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; Schüpp 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
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, González & 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, Naishbit & 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 (Tyliani-kis, 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; Schüeppe et al. 2011).

In recent literature, trap-nest communities are usually split into three groups: bees, wasps and higher trophic enemies (predators and parasitoids; Schüeppe 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 Grand-cour, 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 m² 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 (Bundesamt 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 \( H' = \sum \frac{p_i \log(p_i)}{C_0} \)), and the correlations among landscape measures (Table S4, Supporting information), were used only forest cover in the surroundings (% in the analyses.

**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 Passalocues, Pompredon and Pseuda), other herbivore-predating wasps (Eumenidae and Sphecidae, feeding on Chrysomelidae, Curculionidae, Caelifera and micro-lepidoptera larvae), spider-predating wasps (Pompiliidae 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, Banasik-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 m² 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 R² square values ($R^2_a$) can be used to represent the percentage variance in the data explained by each independent variable (Pereira-Neto et al. 2006); note that $R^2_a$ 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), \( \beta \) the vector of parameters and \( \varepsilon \) the vector of residuals. In our case, we consider \( \varepsilon \sim N(0, \Sigma) \) with

\[
\Sigma = \delta^2 \begin{pmatrix}
1 & ... & 0 \\
... & ... & ... \\
0 & ... & 1
\end{pmatrix} + \lambda \delta^2 \begin{pmatrix}
0 & ... & c_{ij} \\
... & ... & ... \\
c_{ij} & ... & 0
\end{pmatrix}
\]
eqn1

The parameter \( \lambda \) determines the strength of the correlation structure induced by the overlap in landscape and \( \delta^2 \) denotes the variance. To estimate the \( P \)-value of \( \lambda \), 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 independent and identically normally distributed) before checking for normality. This is achieved by the following transformation: \( \tilde{e} = L^T e \), with \( e \) and \( \tilde{e} \) the vector of residuals and of transformed residuals, respectively; \( L^T \) is the transpose of the lower triangular matrix, \( L \), from Cholesky decomposition of \( \Sigma^{-1} \), the inverse of the matrix \( \Sigma \) (\( L^T \) can be thought of as the square root of the matrix \( \Sigma^{-1} \); 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 (Banasek-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 bicolor* 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 (*Eumenes*), digger wasps (*Sphecidae*) and spider wasps (*Pompilidae*). Records were dominated by the spider-predating *Trapsyphe figulas* 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 (klepto-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 (\( F = 1.8, P = 0.003 \)) and for enemies (\( F = 2.0, P = 0.005 \)).

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
The adjusted R² values are given. **P < 0.01, *P < 0.05, †P < 0.1.

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

The prey availability for the analyses of wasps and their subgroups is the abundance of their corresponding prey groups; 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 = 0.056).

**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 (0–16%) with that for the five with highest forest cover (6–17%) (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 ($r = -0.63$, d.f. = 8, $P = 0.053$; 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 $P = 0.013$; Fig. S5b, Supporting information) and (iii) the interaction evenness of hosts increased with greater forest cover ($r = 0.75$, d.f. = 8, $P = 0.012$; Fig. S6, Supporting information). In contrast, for generality, forest cover in the surroundings did not affect the proportion of specialists ($r = 0.03$, d.f. = 8, $P = 0.93$; 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 $P = 0.80$; 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 $\beta = 0.01$, $P = 0.045$; 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, $P = 0.002$, 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 ($r = 0.65$, d.f. = 8, $P = 0.042$) and not to a change in evenness of the interactions at the food web level ($r = 0.17$, d.f. = 8, $P = 0.63$).

### 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 $P < 0.05$.

<table>
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<tr>
<th>Food web metric</th>
<th>Community species richness</th>
<th>Vegetation</th>
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<td>$P$</td>
<td>$\beta$</td>
<td>$P$</td>
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<td>-</td>
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<tr>
<td>Interaction diversity</td>
<td>-0.11</td>
<td>0.220</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Compartment diversity</td>
<td>-1.10</td>
<td>0.004</td>
<td>1.70</td>
<td>0.001</td>
</tr>
</tbody>
</table>

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. 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 ($r = 0.65$, d.f. = 8, $P = 0.039$; Fig. S9, Supporting information) and hosts with only one enemy species ($r = 0.68$, d.f. = 8, $P = 0.030$), 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; Schüpp 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
eenemies 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 under-
lying causes of variation in the quantitative food web
measurements.

In theory, highly diverse communities with higher con-
nectance (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 parti-
tioning 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 ele-
ments of a heterogeneous landscape that bridge agricul-
tural and late succession habitats.

The tree species richness, canopy height and age of for-
est 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 impor-
tance 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 ($r = -0.98, P < 0.001$), so it is possi-
ble that some taxa are responding to the presence of par-
ticular habitats, rather than to heterogeneity itself. For
instance, in contrast to all other taxa, we found that herbi-
vore-predating mason wasps (Eumenidae) were less abun-
dant 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 dis-
tances 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 compens-
tation zones to biocontrol. Furthermore, the species rich-
ness 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 for-
aging rate by temporally and locally specialized foraging
behaviour within the agricultural landscape. In early sea-
son, 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 correla-
tion 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 incor-
porate 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), grass-
lands (Albrecht et al. 2007; Schüpp et al. 2011; Ebeling
et al. 2012; with 170-5, 70-5 and 90-3 brood cells, respec-
tively) and agricultural areas (Holzschuh, Steffan-Dewen-
ter & Tscharntke 2010; 61-3 brood cells). Thus, managed
wildflower strips appear to provide favourable habitat
with access to food resources for pollinators and biologi-
ical control agents. The species richness of plants in the
wildflower strips positively affected the total species rich-
ness 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%, within the range of other studies (e.g. Albrecht et al. 2007 and Schüepp et al. 2011, with 28% 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.

References


Table S3. Higher trophic level ("enemy") species in the 10 experimental wildflower strips.

Table S4. Correlations among variables.

Fig. S1. Arrangement of the 14 trap-nests (red circles) within subplots in the experimental wildflower strips.

Fig. S2. Aerial photo of the study area.

Fig. S3. Trap nests for solitary bees and wasps.

Fig. S4. Relationship between the three sets of environmental descriptors and the trap-nest community in canonical correspondence analyses.

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.