

Plant diversity in a nutshell: testing for small-scale effects on trap nesting wild bees and wasps

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Abstract. Declining plant species richness in agro-ecosystems and thus reduced habitat quality can have cascading effects on ecosystem functioning, leading to reduced pollination and biological control. Here we test if plant diversity can affect arthropod diversity and abundance on a very small scale, manipulating plant species richness (2, 6, 12 and 20 sown species) in small adjacent subplots (6 × 9 m) in 10 wildflower strips in an agricultural landscape. We simultaneously analyzed the effect of plant species richness, vegetation structure, and plant composition on the species richness and abundance of cavity-nesting wild bees, wasps, their prey and natural enemies, and on the structure of their food webs. By separating the trap-nesting species into functional groups according to their prey, we aimed to understand the underlying patterns for the effects of plant diversity. Increasing plant species richness had a significant effect only on spider-predating wasps, the group of wasps trophically most distant from plants. In contrast, bees and food-web structure were unaffected by plant diversity. Spider-predating wasp abundance negatively correlated with the abundance of spiders, suggesting top-down control. Interestingly, the abundance of spiders was the only variable that was strongly affected by plant composition. The hypothesis that the effect of plant diversity decreases with increasing trophic level is not supported by our study, and the mobility of species appears to play a greater role at this small spatial scale.

Key words: biological control; parasitism; plant composition; pollinators; quantitative food webs; resource heterogeneity hypothesis; *Trypoxylon figulus*.

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INTRODUCTION

Biodiversity loss due to intensification in agriculture is an important driver of reduced ecosystem functioning (Cardinale et al. 2006). Plant species richness has often been central to this discussion (Hooper et al. 2005) and has been identified as an important determinant of the

diversity and abundance of consumers (Haddad et al. 2009, Scherber et al. 2010a). Two non-exclusive hypotheses have been formulated to explain the relationship between plant diversity and herbivore abundance and diversity. First, the resource heterogeneity hypothesis (Hutchinson 1959) argues that higher plant diversity offers greater resource heterogeneity, resulting in a

higher diversity of consumers. Second the *more individuals hypothesis* (Srivastava and Lawton 1998) suggests that diverse plant communities are often more productive than simple plant communities (Tilman et al. 2001), and thus the greater quantity of resources available for consumers increases their abundance and diversity. Both hypotheses have found support in previous studies (Knops et al. 1999, Haddad et al. 2009).

At higher trophic levels, predator species may simply respond to increased diversity or productivity of resources provided by their prey in diverse plant communities (*resource heterogeneity* and *more individuals hypotheses* acting at the predator level), although this indirect response with plant diversity may dampen with increasing trophic level (Scherber et al. 2010a). However, predators may also respond directly to structural habitat diversity in diverse and productive plant communities. Consequently, plant diversity could influence positively the structure of predator communities, possibly resulting in top-down effects limiting herbivore abundances more strongly in more diverse plant communities, as predicted by the *enemy hypothesis* (Root 1973). Thus declining plant species richness can have cascading effects, releasing herbivores from this control and leading to reduced ecosystem functioning (Knops et al. 1999, Balvanera et al. 2006). The relationships between abundance and diversity of different trophic levels is therefore difficult to predict, and it is not surprising that recent studies showed varying effects of plant diversity on the abundance or diversity of higher trophic levels, yielding positive (Albrecht et al. 2007, Dinnage 2013), neutral (Ebeling et al. 2012) or negative (Schuldt et al. 2011) relationships. However, positive effects dominate, with a reported decrease in the strength of the relationship for higher trophic levels (Scherber et al. 2010a).

In addition to plant species richness, the composition of the plant community can affect the species richness, abundance and food-web structure of consumers and higher trophic levels (Hooper and Vitousek 1997, Haddad et al. 2001, Viketoft et al. 2009, Scherber et al. 2010b). Usually, plant composition is analyzed separately from plant diversity and structure, either by using multivariate approaches (Fabian et al. 2012), by considering different functional groups

(e.g., grasses, herbs, legumes; Hector et al. 1999, Haddad et al. 2009, Scherber et al. 2010b), or by using dissimilarity matrices in Mantel tests (Ebeling et al. 2012). To our knowledge, studies that simultaneously analyzed the effect of plant diversity, plant composition and structure on insect diversity and abundance and ultimately food-web structure are rare.

The spatial scale at which the studies are conducted can affect the shape and strength of the relationship between plant species richness and the higher trophic levels. For example, the effect of productivity on the species richness of producers and of animals changed from unimodal to linear when increasing the spatial scale of the study (Chase and Leibold 2002). In that case, increased scale was obtained by pooling plots (ponds) of similar productivity, and the change in shape was explained by higher species dissimilarity in more productive plots. More generally, rather than a change in shape, one can expect that the relationships become weaker when considering smaller plots. For example, using hymenopteran-dominated communities in trap-nests, Albrecht et al. (2007) found a significant relationship between plant and bee diversity in 1-ha plots, while no significant relationship could be detected in the 20 m × 20 m plots of the Jena experiment (Ebeling et al. 2012). However, the same experiment yielded many positive results for other groups (Scherber et al. 2010a), and it is likely that this scale-effect is dependent on the mobility of the species considered. Because various species groups may respond differently to plant diversity according to their trophic level (Scherber et al. 2010a) and their mobility, it is interesting to consider the effects of plant diversity at a small spatial scale, since it is here that differences between the groups may be more apparent. Additionally, considering more subtle differences in the ecology of the species, rather than simply their trophic level, could reveal otherwise hidden effects.

Here, we look at the hymenopteran-dominated communities breeding in trap-nests in a plant diversity experiment installed within wildflower strips. These structures are ecological compensation areas consisting of mixtures of typically tall herbs and often established along field margins (Haaland et al. 2011). Among those species likely to colonize wildflower strips, solitary cavity-

nesting bees and wasps (Hymenoptera, Aculeata) provide valuable ecosystem services (Gathmann and Tscharntke 1997) and have been used to monitor the effects of ecological change (Tscharntke et al. 1998, Albrecht et al. 2007, Holzschuh et al. 2010). Cavity-nesting bees act as pollinators and collect pollen or nectar as food for their larvae (Westrich 1989). Cavity-nesting wasps can act as biological control agents (Tscharntke et al. 1998) by collecting phloem-sucking aphids (Aphididae) or other herbivorous arthropods, including larvae of smaller moths (microlepidoptera), leaf beetles (Chrysomelidae) and weevils (Curculionidae). Other species behave as intraguild predators by feeding on spiders (Araneae), which themselves are beneficial as predators in agricultural ecosystems (Schmidt-Entling and Dobeli 2009). Thus, the trap-nest bees and wasps fall in different trophic levels and may respond differently to vegetation composition, diversity and structure, either directly, through the availability of pollen and nectar sources, or indirectly, through the availability of their different prey taxa. Although it is known that prey abundance has important effects on the abundance of predators (Cohen et al. 2003), earlier studies on trap nests included plant species richness, but not specific prey abundances (e.g., Albrecht et al. 2007, Ebeling et al. 2012).

We used mixed effect models to simultaneously analyze the effect of plant composition, plant diversity and vegetation structure on the diversity and abundance of the trap-nest functional groups in a plant diversity experiment. We also reconstructed quantitative food webs describing the feeding links and interaction strength between bee and wasp hosts (the nest-makers) and their enemies, mostly cleptoparasitic flies and parasitoid wasps (Bersier et al. 2002, Tylianakis et al. 2007). We tested the following hypotheses:

- (1) Plant diversity affects the diversity and abundance of bees, wasps and their enemies in trap nests according to the *resource heterogeneity* and *more individuals hypotheses*. These effects can be measured for some groups even on a very small scale.
- (2) The strength of the plant diversity effect differs among insect functional groups, decreasing with increasing trophic level in

the following order: (1) bees, (2) aphid- and other herbivore-predating wasps, (3) spider-predating wasps, and (4) enemies of trap-nesting bees and wasps.

- (3) The complexity of biotic interactions, as measured by quantitative food web metrics, decreases more rapidly than simple species diversity and abundance as plant diversity declines (Tylianakis et al. 2007).

MATERIAL AND METHODS

Wildflower strip manipulations

Wildflower strips are one of several elements in agri-environmental schemes introduced in Europe to counter species declines and provide ecosystem services (Kleijn et al. 2009, Haaland et al. 2011). In Switzerland, they consist of field margins or patches sown with a recommended plant mixture containing 24 herb species and maintained for six years (Nentwig 2000). In spring (April–June) 2007 12 wildflower strips were sown manually in agricultural fields around the village of Grandcour, 10 km south of Lake Neuchâtel in north-west Switzerland (479 m altitude; coordinates: 46° 52' N, 06° 56' E). Annual average air temperatures are 10.1°C and annual precipitation is approximately 941 mm in the region (Confédération suisse, Agroscope 2011). The region is characterized by intensive agriculture embedded in a small-scale mosaic of arable fields, meadows and forests (Fabian et al. 2013).

The wildflower strips (hereafter strips) were each divided into three blocks of 216 m², which were randomly assigned to one of three trophic compositions: (1) control unfenced; (2) fenced with the aim of excluding slugs, micromammals and their main vertebrate predators; and (3) fenced to exclude only the vertebrate predators (as explained in detail in Fabian et al. 2012). These treatments did not affect the trap-nest community analyzed here (see statistical analysis below). Within each trophic treatment, four subplots (6 × 9 m) differing in plant diversity (2, 6, 12, 20 sown species) were randomly assigned (Fig. 1) and established from seeds of the conventional wildflower seed mixture (Günter 2000). The order and species composition of the plant diversity subplots was the same in the three fence treatments within a strip (Fig.

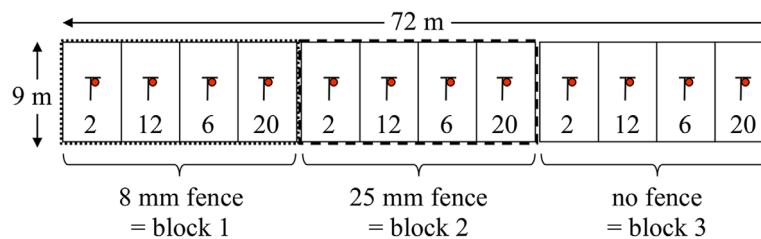


Fig. 1. Experimental set up of 12 trap-nests (red circles) within subplots in wildflower strips. Numbers indicate sown plant species richness. Strips were divided into three blocks of equal size, with 3 fence treatments: (1) fence with 8 mm mesh (dotted-line), (2) fence with 25 mm mesh (dashed-line) and (3) no fence.

1), but differed between strips. Thus, in total each of the 12 strips consisted of 12 subplots (3 fencing $\times$ 4 diversity treatments). In contrast to other biodiversity experiments (e.g., Cedar Creek; Tilman et al. (2001) and Jena Experiment, Roscher et al. (2004)), the plots were not weeded, so that the plant communities are the result of self-assembly following initial sowing. All plant diversity measures were thus based on actual diversity estimates rather than sown values, although the two were correlated ($r = 0.13$, $df = 280$, $P = 0.014$).

Vegetation

In autumn 2008, the percentage cover for each species was visually estimated using the standard method of Braun-Blanquet (Perner et al. 2005) for each subplot. *Plant diversity* was characterized by the total plant species richness. Vegetation structure was characterized by the average *vegetation height* and *plant biomass*. Vegetation height was estimated as the average height of all plants of a subplot. Plant biomass was assessed by measuring the leaf area index (LAI) with a LAI-2000 (LI-COR Biosciences) at 24 random points in each subplot in autumn 2008. The method was calibrated by cutting, drying and weighing 5 biomass samples in 8 subplots, and the resulting linear relationship (Pearson product-moment correlation $r = 0.89$) was used to transform the average LAI values to plant biomass per subplot in dry weight g/m^2 .

Trap nests

Community composition.—Trap nests enabled us to study species richness, abundance, and interactions of above ground nesting hymenopterans and their natural enemies under standardized nest site conditions (Tscharrntke et al. 1998). Trap-

nests consisted of 170–180 20-cm long internodes of common reed *Phragmites australis*, placed in 20-cm long plastic pipes of 10 cm diameter. The diameters of reed internodes ranged from 2 to 10 mm. One trap was placed within each subplot, fixed at a height of 1.3 m on a wooden pole and protected by a 30×30 cm wooden roof. In total, 12 trap nests were positioned in each strip (Fig. 1) from mid-April until October 2008. After collection they were stored at 4°C for at least seven weeks to simulate winter. Twenty-seven nests were destroyed while in place, including nearly all of those in two strips, thus in total 117 trap nests from 10 strips were analyzed.

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 adults for identification. Individuals were identified using the following resources: Megachilidae, Amiet et al. (2007); Sphaecidae, De Beaumont (1964); Pompilidae, Wolf (1972); Eumenidae, Schmid-Egger (2004); Sapygidae, Amiet (2008); and Chrysididae, Bellmann (1995) and Linsenmaier (1997). Several specimens of each species were verified by taxonomists (see Acknowledgments). If no adult emerged, features of the nest and larval food were used to identify the genus or (sub-) family based on Gathmann and Tscharrntke (1999). Empty brood cells of eumenid wasps were assumed to belong to the bivoltine *Ancistrocerus nigricornis*, since it was the only species for which offspring of the first generation emerged before trap collection (Krewenka et al. 2011).

Table 1. Parameter estimates from linear mixed effect models relating species richness and abundance of the trap-nest community and their prey to descriptors of vegetation and prey/predator abundance.

Response variable	Explanatory variable						AIC with/without plant composition correl.
	Plant species richness (log)	Veg. height	Plant biomass	Additional variable		Plant correl. coef. λ	
				Name	Estimate		
Species richness							
Entire community	0.00 ns	0.03 ns	−0.05 ns	NA	...	0.34	94/94
Host species	0.08 ns	−0.07 ns	−0.08 ns	NA	...	0.22	114/112
Bees	−0.05 ns	0.08 ns	−0.03 ns	NA	...	0.06	105/103
Wasps	0.20†	−0.14 ns	−0.09 ns	no. arthropods	0.03 ns	0.49	117/117
Aphid predators	0.15 ns	−0.16 ns	0.08 ns	no. aphids	0.05 ns	<0.01	125/123
Herbivore predators	0.06 ns	−0.01 ns	−0.17 ns	no. herbivores	0.01 ns	0.26	127/125
Spider predators	0.27*	−0.11 ns	0.11 ns	no. spiders	−0.16†	<0.01	112/110
Enemies	−0.08 ns	−0.01 ns	0.01 ns	no. host species	0.42***	0.15	58/56
Abundance (no. cells)							
No. brood cells	−0.05 ns	−0.08 ns	−0.07 ns	NA	...	<0.01	98/96
Bees	−0.06 ns	−0.05 ns	−0.05 ns	NA	...	<0.01	95/93
Wasps	−0.06 ns	−0.11 ns	−0.09 ns	no. arthropods	−0.08 ns	0.26	110/109
Aphid predators	0.10 ns	−0.10 ns	0.06 ns	no. aphids	0.03 ns	<0.01	127/125
Herbivore predators	−0.05 ns	0.01 ns	−0.20†	no. herbivores	0.03 ns	0.28	81/79
Spider predators	0.20*	−0.11 ns	−0.02 ns	no. spiders	− 0.21*	<0.01	17/15
Parasitized cells	−0.06 ns	−0.01 ns	0.02 ns	no. brood cells	0.54***	<0.01	118/119
Abundance of potential prey (D-vac)							
Aphids	−0.01 ns	0.01 ns	0.16 ns	no. aphid pred. no. spiders	0.08 ns 0.03 ns	0.26	120/121
Herbivores	0.14 ns	0.14†	0.11 ns	no. herb. pred. no. spiders	−0.08 ns 0.27**	0.14	76/74
Spiders	−0.07 ns	−0.05 ns	0.01 ns	no. spider pred. no. herbivores	−0.13† 0.21*	0.56	67/76

Notes: Additional variables measuring prey or predator abundance were added to the models as explained in *Material and Methods*. Values of parameters come from REML models, with strips as random factors and the plant composition in the different subplots included as a correlation structure. Response variables were all Box-Cox power transformed, except species richness of aphid-predating wasps and abundance of spider-predating wasps, which were logarithmic transformed. Abbreviations are: veg., vegetation; correl., correlation; coef., coefficient; no., number of; pred., predator; herb., herbivore; NA, not available; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; † $P < 0.1$; ns $P > 0.1$.

Species richness and abundance (number of brood cells) in each subplot were recorded for the entire trap-nest community and separately for the following groups: hosts, enemies, pollen- and nectar-collecting bees (Apidae), all wasps, and the individual wasp functional groups predating on herbivores (Eumenidae and Sphecidae, feeding on Chrysomelidae, Curculionidae, Caelifera, and microlepidoptera larvae), on aphids (Sphecidae of the genera *Passaloecus*, *Pemphredon*, and *Psenulus*), and on spiders (Pompilidae and Sphecidae of the genus *Trypoxylon*) (see Table 1).

Food-web metrics.—Quantitative host-enemy interaction food webs were constructed based on the pooled data from the three equal diversity subplots of each strip, and three quantitative food-web metrics were calculated following Bersier et al. (2002), using the bipartite package (Dormann et al. 2009) in R (R Development Core

Team 2012). *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. *Interaction diversity* is a measure of the Shannon diversity of interactions that takes both the number and the evenness of interactions into account (Tylianakis et al. 2007). For comparison, qualitative food-web metrics were calculated based on binary presence/absence interaction data. We analyzed three additional qualitative food-web metrics. *Connectance* is the proportion of potential links that are realized. *Nestedness* is a measure of departure from a systematic arrangement of species by niche width whereby the niches of more specialized species fall within those of more generalized species, ranging from 0 to 100, high to low nestedness (Atmar and Patterson 1993). The *number of compartments* is the number of

subwebs within a web, where a subweb is a set of interconnected species with no links to members of other subwebs (Tylianakis et al. 2007).

Availability of arthropod prey

To estimate arthropod abundance in each subplot of the 10 strips, vacuum (hereafter D-vac) samples 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). A foliage Hoover type SH 85C (Stihl, Dieburg, Germany) was used to sample for two minutes from an area of 1 m² in the center of each subplot, working systematically along each strip to minimize disturbance (Fig. 1). Collected arthropods were stored in ethanol and grouped into orders. Aphid (Aphidina) and spider (Araneae) abundances served as estimates of food availability for aphid- and spider-predating wasps, respectively. Total abundances of butterfly larvae (Lepidoptera), Psocoptera, beetle larvae (Coleoptera) and grasshoppers (Caelifera) per subplot (Appendix: Table A3) served as estimates of food availability for herbivore-predating wasps. For the analysis of total wasp species richness and abundance, the summed abundance of all these groups was counted as “arthropods”.

Statistical analyses

All analyses were carried out using R version 2.12.0 (R Development Core Team 2012). To determine the best structure of the random factors, we first analyzed linear models with the response variables bee, wasp and enemy species richness and abundance and tested for differences between strips and between trophic (fence) treatment blocks. Models with only strips as random factor always performed best based on Akaike Information Criterion (AIC), compared to models with either trophic treatment, or strip and trophic treatment as random factors, thus we used the ten strips as random factors in all following analyses.

We analyzed the data using a linear mixed effect model with a correlation structure induced by the similarity in plant species composition between subplots. Our model is given by

$$y_{i,j} = \beta_0 + \beta_1 \log(S)_{i,j} + \beta_2 (\text{Height})_{i,j} + \beta_3 (\text{Biomass})_{i,j} + \beta_4 (\text{Additional})_{i,j} + z_j + \varepsilon_{i,j}$$

where the indices i and j denote the subplot and the wildflower strip, respectively. As response variables ($y_{i,j}$), we tested: the species richness and number of brood cells of all trap nest species, hosts, enemies, bees, wasps, and the three wasp functional groups, and the abundance of aphids, other herbivores, and spiders from the D-vac samples. The following covariates were used: the natural logarithm of number of plant species ($\log(S)$), the average vegetation height (Height) and the average plant biomass (Biomass). As additional explanatory variables (Additional), we used: (1) the abundance of D-vac collected arthropods, aphids, other herbivores, and spiders in the analysis of the abundance and species richness of all wasps, aphid-, other herbivore- and spider- predating wasps, respectively; (2) the host species richness and number of brood cells in the analysis of enemy richness and number of parasitized cells, respectively; (3) the abundance of the respective predatory wasp group in the analysis of the abundance of D-vac collected aphids, other herbivores and spiders and (4) the abundance of D-vac collected spiders for aphids and herbivores, and of herbivores for spiders. The parameter β_0 denotes the intercept and β_{1-4} denote the parameter estimates for the slopes on each variable. The 10 wildflower strips were considered as random factors with $z_j \sim N(0, \sigma_z^2)$, where σ_z^2 denotes the random effect variance. The similarities in plant species composition between subplots were included as correlation structure in the residuals. Specifically, we do not consider the residuals as independent (which is the usual assumption in linear models). In our model the correlation between the residuals from subplot (i_1, j_1) and (i_2, j_2) is proportional to their vegetation similarity measured as the Bray-Curtis index (Bray and Curtis 1957), i.e., $\varepsilon_{i,j} \sim N(0, \Sigma)$, where the elements of the variance-covariance matrix are given by

$$\Sigma_{(i_1, j_1), (i_2, j_2)} = \begin{cases} \sigma^2 & \text{if } (i_1, j_1) = (i_2, j_2) \\ \sigma^2 \times (\text{Bray-Curtis})_{(i_1, j_1), (i_2, j_2)} \times \lambda & \text{if } (i_1, j_1) \neq (i_2, j_2). \end{cases}$$

The parameter λ determines the strength of the

correlation structure induced by the similarity in plant species composition, and is estimated at the same time as the other parameters. Note that for $\lambda = 0$, our model is simply equivalent to a standard linear mixed effect model. In order to determine if the correlation structure between the subplots induced by the plant composition was significant, we fitted models with and without inclusion of the correlation structure by maximum likelihood (see Chapter 9.4.2 in Davison 2003) and then computed the AIC (Zuur et al. 2009). Finally, the parameters were estimated using restricted maximum likelihood (REML, see Chapter 12.2 in Davison 2003). We examined Q-Q plots and Shapiro-Wilk tests of the normalized residuals of the models and Box-Cox transformed the response variables when necessary, to meet the assumptions of normality (Fox and Weisberg 2011). All continuous explanatory variables were scaled to zero mean and unit variance to facilitate comparison of their relative importance (Oksanen et al. 2011). The REML and ML codes can be provided upon request.

The food-web metrics (vulnerability, generality, interaction diversity, connectance, nestedness and number of compartments) were analyzed using the same procedure, with the explanatory variables: plant species richness (log), vegetation height, plant biomass and trap-nest species richness (to account for the possible dependence of the food-web metrics on the latter; Banasek-Richter et al. 2009).

The species composition of the entire community and of the four trophic guilds was analyzed with respect to (1) plant species richness and effective number of plant species (based on the Shannon diversity, see Jost 2006), vegetation height and biomass, and (2) vegetation composition of the 40 most abundant plant species over all strips, using constrained correspondence analyses (CCA) in *vegan* (Oksanen et al. 2011). Trap nest species with less than ten individuals were down-weighted; the effect of the strip identity was removed (“partialled out”) as conditioning variable. The importance of the predictors was tested using the function *anova* with 9999 permutations. Plant species that significantly affected the composition of the trap nest community were identified using the function *ordistep* with backward stepwise model selection using 9999 permutations.

RESULTS

In total we recorded 13,795 brood cells of 38 host taxa identified at the species level, and 16 at coarser level in the 117 trap nests. Bees were represented by 13 species in 9442 brood cells and wasps by 25 species in 3926 brood cells (Appendix: Table A1). The most abundant bee species was the Red Mason bee, *Osmia bicornis* (Family Megachilidae), with 6666 brood cells. The most abundant wasp species were the spider-predating digger wasp, *Trypoxylon figulus* (family Sphecidae), and the caterpillar-predating mason wasp, *Ancistrocerus nigricornis* (family Eumenidae), building 1659 and 931 brood cells, respectively. We found 36 taxa of higher trophic enemies of the orders Hymenoptera (cleptoparasites and parasitoids), Diptera (parasites), Coleoptera (predators) and Acari (parasites). Ten attacked bees, ten attacked wasps, eight attacked both bees and wasps, and eight attacked undetermined hosts. The most common enemy species were the gregarious chalcid wasp *Melittobia acasta*, which attacked 23 host species in 523 cells (Appendix: Table A2) and the cleptoparasitic drosophilid *Cacoxenus indagator*, attacking three bee species in 1281 cells. Mortality due to natural enemies was 20.3% for bees and 17.3% for wasps. Full species lists can be found in Appendix: Tables A1 and A2; and means for variables are given in Table A3.

Trap nest species richness and abundance

Bee richness and abundance and total wasp abundance were not related to plant species richness ($P > 0.1$), but the relationship between the species richness of wasps and of plants approached significance (parameter value = 0.20, $P = 0.053$, Figs. 2A, B and 3A, B). Among the individual trophic groups, only spider-predating wasps showed a significant effect of plant species richness, with positive relationships for both species richness and abundance (Table 1, Figs. 2B and 3B). The abundances of spiders and spider-predating wasps were negatively correlated, while the abundances of spiders and herbivores were positively correlated. The abundance and species richness of the enemies were strongly positively related to the abundance and species richness of their hosts, respectively (Fig. 4). Based on the AIC, mixed

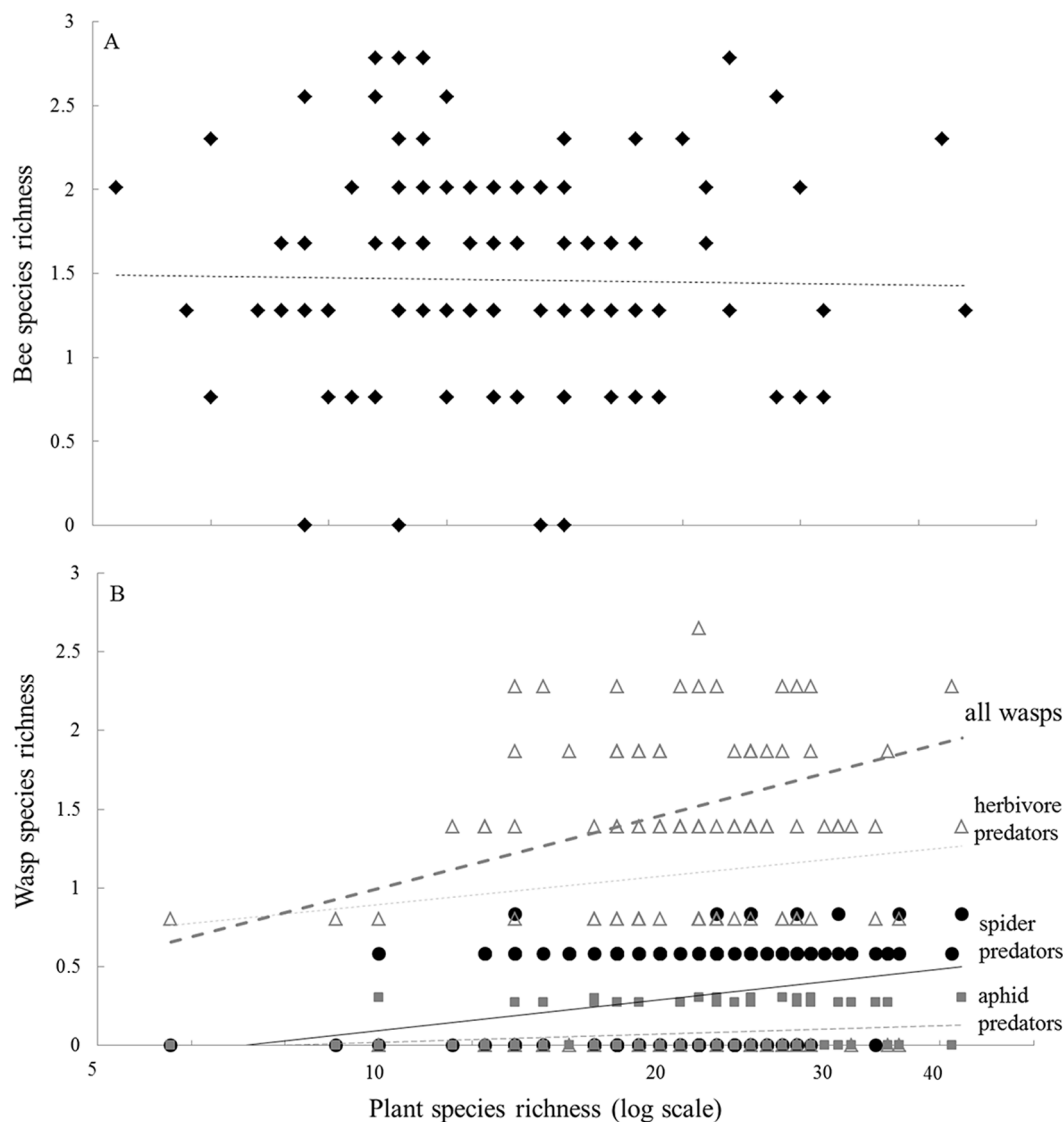


Fig. 2. Relationship between plant species richness and species richness of (A) bees, and (B) wasps: aphid-predating (squares and dashed line), herbivore-predating (triangles and dotted line), and spider-predating wasps (circles and constant black line). Upper grey dashed line indicates the relationship for overall wasp species richness. All response variables were Box-Cox Power transformed; lines are from linear regression analyses.

effect models without the plant composition as correlation structure performed better than models including this term, for all cases but one. Only the model for spider abundance in D-vac samples performed significantly better when plant composition was included as correlation structure. The coefficient λ , determining the strength of the correlation induced by similarity in plant composition, was highest for the abundance of spiders and was generally

larger for wasps than for bees (Table 1).

Food-web structure

The pooled quantitative food web is depicted in Fig. 5. None of the quantitative or qualitative food-web metrics were affected by plant species richness, but almost all were significantly affected by the trap nest species richness (Table 2). Connectance was affected by vegetation height, but no other food-web metrics were affected by

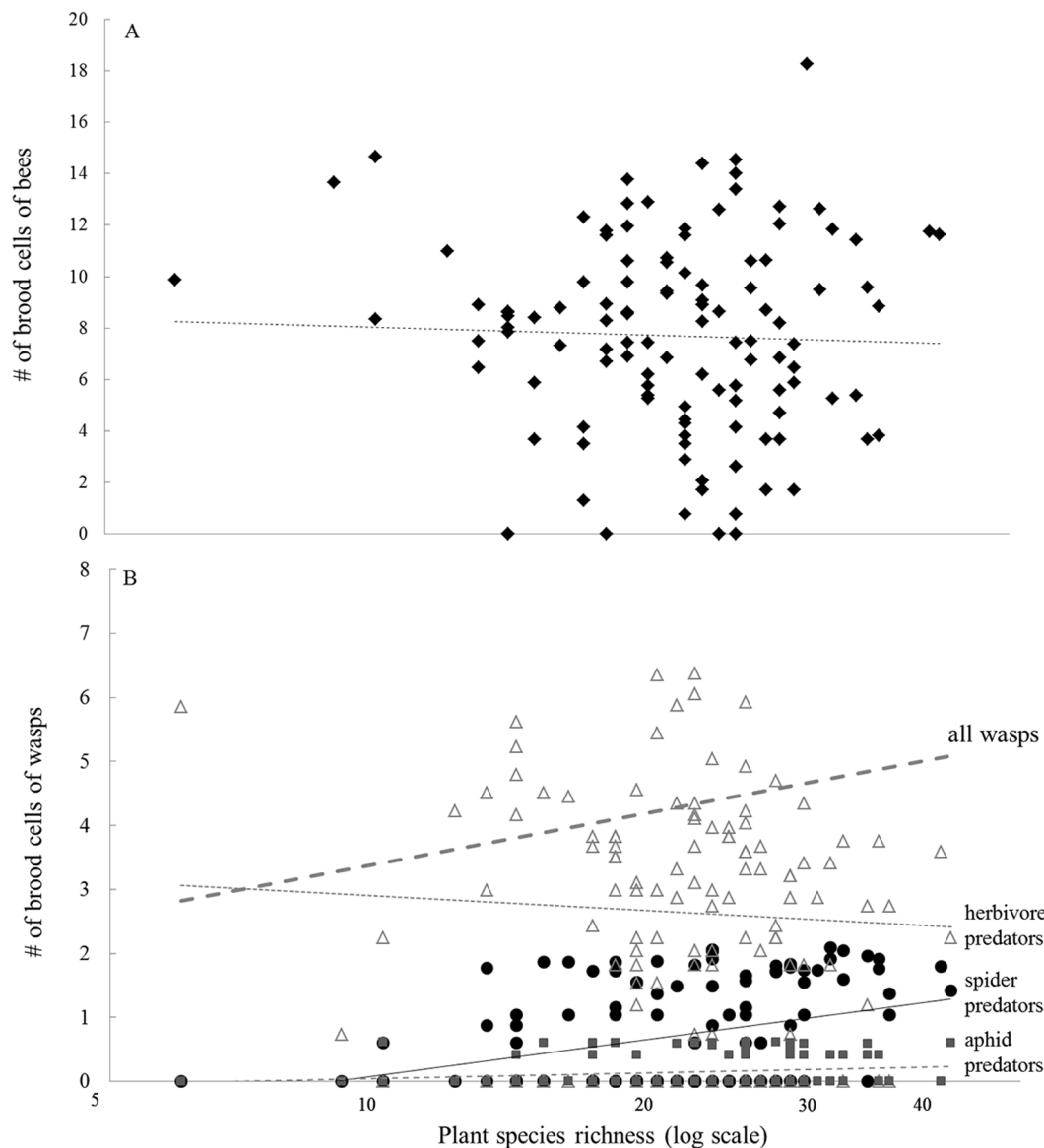


Fig. 3. Relationship between plant species richness and number of brood cells of A) bees, and B) wasps, aphid-predating (squares and dashed line), herbivore-predating (triangles and dotted line), and spider-predating wasps (circles and constant black line). Upper grey dashed line indicates the relationship for overall wasp species richness. All response variables were Box-Cox Power transformed; lines are from linear regression analyses.

vegetation height or biomass. For all food-web metrics, the AIC favors the model without plant composition included.

Vegetation effects on trap nest community composition

The multivariate analysis of the effect of the vegetation on the species composition of the

entire trap nest community revealed effects approaching significance for plant species richness ($\chi^2 = 0.06$, $P = 0.07$; see Fig. 6) and composition ($\chi^2 = 2.43$, $P = 0.09$). Splitting the data into trophic guilds, we found that the community of bees was not affected by the vegetation measures or by the plant composition (all $P > 0.1$). In contrast, wasps were significantly

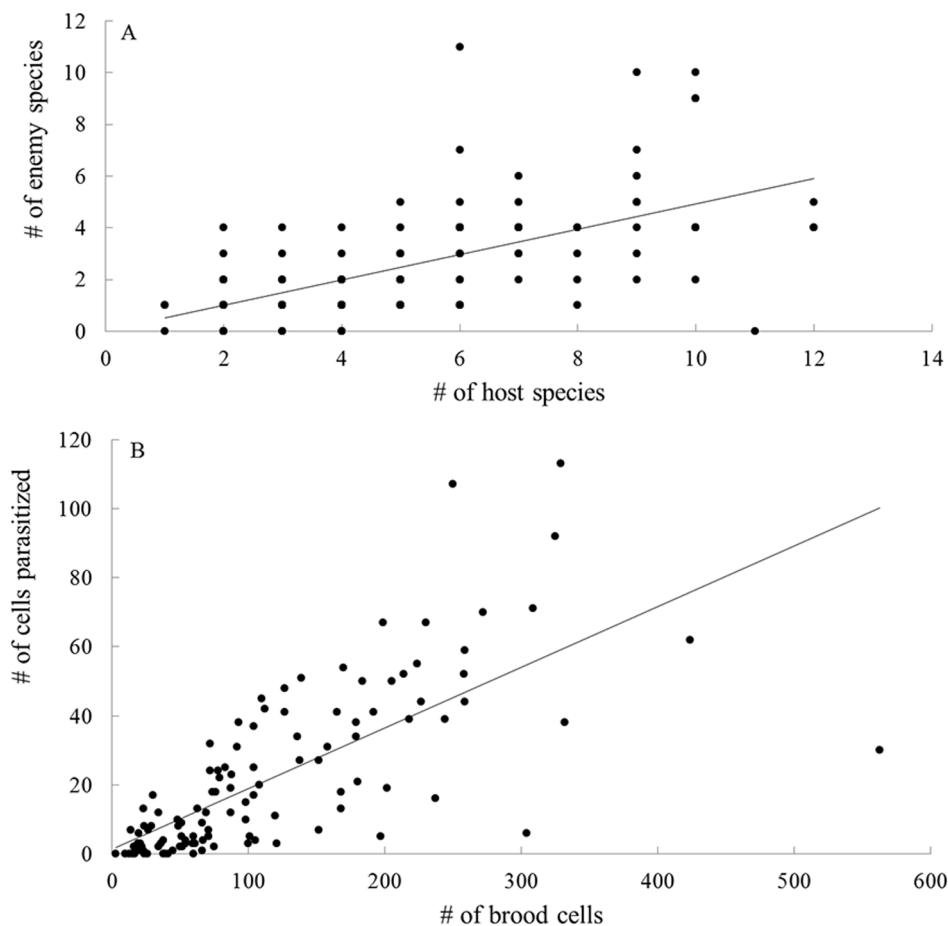


Fig. 4. Relationship between (A) enemy and host species richness and (B) number of cells parasitized and number of brood cells, both fitted by linear regression lines.

affected by plant species richness ($\chi^2 = 0.18$, $P = 0.01$) and average vegetation height ($\chi^2 = 0.13$, $P = 0.03$). The latter effect was due to aphid-predating wasps ($\chi^2 = 0.35$, $P = 0.05$), and these wasps were also strongly influenced by the plant composition ($\chi^2 = 5.07$, $P = 0.01$; Fig. 7).

Among the aphid-predating wasps, different species seemed to be associated most strongly with certain plant species, for instance, members of the genus *Pemphredon* with *Stellaria media*; *Passaloecus vandellii* with *Cerastium* sp.; *Passaloecus gracilis* with *Cirsium arvense*, *Holcus lanatus* and *Convolvulus arvensis*; most species of *Passaloecus* with *Pastinaca sativa*; *Psenulus pallipes* with *Equisetum arvense* and *Lolium perenne*; the latter two plant species were negatively associated with *Passaloecus* species.

DISCUSSION

The aim of our study was to explore if relationships between plants and higher trophic level communities were present at a small spatial scale. We found that plant species richness and composition had limited effects on the trap-nest community. However, contrary to our prediction that the strength of the relationship would diminish with increasing trophic level, the strongest effects were found for wasps. In particular, significant effects were found for the richness and abundance of spider-predating wasps, the group the most distantly associated with plants. Furthermore, none of the qualitative or quantitative food-web metrics were related to plant species richness. Thus, contrary to our

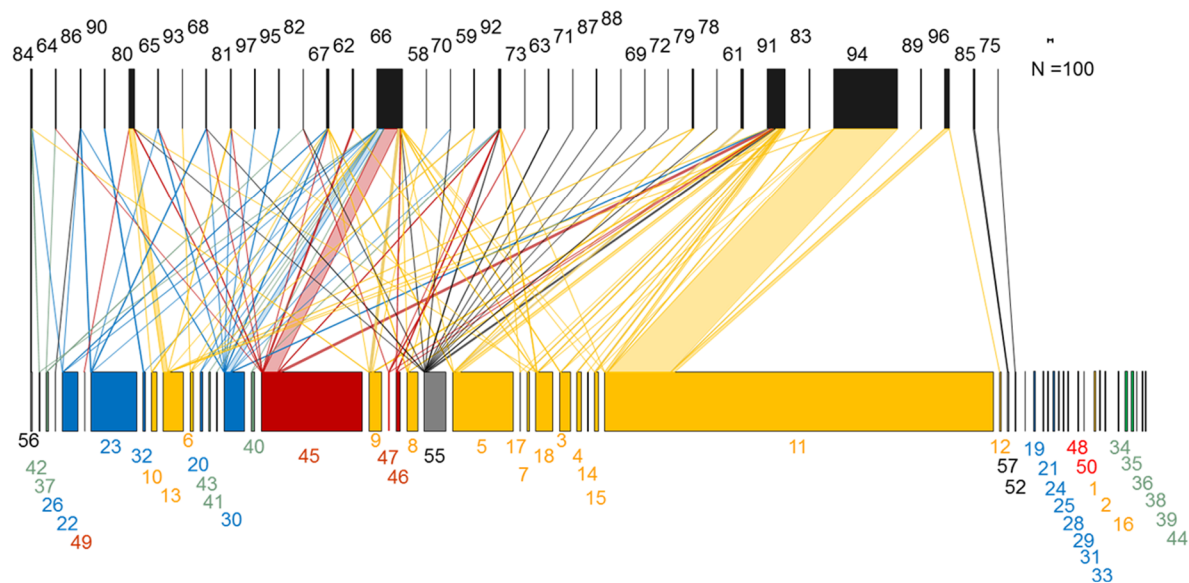


Fig. 5. Quantitative host–enemy food web from all diversity plots. Width of bars represents host and enemy abundance and width of links total number of interactions. Species richness: 34 hosts (lower bars) and 36 enemies (upper bars). Host functional groups: bees (yellow), aphid-predating wasps (green), herbivore-predating wasps (blue), spider-predating wasps (red) and undetermined groups (grey). Species codes are given in Appendix: Tables A1 and A2. Hosts and enemies are ordered to minimize the overlap of interactions.

expectation, the effect of plant diversity on food-web structure was not stronger than on simple community richness.

Our results are intriguing since groups most closely linked to plants—i.e., bees—showed no effect, while higher trophic levels did. Species richness of wasps approached significance and,

intriguingly, the richness and abundance of spider-predating wasps were positively affected by plant species richness. Thus our results support the *resource heterogeneity* and *more individuals hypotheses* for wasps, but not for bees. Ebeling et al. (2012) also found no relationship between plant diversity and brood cell densities

Table 2. Parameter estimates from linear mixed effect models relating food-web metrics to descriptors of vegetation and trap nest species richness.

Food-web metrics	Explanatory variable					AIC with/without plant composition correl.
	Plant species richness (log)	Veg. height	Plant biomass	Trap nest species richness	Plant correl. coeff. λ	
Quantitative						
Vulnerability	−0.12 ns	0.03 ns	0.17 ns	0.37*	0.15	28/26
Generality	0.06 ns	0.13 ns	−0.20 ns	0.21 ns	0.08	48/46
Interaction diversity	−0.11 ns	0.14 ns	−0.11 ns	0.59**	0.07	37/34
Qualitative						
Vulnerability	−0.19 ns	−0.02 ns	0.27 †	0.50**	<0.01	29/27
Generality	0.11 ns	0.06 ns	−0.18 ns	0.42*	<0.01	41/39
Interaction diversity	0.01 ns	0.16†	0.03 ns	0.28***	<0.01	7/5
Connectance	0.02 ns	−0.31*	0.14 ns	−0.68***	<0.01	29/27
Nestedness	0.02 ns	0.01 ns	0.21 ns	−0.57***	<0.01	33/31
No. compartments	0.11 ns	0.06 ns	−0.18 ns	0.42*	<0.01	41/39

Notes: Values of parameters from REML models, with strips as random factors and the plant composition in the different subplots included as a correlation structure. Abbreviations as in Table 1.

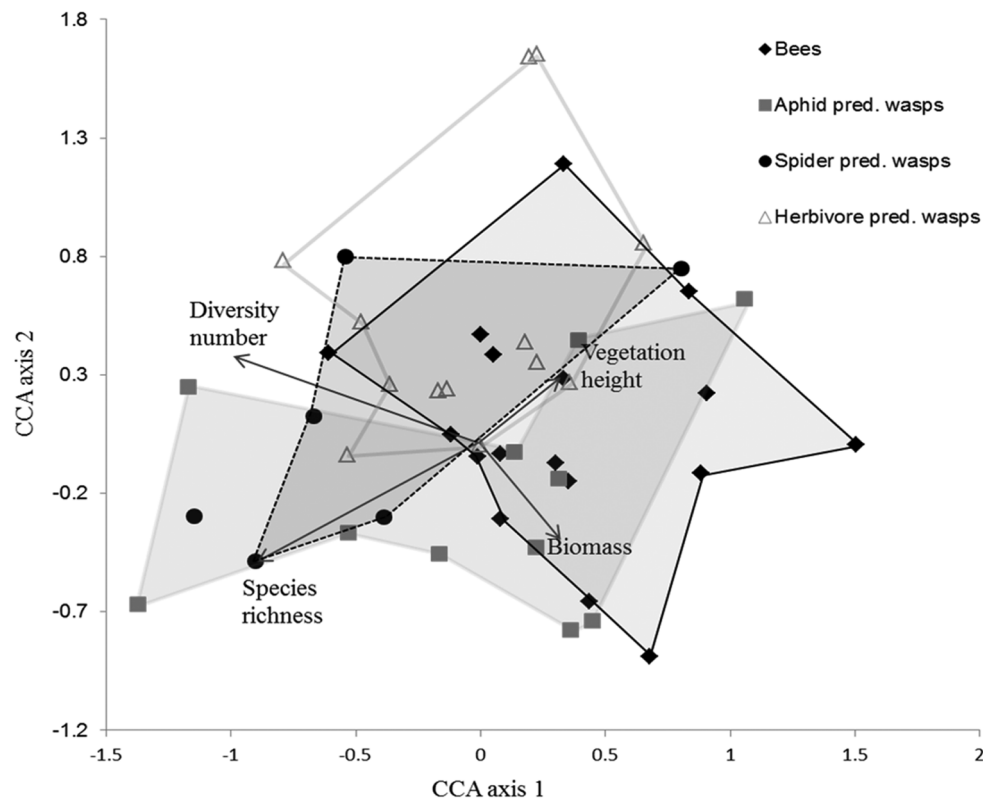


Fig. 6. Canonical correspondence analysis for trap-nesting bee and wasp communities with vegetation measurements as explanatory variables. Planes connect trophic guilds of: bees (diamonds), aphid-predating (squares), herbivore-predating (triangles) and spider-predating (circles) wasps.

of bees. Their diversity plots were, similar to our experiment, within a short distance of each other. In contrast, Albrecht et al. (2007) found a significant increase in bee abundance and species richness with increasing plant diversity; the distance between their sites was on average 5 km and their average size was 1 ha. Thus, mobility relative to the spatial scale of the experiment, rather than trophic level, may be most important in determining the response to plant diversity.

Species that are most strongly limited in their mobility by the weight of their prey might profit most from high plant diversity in the proximity of their nests. Generally, spider-predating wasps carry greater loads in relation to their body size than the other trap-nesting groups. Body-size ratios for females of the most common wasp species and the size of their most abundant prey are the following: (1) 0.33 for aphid-predating wasps, *Passaloecus borealis* (5.5–6.5 mm; De

Beaumont 1964) with aphids (1–3 mm); (2) 0.39 for herbivore-predating wasps *A. nigricornis* (10–13 mm; Schmid-Egger 2004) with Tortricidae caterpillars (3–6 mm); and (3) 0.52 for spider-predating wasps *Trypoxylon figulus* (9–12 mm; De Beaumont 1964) with *Theridion impressum* (5–6 mm). Thus, spider-predating wasps may be most strongly limited by the distances over which they must transport their prey, and hence seem to minimize this by selecting breeding sites in resource-rich patches in terms of spiders, as shown for *Argiope bruennichi* (Bruggisser et al. 2012) and for carnivore (including spiders) abundance (Scherber et al. 2010a). Such small-scale effects may be difficult to discover at large spatial scales, where landscape and metacommunity effects may be key drivers for the community structure of these wasps (Fabian et al. 2013). Interestingly, the local study of Ebeling et al. (2012) found weak but positive effects of plant diversity on wasps, while no effect was

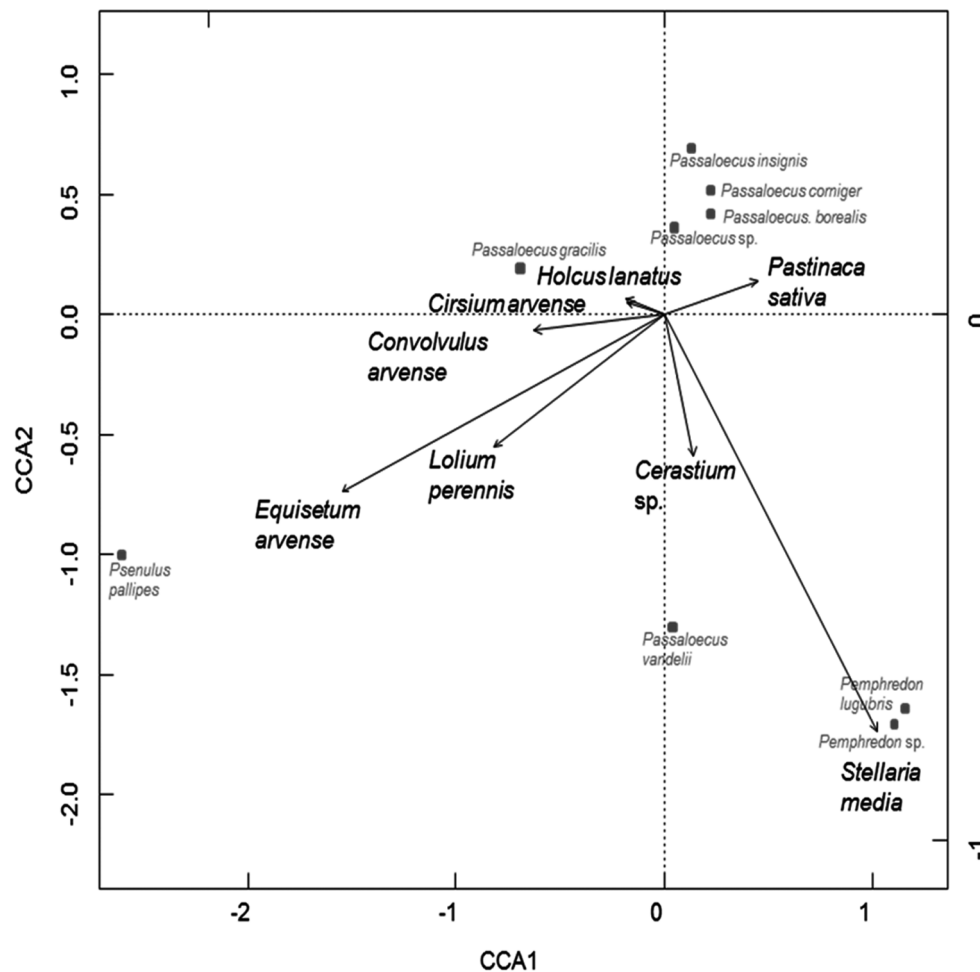


Fig. 7. Canonical correspondence analysis for the aphid-predating wasp community (in grey) with the most influential plant species as explanatory variables (in black). CCA axis 1 explains 25.5% ($\chi^2 = 0.66$, $P = 0.005$) and CCA axis 2 explains 19.9% ($\chi^2 = 0.57$, $P = 0.005$) of the variation.

discovered at a regional scale by Albrecht et al. (2007).

When analyzing the prey community in D-vac samples, we found no effect of plant species richness on the abundance of spiders, herbivores, or aphids. It is possible that, for spiders at least, we could not detect an effect because it was masked by top-down control, in the form of stronger predation pressure by spider-predating wasps in plots with higher plant diversity. The most common of the wasps, *Trypoxylon figulus*, can have a substantial negative effect on spider populations (Blackledge et al. 2003), because one female can catch 100–300 spiders in the course of a summer (Bristowe 1941). In our study every

brood cell was filled with 5–15 spiders. Thus, with an average of ten spiders per larva, the 1732 brood cells would contain 17320 spiders caught by *Trypoxylon* wasps. Furthermore, the wasp populations were concentrated in only some of the strips: although five strips contained only 0 to 28 brood cells per strip, five others had much greater numbers, with between 102 and 583 cells. Within the same system, strong regulation of spider abundance by hymenoptera is seen in *Argiope bruennichi* by hornets (Bruggisser et al. 2012).

The complexity of biotic interactions is expected to be more strongly affected by a decrease in plant diversity than simple species diversity and

abundance (Albrecht et al. 2007, Tylianakis et al. 2007). Although the diversity and abundance of higher and lower trophic levels in the trap nests were strongly positively correlated, contrary to our expectation, we detected no effect of plant diversity on the quantitative or qualitative food-web metrics. This absence of relationship may be simply due to the fact that only a small subset of the whole community, namely spider-predating wasps, responds to plant diversity. Interestingly, connectance was negatively correlated with vegetation height, which might be due to a decreased accessibility of the trap nests for higher trophic levels when *Dipsacus fullonum*, the tallest species of our system, was abundant. Indeed, adding the logarithmically transformed cover of *Dipsacus fullonum* to the model shows a negative relationship between connectance and *D. fullonum* cover (parameter estimate = -0.29 , $P = 0.023$). Thus, the architecture of the vegetation can override the effects of plant diversity on food-web complexity.

In contrast to other analyses that simply treated species diversity (e.g., Albrecht et al. 2007, Tylianakis et al. 2007, Haddad et al. 2009, Scherber et al. 2010a, Ebeling et al. 2012), we accounted for plant composition by including a correlation structure in the residuals of the mixed-effect models. This is important because a change in plant diversity cannot be achieved without altering plant composition. In our case however, for all groups except spiders, models with plant composition performed worse than models without. Earlier studies similarly found that the abundances of spiders were strongly affected by the plant community, acting through species composition (Schaffers et al. 2008), diversity (Bruggisser et al. 2012), or vegetation structure (Pearson 2009, Bruggisser et al. 2012). Moreover, the abundances of spiders and of herbivores were strongly positively correlated in our study, reflecting a bottom-up effect. For web-building spiders, habitat use is strongly dependent on high prey abundance and on vegetation structure, which is closely linked to plant composition. Thus, habitat selection might explain this effect for spiders. The absence of an effect of plant composition for the other species groups may reflect the small-scale of the study relative to their mobility. In general, however, plant composition should be included in biodi-

versity models and may reveal unexpected results.

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Bee and wasp species in 117 trap nests, their number of occupied brood cells, and the number of cells attacked by their natural enemy species. Abbreviations are: Code, species code used in Fig. 5; p/n, pollen and/or nectar; a, aphids; h, herbivores; s, spiders; na, not available; No. cb, number of cells built; No. ca, number of cells attacked.

Code	Species	Larval food	No. cb	No. ca
	Apidae			
1	<i>Hylaeus communis</i>	p/n	28	0
2	<i>Hylaeus difformis</i>	p/n	7	0
3	<i>Hylaeus</i> sp.	p/n	212	13
4	<i>Chelostoma florisomne</i>	p/n	76	8
5	<i>Heriades truncorum</i>	p/n	1094	139
6	<i>Megachile centuncularis</i>	p/n	78	6
7	<i>Megachile ericetorum</i>	p/n	44	10
8	<i>Megachile versicolor</i>	p/n	202	27
9	<i>Megachile</i> sp.	p/n	200	79
10	<i>Osmia adunca</i>	p/n	100	2
11	<i>Osmia bicornis</i>	p/n	6666	1427
12	<i>Osmia brevicornis</i>	p/n	21	4
13	<i>Osmia caerulea</i>	p/n	332	118
14	<i>Osmia gallarum</i>	p/n	4	4
15	<i>Osmia caerulea/gallarum</i>	p/n	43	30
16	<i>Osmia cornuta</i>	p/n	2	0
17	<i>Osmia</i> sp.	p/n	11	5
18	Apiformes sp.	p/n	322	42
	Eumenidae			
19	<i>Alastor atrops</i>	h	1	0
20	<i>Allodynerus rossii</i>	h	55	5
21	<i>Ancistrocerus antilope</i>	h	54	0
22	<i>Ancistrocerus gazella</i>	h	331	26
23	<i>Ancistrocerus nigricornis</i>	h	931	21
24	<i>Ancistrocerus parietinus</i>	h	11	0
25	<i>Ancistrocerus</i> sp.	h	11	0
26	<i>Euodynerus notatus</i>	h	5	2
27	<i>Gymnomerus laevipes</i>	h	18	0
28	<i>Microdynerus timidus</i>	h	60	0
29	<i>Symmorphus gracilis</i>	h	18	0
30	Eumenidae sp.	h	298	160
	Sphecidae			
31	<i>Ectemius continuus</i>	h	1	0
32	<i>Isodontia mexicana</i>	h	31	6
33	<i>Nitela</i> sp.	h	5	0
34	Sphecidae sp.	a	13	0
35	<i>Passaloecus borealis</i>	a	70	0
36	<i>Passaloecus gracilis</i>	a	61	0
37	<i>Passaloecus insignis</i>	a	43	5
38	<i>Passaloecus corniger</i>	a	11	0
39	<i>Passaloecus vandeli</i>	a	3	0
40	<i>Passaloecus</i> sp.	a	70	6
41	<i>Pemphredon lugubris</i>	a	20	1
42	<i>Pemphredon</i> sp.	a	16	5
43	<i>Psenulus pallipes</i>	a	22	2
44	<i>Psenulus</i> sp.	a	2	0
45	<i>Trypoxylon figulus</i>	s	1659	421
46	<i>Trypoxylon</i> sp.	s	73	18
	Pompilidae			
47	<i>Agrenioides cinctellus</i>	s	19	5
48	<i>Auplopus carbonarius</i>	s	3	0
50	<i>Dipogon subintermedius</i>	s	5	0

Table A1. Continued.

Code	Species	Larval food	No. cb	No. ca
49	<i>Dipogon</i> sp.	s	6	2
	Others			
52	Symphyta sp.	na	6	4
55	undetermined host	na	392	62
56	Host Braconidae 1	na	12	12
57	Host Braconidae 2	na	17	17
Total no. brood cells		13795	2695	

Table A2. Enemies of bees and wasps in 117 trap nests and the number of brood cells attacked. Species codes are used in Fig. 5. A dagger (†) indicates morphospecies.

Code	Species	No. cells attacked
	Hymenoptera	
	Apidae	
59	<i>Coelioxys inermis</i>	4
58	<i>C. inermis/mandibularis</i>	3
61	<i>Stelis breviscula</i>	32
	Chrysididae	
62	<i>Chrysis cyanea</i>	21
63	<i>C. ignita</i>	3
64	<i>Omalus auratus</i>	5
65	Chrysididae sp.	7
	Eulophidae	
66	<i>Melittobia acasta</i>	523
	Ichneumonidae	
67	<i>Ephialtes manifestator</i>	28
68–72	Ichneumonidae spp. 1–5†	16
73	Cryptinae sp.	1
75	Tryphoninae sp.	1
76	Campopleginae sp.	3
	Gasteruptiidae	
78	<i>Gasteruption assectator</i>	2
	Sapygidae	
79	<i>Sapyga decemguttata</i>	14
80	<i>S. quinquepunctata</i>	110
81	Sapygidae sp.	7
	Chalcidoidea	
82	Pteromalidae sp.	1
	Toryminae	
83	<i>Monodontomerus obsoletus</i>	14
	Braconidae	
84–89	Braconidae sp. 1–6†	66
90	<i>Isodontia</i> parasites	3
	Coleoptera	
91	<i>Trichodes alvearius</i>	376
92	<i>Megatoma undata</i>	69
	Diptera	
93	<i>Anthrax anthrax</i>	12
94	<i>Cacoxenus indagator</i>	1281
95	Diptera larvae	2
	Acari	
96	<i>Chaetodactylus osmia</i>	90
	Undetermined	
97	Species 1	1
	Total	2695

Table A3. Information on the distributions (arithmetic means $\pm$ SE, minimum and maximum values) of the variables measured in the 117 subplots or in the 39 pooled food webs. These variables describe the species richness and abundance of the different species groups sampled from trap nests and D-vacs, the quantitative and qualitative food-web metrics, and the vegetation measures.

Variable	Mean $\pm$ SE	Min	Max
Species richness (trap nest)			
Entire community	9.5 $\pm$ 0.4	2	21
Bee species	1.8 $\pm$ 0.1	0	6
Wasp species	3.1 $\pm$ 0.2	0	10
Aphid predators	0.5 $\pm$ 0.1	0	5
Herbivore predators	1.5 $\pm$ 0.1	0	4
Spider predators	0.6 $\pm$ 0.1	0	2
Enemies	2.8 $\pm$ 0.2	0	10
Abundance (trap nest)			
No. brood cells	118.0 $\pm$ 9.1	6	568
Bee cells	80.7 $\pm$ 7.6	0	529
Wasp cells	34.0 $\pm$ 3.7	0	238
Aphid predator cells	2.7 $\pm$ 0.8	0	58
Herbivore predator cells	15.6 $\pm$ 1.8	0	90
Spider predator cells	15.1 $\pm$ 3.2	0	22
Cells parasitized	23.0 $\pm$ 2.3	0	122
Prey abundance (D-vac sampling)			
Aphids (Aphidina)	52.6 $\pm$ 4.6	1	791
Spiders (Araneae)	24.1 $\pm$ 4.1	5	130
Herbivores	9.7 $\pm$ 0.6	0	33
Beetles (Coleoptera larvae)	6.1 $\pm$ 0.7	0	27
Butterflies (Lepidoptera larvae)	2.8 $\pm$ 0.2	0	16
Barklice (Psocoptera)	1.0 $\pm$ 0.0	0	8
Grasshoppers (Caelifera)	0.3 $\pm$ 0.0	0	3
Quantitative food-web metrics			
Vulnerability	1.5 $\pm$ 0.1	1.0	3.7
Generality	1.5 $\pm$ 0.1	1.0	3.9
Interaction diversity	2.0 $\pm$ 0.1	0.6	2.9
Qualitative food-web metrics			
Vulnerability	1.8 $\pm$ 0.1	1.0	3.5
Generality	2.0 $\pm$ 0.1	1.0	5.1
Interaction diversity	2.0 $\pm$ 0.1	1.1	2.9
Connectance	0.3 $\pm$ 0.0	0.2	0.5
Nestedness	38.0 $\pm$ 1.9	20.9	63.1
No. compartments	2.8 $\pm$ 0.1	1	4
Vegetation			
Species richness	22.4 $\pm$ 0.6	6	42
Biomass (g/m ²)	525.5 $\pm$ 14.4	247.8	1271.2
Height (m)	1.4 $\pm$ 0.0	0.4	2.1