Plant–pollinator interactions along an urbanization gradient from cities and villages to farmland landscapes

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Abstract. Urbanization affects pollinator diversity and plant–pollinator networks by changing resource availability locally and in the surrounding landscape. We experimentally established ($N = 12$) standardized plant communities in farmland, villages, and cities to identify the relative role of local and landscape effects on plant–pollinator communities along this urbanization gradient. We found that the number of flower visits by solitary bees, but not bumblebees, was highest in cities and lowest in farmland, with villages being intermediate, whereas syrphid flies exhibited lowest numbers in cities. Villages supported the richest pollinator communities, as they appeared to benefit from both farmland and city communities. Plant–pollinator network metrics such as robustness, interaction evenness, and interaction diversity decreased with increasing urbanization, although local plant richness increased toward urban areas. In conclusion, pollinator communities were most diverse and stable in farmland and village sites, despite the high plant richness in cities. The different composition of pollinator communities along the urbanization gradient suggests considering all three landscape types for conservation schemes.

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INTRODUCTION

The predominant landscape type worldwide is farmland interspersed with urban areas, but urbanization is steadily growing in importance. Farmland areas often support lower insect diversity than urban areas (Bates et al. 2011), depending on local habitat quality and surrounding landscape structure. The surprising diversity of flower-visiting taxa (Baldock et al. 2015, Sirohi et al. 2015) is linked to the generally higher plant richness in urban areas, mostly due to the presence of many non-native plants in urban gardens (Pyšek 1998) that can play an important role as pollen and nectar resources (Ahrne et al. 2009).

The majority of studies comparing farmland with urban areas find that wild bees are more diverse and abundant in urban areas (Verboven et al. 2014, Hall et al. 2016). However, Ahrne et al. (2009) and Verboven et al. (2014) found that bumblebee and syrphid fly richness both show a negative relationship with increasing urbanization. These contrasting results illustrate that urbanization effects on pollinators may be diverse.

Pollinators need floral resources and nesting sites to survive (Westrich 1996, Ebeling et al. 2008); these are provided by green spaces in urban areas where plant diversity and floral resources are abundant. Private gardens and parks offer many floral resources with high plant richness and high temporal stability (Fetridge et al. 2008). This resource stability may not be found in farmland, where mass-flowering crops can support some pollinator species, but only for

a limited time period per year (Westphal et al. 2003). Wild bee pollinators require seminatural habitats as nesting resource, whereas syrphid flies are not linked to seminatural habitat availability in the landscape (Jauker et al. 2009). Syrphid flies are present at much higher diversity and abundance in farmland landscapes with no seminatural habitats than wild bees (Verboven et al. 2014, Baldock et al. 2015) and may also be effective pollinators (Orford et al. 2015). Hence, pollinator communities can be expected to show different responses to urbanization, depending on the pollinator group considered.

Pollinator richness and species composition influence the structure of plant–pollinator networks (McCann 2000, Dunne et al. 2002). The structure of a plant–pollinator network provides information on many aspects of the community, such as network stability (correlated with pollinator richness; Grass et al. 2018). Pollinator richness and species composition depend on the local plant community (Memmott 1999) but are also influenced by the surrounding landscape. It

is therefore difficult to disentangle the influences of local from landscape features on plant–pollinator networks.

In the present study, we test how pollinator communities change across an urban–rural gradient, comparing farmland with villages and cities, and how plant–pollinator network structure is altered in these different landscapes. We used standardized plant communities to observe pollinators, which is an approach that allows strong inference (due to its experimental nature) and generalizations that extend beyond previous studies (Geslin et al. 2013, Theodorou et al. 2017).

METHODS

Study sites

The study was conducted in north-central Germany, in the southern part of the federal state of Lower Saxony, within a 30 km radius of Göttingen (51°32′28.61″ N, 9°54′56.89″ E). We sampled along an urbanization gradient from farmland and villages to cities, including grassy
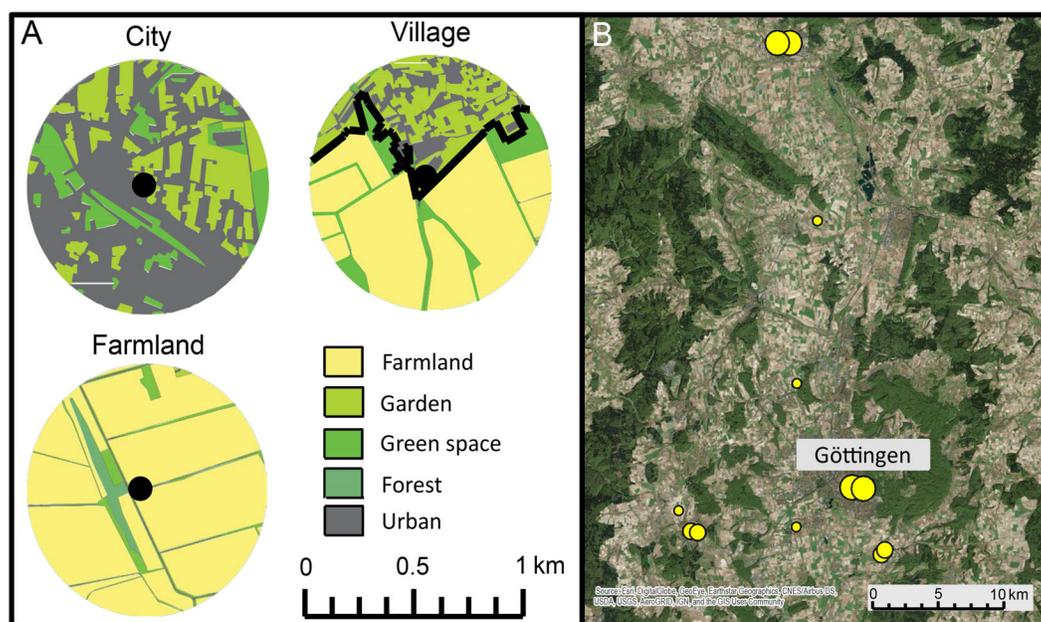
Fig. 1. (A) Example GIS maps (ArcGIS, v. 10.4.1; ESRI, Redlands, California, USA) of the three different landscape types used (only three example landscape buffers are shown). Buffers were 500 m in radius with colors denoting land-use types in each landscape. The black dot in the center denotes the local study site, and the black line in the village landscape indicates the border of the urban area. (B) Yellow points indicate the sites in the surroundings of Göttingen, and point sizes denote urban area type. Small = farmland; medium = village; and large = city. Basemap source: ESRI basemap (Microsoft Bing Maps).

field margins in pure farmland, and gardens (~800–1000 m^2) in villages and cities. Farmland sites were at least 500 m from the nearest house. Village sites were close to the village edge and were surrounded by a 500-m buffer comprising approximately 50% urban area and 50% farmland. City sites were at least 500 m from the city edge and were surrounded by a buffer of 100% urban area (Fig. 1). The urbanization gradient was constructed in this way to test the influence of amount of farmland in the landscape and the level of urbanization. $N = 12$ sites were used: four farmland sites (maximum distance 30 km from Göttingen), two villages (two gardens each; Dransfeld, 51°50′06.01″ N, 9°76′23.95″ E and Diemarden, 51°48′72.82″ N, 9°98′05.67″ E), and two cities (two gardens each; Göttingen and Einbeck, 51°49′13.29″ N, 9°52′6.14″ E; separated by a minimum of 500 m inside the city border).

Experimental plant plots

Experimental plant patches were established in April 2015 (size 80 × 80 cm) in each of the 12 sites (Fig. 2). We standardized soil conditions by using a soil mix at all sites (mix from volcanic clay, peat, lime carbonate, and NPK fertilizer; 180 mg/L N, 180 mg/L P; 260 mg/L K; 130 mg/L Mg, and 100 mg/L of S with a pH of 5.9). Approximately 30 mL of NPK fertilizer was added when the seeds were planted, which contained equal parts N (8%) and P (8%). The numbers of plant seeds used were standardized to approximately 20 seeds per plant species and were evenly scattered over the soil. The plant species used were *Phacelia tanacetifolia* (Benth.) and *Sinapis arvensis* (L.). Plant patches were watered once a week with 10 L of water and fertilized once more after one month. The perennial garden plants *Veronica spicata* (L.) and *Astilbe*

Fig. 2. Experimental plant plot in an urban garden. Plant species are, from top to bottom, *Sinapis arvensis, Phacelia tanacetifolia, Astilbe chinensis,* and *Veronica spicata.*

chinensis (Maxim.) were bought from a commercial supplier (Baumschule Jenssen, Göttingen, Germany) and transplanted to the experimental plots in June. This mixture of four plant species included plants with high-quality pollen and nectar that are attractive to pollinators. The plant species covered a wide range of flower types, both open and tubular, and a mixture of colors: yellow, white, and purple (Pritsch 2018). All plant species flowered simultaneously at the start of July for two weeks.

Pollinator observations

Insect observations were run in early July 2015 for 15-min intervals at two different times of the day (total observation hours = 6): morning (10:00–11:30) and midday (12:45–14:30); these times were centered on midday (13:15), calculated as the midpoint between sunrise and sunset. Observations were run in early July as midsummer is when pollinator richness is high in urban and agriculture areas (Leong et al. 2016). Six sites were visited each day, three per time period, and the order in which they were visited was randomized. Observations were conducted on a corner of each plant plot (50 × 50 cm) that included all plant species. We observed all insect pollinators that visited a flower, identified them to genus or species level, and counted the number of visits (landing on a single flower equals one visit) for each insect until it left the plant plot. If it was not possible to identify an individual to species level, we identified it as accurately as possible (e.g., to genus level) and assigned a morphospecies to it. We also recorded which plant species each insect pollinator was observed on. Insect pollinators included solitary bees (i.e., non-bumblebees), bumblebees, butterflies, syrphid flies, non-syrphid flies, wasps, and honeybees. To assess the plant species richness neighboring the plant plots, we counted all plant species within a radius of 20 m that were flowering at that time.

Statistics

We found no differences in pollinator richness and their abundance between morning and midday observations; thus, abundances were summed for every observation day. All analyses were performed using R (version 3.5.1; R Core Team 2018). The response variables (number of pollinator visits, plant richness, and pollinator morphospecies richness) were modeled as functions of landscape type (a factor with three levels) and plant species richness (numeric). Plant species richness was influenced by landscape type and was always tested in separate models.

We used a series of generalized least squares (GLS) models and linear mixed-effects models (LME; all final models were fitted using REML) to account for potential spatial non-independence in our data: a GLS model without heterogeneity, a GLS model with spherical autocorrelation (longitude, latitude), and an LME model with random effects for every site ($N = 12$). These models were ranked using Akaike's information criterion, corrected for sample sizes (AIC_c; information-theoretic approach; Mazerolle 2016). For all variables, the models with the lowest AIC_c were simple GLS models without a correlation structure or random effect.

For plant richness and pollinator visit data, we tested which distribution fitted each response variable best, using the fitdistrplus package (Delignette-Muller and Dutang 2015). In all cases, models with a lognormal distribution had lowest AIC_c values, hence we log-transformed all response variables. Corresponding negative binomial or Poisson models did not fit the data adequately. Results were plotted using the effects package (Fox and Weisberg 2018).

The proportional abundance of the seven different pollinator groups was tested using multinomial models (Venables and Ripley 2002) against the explanatory variables. Bipartite networks ($N = 12$) were created from the plant–pollinator interactions for each site and their structure analyzed with network-level metrics using the bipartite package (Dormann et al. 2008). The network-level metrics used were robustness, interaction evenness, and Shannon diversity of interactions (based on Blüthgen et al. 2006). Robustness is a measure of the stability of the network; specifically, it is calculated by measuring the area below the extinction curve generated as a measure of the robustness of the network to the loss of species (Memmott et al. 2004, Burgos et al. 2007).

Results

We observed 18 pollinator morphospecies in farmland, and 16 morphospecies in both villages
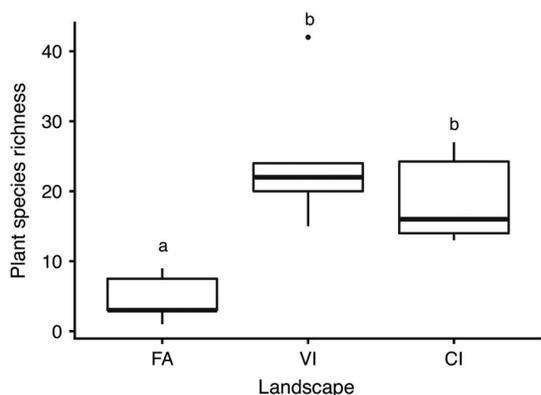
Fig. 3. Flowering plant species richness within a radius of 20 m around experimental plant patches in different landscapes along an urbanization gradient. N_{FA} = 4; N_{VI} = 4; N_{CI} = 4; FA, farmland; VI, village; CI, city. Bars that do not share the same letter show significant differences ($P < 0.05$). Boxplots show median (thick horizontal line), the interquartile range (25th–75th percentile; box), and ±1.5 times the interquartile range (whiskers).

and cities. There were a total of 117 individuals in farmland, 117 in villages, and 92 in cities, and the total number of flower visits by these individuals was 525 in farmland, 540 in villages, and 368 in cities. Flower visitor taxonomic groups were classified into solitary bees, bumblebees, honeybees, syrphid flies, non-syrphid flies, butterflies, and wasps. Plant species richness was positively correlated with the level of urbanization as plant richness was higher in villages and cities compared to farmland (Fig. 3).

Pollinator visitation

The pollinator group identity and the amount of urban area influenced the number of visits by pollinating insects with solitary bees and syrphid flies visiting flowers most often, but in different landscape types (Fig. 4, Table 1). The visits by syrphid flies were higher in farmland and villages than in cities, and solitary bee visitation rates were higher in experimental plant plots within urban areas rather than in farmland. Bumblebees, butterflies, and non-syrphid flies showed a negative trend with increasing urbanization (Fig. 4). Honeybees and wasps visited flowers within urban areas and were not present at farmland sites (Fig. 4).

The proportional abundance of pollinator groups was significantly influenced by landscape
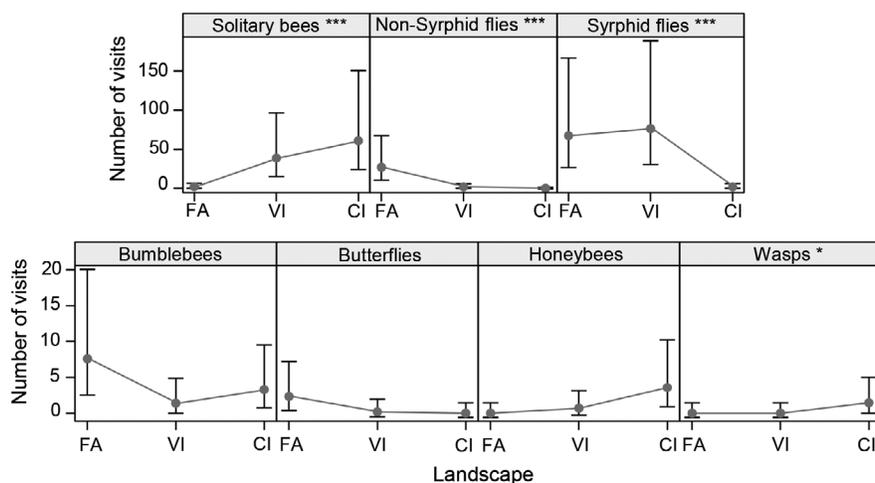
Fig. 4. Numbers of pollinator visits for each pollinator group with 95% confidence intervals (fitted values ±95% pointwise confidence intervals) from a combined GLS model with an interaction term between pollinator group and landscape. Syrphid flies had more visits in farmland and villages than in cities ($P < 0.001$). Solitary bees showed the opposite trend with more visits in urban areas than in farmland ($P < 0.001$). Bumblebees, butterflies, and honeybees showed a nonsignificant trend with a lower visitation rate in urban than in farmland landscapes ($P > 0.1$). Wasps were mainly present in cities ($P = 0.03$). N_{FA} = 4; N_{VI} = 4; N_{CI} = 4; FA, farmland; VI, village; CI, city. Significance values are taken from individual models and are indicated as *$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$.

Table 1. Chi-square values, degrees of freedom (df), and level of significance for generalized least squares models (all with log-transformed response variables).

Response variable	Variable	df	χ^2 value	$P\ (>\chi^2)$
Plant richness	Landscape	2	29.16	<0.001
Solitary bee visits	Landscape	2	16.77	<0.001
Non-syrphid fly visits	Landscape	2	38.97	<0.001
Syrphid fly visits	Landscape	2	63.16	<0.001
Bumblebee visits	Landscape	2	4.87	0.088
Butterfly visits	Landscape	2	3.70	0.157
Honeybee visits	Landscape	2	3.53	0.171
Wasp visits	Landscape	2	11.42	0.003
Pollinator morphospecies richness	Landscape	2	3.45	0.178
Solitary bee visits	Plant richness	1	2.92	0.088
Non-syrphid fly visits	Plant richness	1	3.54	0.060
Syrphid fly visits	Plant richness	1	0.06	0.811
Bumblebee visits	Plant richness	1	7.19	0.007
Butterfly visits	Plant richness	1	2.87	0.090
Honeybee visits	Plant richness	1	2.82	0.093
Wasp visits	Plant richness	1	0.04	0.850
Pollinator morphospecies richness	Plant richness	1	0.35	0.555

type (Fig. 5) and was influenced by plant richness in the direct surroundings. With high urbanization, fewer pollinators per group were present. Pollinator morphospecies richness was highest in farmland areas where plant richness was lowest (Fig. 6).

Plant–pollinator community structure and network metrics

Community composition also changed in the different landscapes, with solitary bees dominating in urban areas and syrphid flies dominating in farmland landscapes but overlapping in the village landscapes (Figs. 4, 7). Wasps and honeybees were found in urban areas, whereas butterflies and non-syrphid flies were present in farmland sites but were rare in village and city sites (Figs. 4, 7). Also, plant–pollinator networks were more robust in farmland and in villages compared with cities (Fig. 8) and had the highest interaction evenness in farmland compared to urban areas. The Shannon diversity of interactions was highest in farmland and in villages compared with cities.

DISCUSSION

In this study, we investigated plant–pollinator community structure, using observations on experimental study plots along a farmland and village to urban landscape gradient.

We found that flower visitation rates strongly differed between cities, farmland, and villages, depending on pollinator group identity.
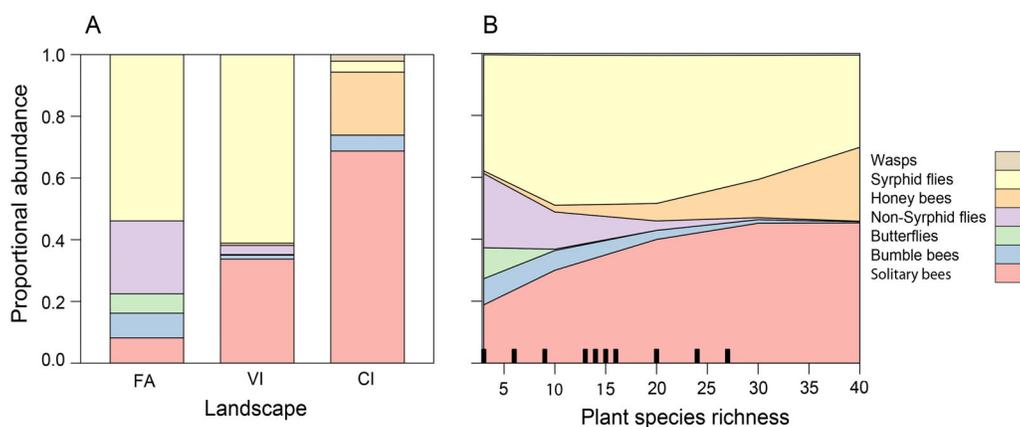
Fig. 5. Proportional abundance of pollinator taxa in the different landscapes, based on a multinomial model. Probabilities were calculated using the allEffects function in the effects package in R, back-transforming probabilities from a logit scale with reference to the baseline category (bees; Fox 2003, Fox and Hong 2009). Syrphid flies were present significantly more often in farmland and village landscapes, while solitary bees were present significantly more often in city landscapes. N_{total} = 12; N_{FA} = 4; N_{VI} = 4; N_{CI} = 4; FA, farmland; VI, village; CI, city.
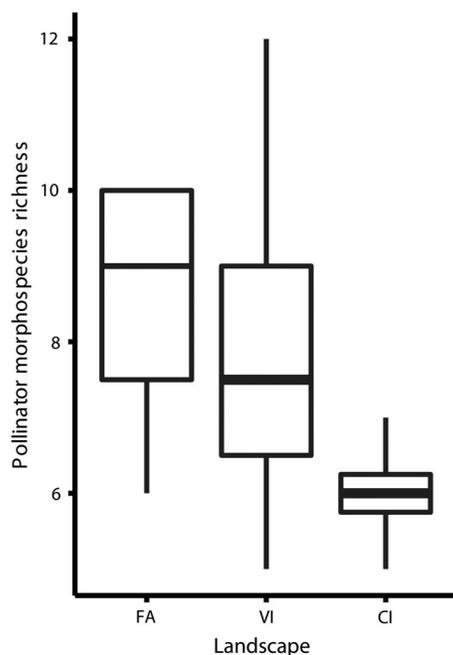
Fig. 6. Morphospecies richness decreased with increasing urbanization. N_{FA} = 4; N_{VI} = 4; N_{CI} = 4; FA, farmland; VI, village; CI, city. Boxplots show median (thick horizontal line), the interquartile range (25th–75th percentile; box), and ±1.5 times the interquartile range (whiskers).

Morphospecies richness of pollinators was higher in farmland than in cities, with villages being intermediate. Interestingly, landscape type influenced the identity of the dominant pollinator groups, with farmland dominated by syrphid flies and cities by solitary bees. This study used an experimental approach to assess the influence of the level of urbanization on plant–pollinator community structure. Thus, sample sizes were smaller than in purely observational studies.

Pollinator visitation

Our results clearly show that plant species richness was higher in urban areas, but that pollinator richness decreased in urban areas. The pollinators we observed were generalists, as they visited all plant species regardless of the landscape type. The pollinator group identity influenced the number of pollinator visits, as solitary bees were mainly present in cities and all flies were mainly present in farmland, while both were present in villages. These changes in

pollinator richness and community composition contributed to the differences in network structure, where robustness, interaction evenness, and Shannon diversity were all highest in farmland and lowest in cities, with villages at intermediate levels. In our study, visitation rates to surrounding flowers were not recorded; therefore, we could not determine if the lower numbers of certain pollinator types (e.g., solitary bees) observed in urban areas were due to the landscape type or because the pollinators had more other options.

Theodorou et al. (2017) used experimental plant communities to separate the influence of local from landscape influences and also found that bee richness is positively influenced by high flowering richness in urban areas. We did not observe many pollinator morphospecies at our experimental plant plots, possibly because the four plant species were flowering for only a short time period and attracted just a small range of pollinators. But we observed little change in the pollinator morphospecies present from our first to second round of observations; thus, the differences between treatments appear to be fairly robust for this time of the year. However, patterns may change with season and year.

Solitary bees were present in farmland sites in low numbers, presumably because plant plots in these sites were surrounded only by farmland with few floral resources and seminatural areas within the 500 m radius considered. Solitary bees disperse several hundred meters throughout the landscape (Gathmann and Tscharntke 2002). Even though there are suitable nesting sites in farmland areas and some floral resources, these are not necessarily close enough to provide suitable resources for solitary bees to survive (Westrich 1996). Gardens in urban areas provided good habitat for solitary bees as there were higher solitary bee abundances in cities than in villages. *Heriades truncorum*, for example, was dominant in cities, while its numbers decreased along the urban gradient, with lower abundance in villages and farmland. This supports findings from Banaszak-Cibicka and Zmihorski (2012) and Fortel et al. (2014), in that plant species richness was highest in villages and cities, and solitary bee richness increased in areas with high plant richness (Ebeling et al. 2008).

Syrphid flies showed the opposite relationship, as they were present mostly in farmland and
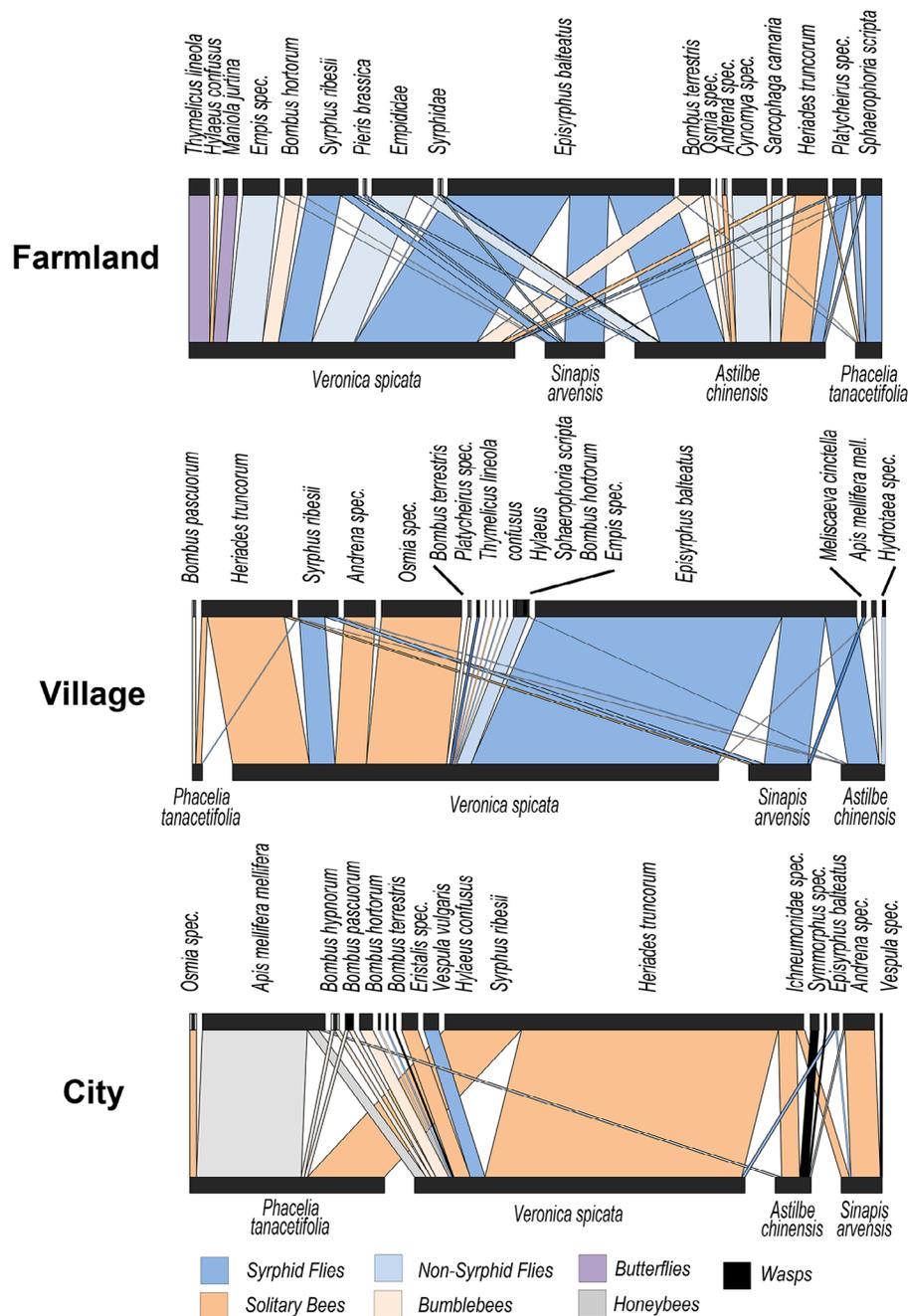
Fig. 7. Plant–pollinator networks in the different landscape types. Webs were aggregated by summing each taxon's abundance across all sub-sites within each landscape: $N_{Farmland}$ = 4; $N_{Village}$ = 4; N_{City} = 4; lower section = plant species; upper section = pollinator morphospecies. Wider bars indicate more pollinator visits than smaller bars. Dark-blue bars indicate visits of syrphid flies; light-blue bars indicate non-syrphid flies. Dark-orange and light-orange bars indicate solitary bees and bumblebee visits. Bars for wasp visits are black, and bars of honeybee visits are gray.
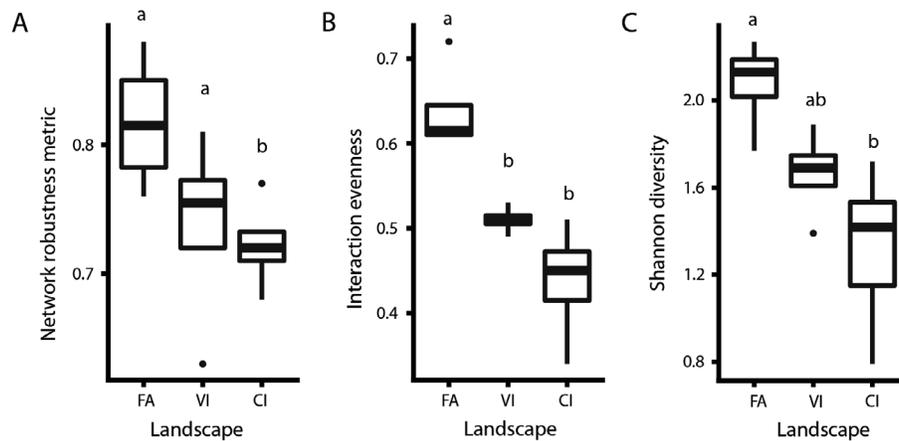
Fig. 8. Network metrics tested against the influence of landscape. Insect communities had significantly higher robustness ($P = 0.014$), interaction evenness ($P = 0.007$), and Shannon diversity ($P = 0.005$) in farmland landscapes. $N_{FA} = 4$; $N_{VI} = 4$; $N_{CI} = 4$; FA, farmland; VI, village; CI, city. Boxes that do not share the same letter show significant differences ($P < 0.05$). Boxplots show median (thick horizontal line), the interquartile range (25th–75th percentile; box), and ±1.5 times the interquartile range (whiskers).

villages, with low abundance in cities. This pattern was especially apparent for *Episyrphus balteatus* as it dominated networks in farmland and village sites but was rarely observed in city sites. This agrees with findings from Jauker et al. (2009) and Bates et al. (2011). Syrphid larvae are ubiquitous in crop fields (Tenhumberg and Poehling 1995). The adults feed on pollen and nectar (Haslett 1989) and so require floral resources, but as they do not require specific nesting habitat and are very mobile, then the fragmentation of floral resources throughout farmland landscapes is not such a problem. Further, *E. balteatus* larvae are the most frequent predators of cereal aphids, which might explain their dominance (Haenke et al. 2009). These differing resource requirements may explain why we did not observe syrphid flies in the pure urban habitat. Any selection of plant species for experimental patches will never be perfectly attractive to all pollinator groups, which could explain why few non-syrphid fly pollinators were observed in our study.

Honeybees were only present within village and city sites, which indicates that managed honeybee hives were present close to the experimental plant plots. Earlier studies showed that honeybees may compete with wild bees and other pollinators for resources (Henry and Rodet 2018, Wojcik et al. 2018). The presence of honeybees within our sites may have changed the visitation rate and occurrence of other pollinators on our experimental plant plots.

There were few floral resources in farmland landscapes, as we sampled in areas that were not managed to promote pollinators (i.e., flower strips planted by farmers); this means the pollen-rich flowers used in our experiment may have attracted a disproportionate number of pollinators in farmland. Therefore, the higher pollinator richness in farmland sites may be because our experimental plant plots attracted more pollinators in farmland areas than they did in villages and cities, where the reverse may be true as these landscapes had higher plant richness in their surroundings, which may mean that we observed disproportionately fewer pollinators in villages and cities.

Plant–pollinator community structure and network metrics

The structure of plant–pollinator networks was more robust and stable in farmland and villages, where more pollinators were present than in cities. The higher diversity and higher interaction evenness indicate few dominating morphospecies. This absence of dominating interaction links in a network contributes to network stability and robustness, explaining why these networks were more robust in farmland sites (May

1973, Tylianakis et al. 2010). Our results of higher interaction evenness in farmland sites contradict those by Geslin et al. (2013) who found that interaction evenness was highest in an urban area compared with farmland, but they found higher numbers of interactions in farmland. The pollinator group present determined the patterns found: There was low interaction evenness in cities with fewer pollinators, which were dominated by solitary bees. In villages and farmland, there was higher pollinator richness with no dominant morphospecies, resulting in higher evenness of interactions.

Urban areas do support pollinator insect communities, but they are not optimal habitat, as resources are patchy and often isolated with many barriers to pollinator dispersal in the form of roads and buildings (Turrini and Knop 2015). The level of urbanization had a strong influence on the pollinator community, as we found that the pollinator community in villages was a mixture of that found in urban areas and in farmland. This agrees with findings from Bates et al. (2011) who found more syrphid flies in farmland than in urban areas and with Sirohi et al. (2015) who found that native bee richness in urban areas was higher than in nearby farmland. The city sites we set up were completely surrounded by built-up areas, whereas the village sites were composed of approximately half built-up area and half farmland, a similar habitat type to what is present on the edge of cities that border on farmland. Villages supported a mixture of the urban pollinator community and the farmland pollinator community, which is likely due to the mixed landscape type. To promote pollinator communities, we therefore suggest that habitat enrichment efforts should focus on preserving natural habitats and increasing floral resources in farmland areas and in urban areas that border on farmland in both villages and cities.

CONCLUSIONS

Assuming that our experimental approach was able to capture pollinator community patterns in cities, villages, and farmland, we can conclude the following from our study: Firstly, different pollinator groups were supported by different landscape types—that is, if the aim is to enhance or conserve overall pollinator biodiversity, then a mixture of different landscape types will be optimal. Secondly, cities or large urbanized areas alone will generally yield rather poor pollinator communities and unstable networks, despite their apparent richness in flowers and ornamental plants. Enriching the interface between urban and farmland landscapes will be an important tool to increase pollinator biodiversity and network robustness.

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Data Accessibility

Data are available from the Dryad repository: https://doi.org/10.5061/dryad.4mw6m906s.