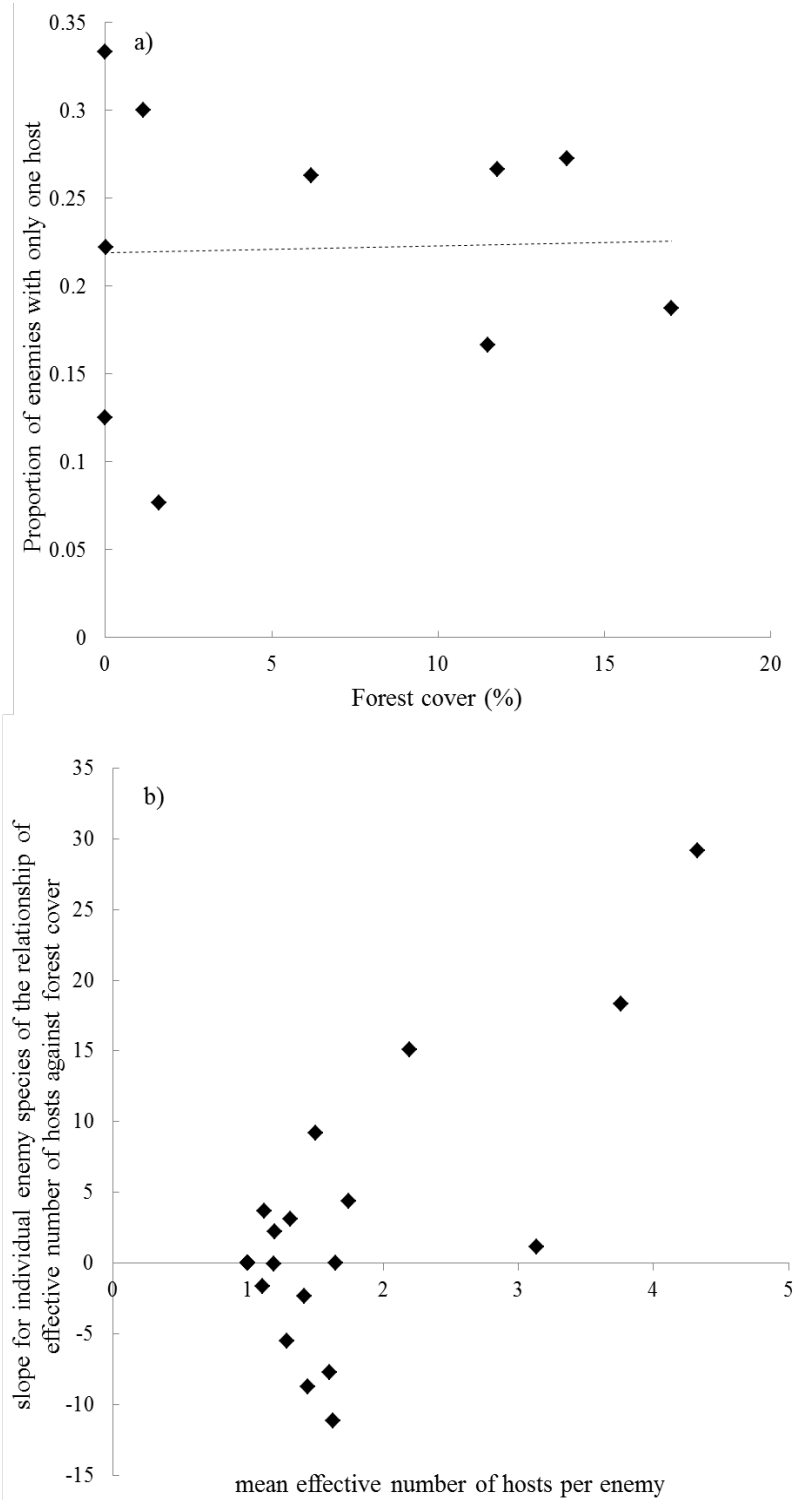


Fig. S7. Potential explanations for the relationship between forest cover and generality. The relationship between a) the proportion of enemies that have only a single host and forest cover, and b) the values of the slopes for individual enemy species in the effective number of hosts regressed against forest cover and their mean effective number of prey over all 10 strips. Enemies with the highest number of hosts are also those showing the strongest positive effect of forest cover.

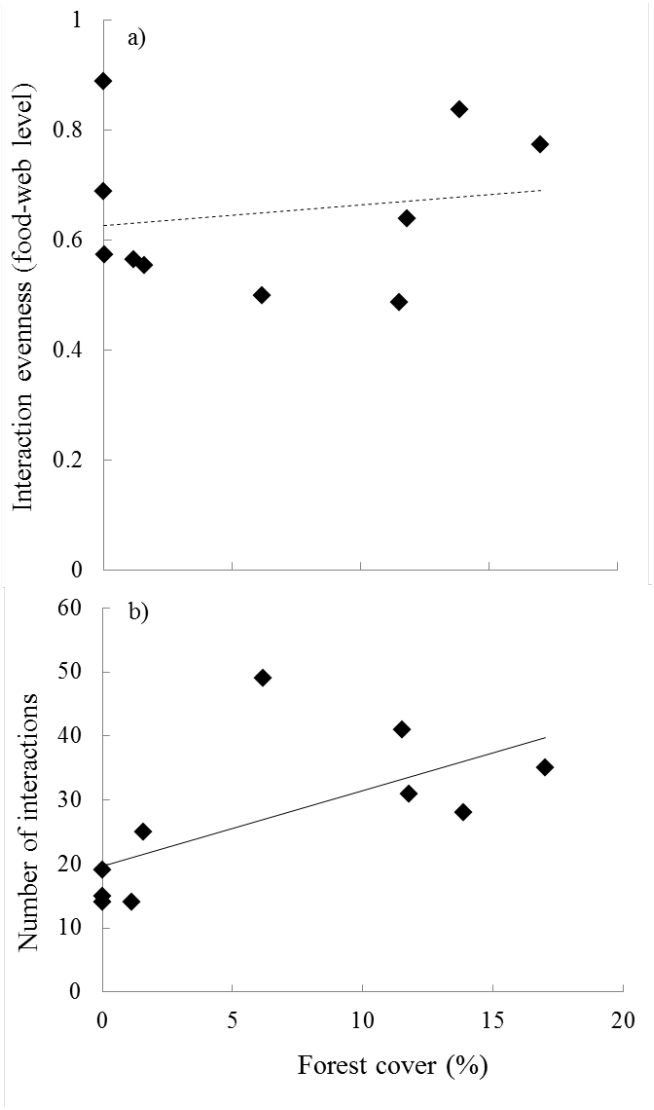
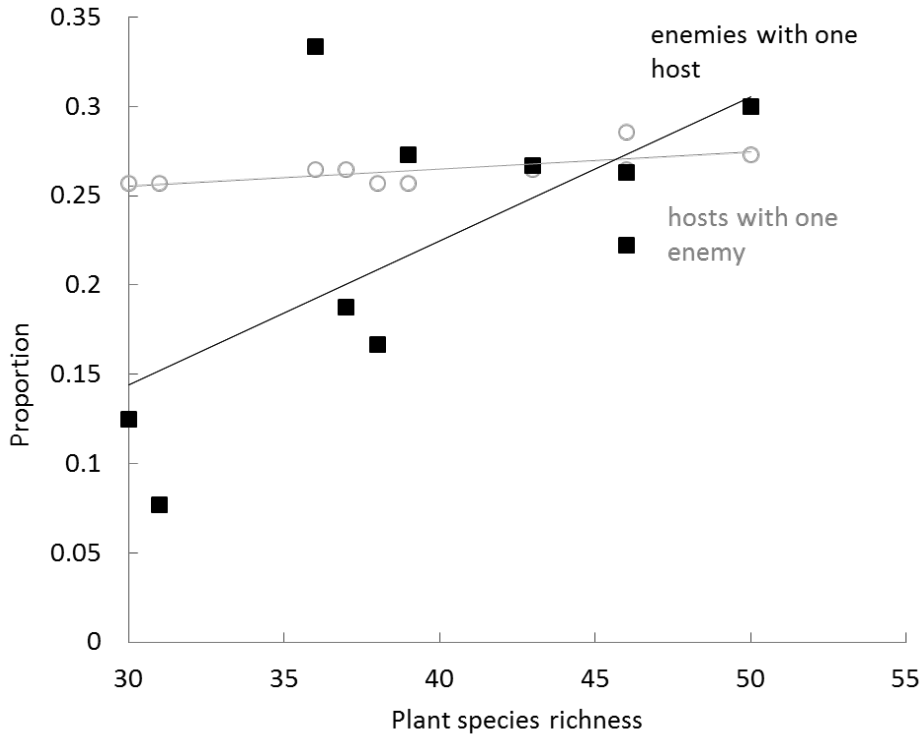


Fig. S8. Potential explanations for the relationship between forest cover and interaction diversity: a) the total interaction evenness for each food web as a function of forest cover and b) the total number of interactions of each food web as a function of forest cover.



817

818 **Fig. S9.** A potential explanation for the relationship between plant species richness and
819 compartmentalisation: the proportion of "specialist" hosts with only one enemy (grey circles)
820 and of specialist enemies with only one host (black squares) both increase significantly with
821 plant species richness.

4 Supplementary References

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