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The structure of flower visitor networks in relation to pollination across an agricultural to urban gradient

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Summary

1. Pollination is a major ecosystem service in which insects, particularly bees, play an important role for the reproduction of most angiosperms. Currently, this service is considered under threat due to reported bee declines. Moderately urbanised areas could be important for pollinators and pollination; however, compared to agricultural and natural systems, they are poorly studied.

2. Here, we investigated the relative effects of local habitat quality and anthropogenic land use across an agricultural to urban gradient for local plant and flying insect communities. We quantified local flower visitor networks and related network architecture to these local and landscape factors using structural equation modelling. Flower visitor network architecture is often assumed to act as a surrogate for the ecosystem service of pollination. To test this idea, we related network metrics to pollination of four experimental, insect pollinator-dependent plant species.

3. Overall, local land use markedly influenced plant and flying insect communities. Flower richness and bee richness were higher in urban compared to agricultural areas. Flower visitor network metrics (e.g. linkage density) increased with the proportion of urban area surrounding a site. Also, relative to agricultural areas, urban flower visitors were more generalised and foraged from a higher number of plant species, likely a consequence of higher urban flowering plant richness. However, urban bees also visited a lower proportion of the available flowering plants (higher specialisation). Surprisingly, linkage density, network specialisation and flower visitor generality were not related to pollination of our four experimental plants *per se*. Rather, it was the proportion of urban cover, flying insect abundance and bee richness that were positively related to pollination.

4. Our findings show strong effects of local land use on plant and flying insect communities and flower visitor interaction networks. We observed increased overall visitation rates and pollination services to our experimental plants in urban compared to agricultural areas, despite increased urban flower visitor generality. Indeed, flower visitor network metrics were a poor proxy of provision of the ecosystem service of pollination. Nevertheless, our results point to potential facilitating effects of diverse urban floral and bee communities for pollination.

Key-words: *Borago officinalis*, flower visitor generality, land use change, linkage density, local habitat, network specialisation, *Sinapis alba*, *Trifolium pratense*, *Trifolium repens*, urbanisation

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Introduction

Animal pollinators, especially bees, are an important component of terrestrial biodiversity by providing essential pollination services to many wild and crop plants (Klein *et al.* 2007; Ollerton, Winfree & Tarrant 2011; Garibaldi, Steffan-Dewenter & Winfree 2013). However, during the last decades, numerous reports have shown declines in numbers of both wild and managed pollinators in the Northern Hemisphere (Biesmeijer, Roberts & Reemer 2006; Bartomeus *et al.* 2013; Koh *et al.* 2016) that could have major ecological and economic consequences (Potts *et al.* 2010).

Two of the main factors threatening global biodiversity, including pollinator diversity, are anthropogenic habitat alteration and habitat degradation resulting from the conversion of (semi-) natural to human-dominated habitats (Brown & Paxton 2009; González-Varo, Biesmeijer & Bommarco 2013). Increasing urbanisation and agricultural intensification, acting as global drivers of land use change, are both suggested to have negative effects on pollinator biodiversity (Tscharntke *et al.* 2005; McKinney 2008; Vanbergen 2013). Yet, paradoxically, several studies have shown that moderate degrees of urbanisation and agricultural land use could have neutral or even positive effects on pollinators (McKinney 2008; Carré, Roche & Chifflet 2009; Banaszak-Cibicka & Żmihorski 2011) and pollination (Cussans *et al.* 2010; Verboven *et al.* 2014; Theodorou *et al.* 2016). Moderate land use may increase landscape heterogeneity and the availability of suitable habitats and resources, thus increasing niche diversity, enhancing bee biodiversity and, as a consequence, pollination service provision (Winfree, Bartomeus & Cariveau 2011; Breitbach *et al.* 2012).

Bee pollinators rely on flowers as a source of food in the form of nectar and pollen. Therefore, floral resources can be a limiting factor for pollinator populations (Roulston & Goodell 2011). Pollinator communities also respond positively to small-scale habitat features associated with nesting and floral resources (Murray *et al.* 2012; Theodorou *et al.* 2016), regardless of land use change (Winfree, Bartomeus & Cariveau 2011). Thus, habitat change and disturbance in moderately urbanised and agricultural areas could potentially support pollinator populations, if they provide pollinators with novel foraging and nesting resources (Winfree *et al.* 2009; Carré, Roche & Chifflet 2009; Fortel *et al.* 2014; Senapathi, Carvalheiro & Biesmeijer 2015).

Many studies have so far focused on the effects of anthropogenic habitat use on the diversity of pollinators and their host plants as well as on plant–pollinator community composition (e.g. Angold, Sadler & Hill 2006; McKinney 2008; Winfree *et al.* 2009). However, the effects of land use change and local habitat on plants and insect pollinators are also likely to influence their mutualistic interactions, thereby impacting the architecture of their networks (Fortuna & Bascompte 2006; Ferreira, Boscolo & Viana 2013; Weiner *et al.* 2014). The structure and complexity (e.g. linkage density) of these mutualistic networks could be important in promoting community stability and functioning (Bastolla *et al.* 2009; Tylianakis *et al.* 2010; Parrott 2010; Blüthgen & Klein 2011; Kaiser-Bunbury & Blüthgen 2015). For instance, recent studies have shown that urbanisation affects network topology (Geslin *et al.* 2013; Baldock, Goddard & Hicks 2015); network-level specialisation was found to be lower (Baldock, Goddard & Hicks 2015) and interaction evenness higher (Geslin *et al.* 2013) in urban compared to agricultural areas. Furthermore, urban flower visitors were found to be more generalistic in their diet (Baldock, Goddard & Hicks 2015), suggesting that in urban areas, the same pollinators may become less effective due to augmented transfer of heterospecific pollen (Kremen, Williams & Aizen 2007; Leong, Kremen & Roderick 2014). However, despite the growing body of theory and use of visitation networks to provide information about resource use by flying insects, little is known to date about how network structure impacts ecosystem functioning and service provision (Ferreira, Boscolo & Viana 2013; Kaiser-Bunbury & Blüthgen 2015).

In this study, we quantified local flower visitation networks to examine how local habitat factors and the gradual change in dominant land use type from agricultural to urban in the surrounding landscape affect plant–pollinator communities and their interactions. We then determined their relative impacts on the ecosystem service of pollination by concurrently performing a landscape-scale pollination experiment using potted greenhouse-raised, insect pollinator-dependent plants. We focused on the following three main questions: (i) what are the direct and indirect effects of land use and local habitat on local plant–pollinator communities and (ii) their interaction networks; and (iii) what are the relative effects of habitat, flower visitor community structure, network complexity, network specialisation and flower visitor generality on pollination *per se*? Based on previous studies (e.g. Baldock, Goddard & Hicks 2015), we predicted richer bee and flowering plant communities in urban compared to agricultural areas and a resulting shift towards higher generalism by urban flower visitors due to the more abundant and diverse urban floral resources available to them. Because seed set of self-incompatible plants could be affected directly by the lack of compatible pollen donor plants and absence of pollinators, we also predicted that community-rich urban areas would have a stronger positive effect on pollination (i.e. facilitation), counteracting the potential decreased pollination effectiveness (seed set resulting from a single visit) of urban flower visitors.

Materials and methods

STUDY SITES

Our study was conducted during July and August 2013 in the federal state of Saxony-Anhalt (Germany). We focused on agricultural and urban landscapes, which represent the two dominant land use types in the region. Using land cover maps within a GIS, we pre-selected nine independent sites that differed in their degree of agricultural to urban land cover (see Appendix S1: Tables S1

and S2, Supporting Information). Within each site, we selected a 25 × 25 m plot near its geographic centre with diverse floral resources, and ensured a minimum distance of 3 km between sites (see Appendix S1: Fig. S1).

LOCAL FLOWER RICHNESS, FLYING INSECTS AND LOCAL HABITAT VARIABLES

Local communities of flying insects within each site were sampled in two rounds. The first round was conducted in July, when plants belonging to the first experimental community were placed at all nine sites (see Experimental plant communities). Similarly, the second round of sampling was performed in August during the field exposure of the second experimental plant community. Each sampling round lasted for four warm non-windy days per site (see Appendix S1: Table S1) and encompassed the entire duration of exposure of local pollinators to experimental plant communities.

Flying insect abundance and bee genus richness were quantified using two sets of blue, yellow and white pan traps (21 × 17 × 2·8 cm) placed on the ground. Each pan trap was two-thirds filled with unscented soapy water and emptied every day of the 4-day-long sampling period per site per round (July and August). Insects were collected from traps and stored in 70% ethanol. Pan traps are a standardised and commonly used method for collecting flying insects. As for other flying insect sampling methods, pan traps also have disadvantages such as potential taxonomic bias and undersampling of large insects. However, in a comparative study, pan traps were found to be the most efficient sampling method across geographical regions in Europe (Westphal, Bommarco & Carré 2008). Relative to other flower visitors, the majority of visits to our experimental plants and local networks were performed by bees (see Results section), and thus, we only identified pan-trapped bees to genus while other pan-trapped organisms were identified only to family. We used a Chao estimator to evaluate bee genus richness within sites using the R package 'vegan' (Oksasen, Blanchet & Kindt 2015).

While pan-trapping insects, we also quantified per site local flowering plant richness and percentage of bare soil as estimators, respectively, of the availability of floral resources and, for ground-nesting bees, that is, all species of Andrenidae and most Colletidae and Halictidae (Potts *et al.* 2005), nesting resources (see Appendix S1: Table S2). To do so, during each of the two sampling rounds, 10 1-m^2 quadrats were randomly placed in each plot. There was no mass flowering crop in the near vicinity of any of our sites during either round of sampling.

LAND USE INDEX

At each sampling site, we also quantified habitat composition at six spatial scales (250, 500, 750, 1000, 1500 and 2000 m) using Quantum GIS software (Quantum GIS Development Team 2014) and land cover data obtained from Geofabrik GmbH (http://www.geofabrik.de/) (see Appendix S1: Table S3). We calculated landscape diversity (H_s) for each site at each radius as: $H_s = -\sum p_i \times \ln p_i$, where p_i is the proportion of each land cover of type i (Krebs 1989).

To identify the scale at which the surrounding land cover had the most power to explain insect occurrence, we correlated flying insect abundance and bee genus richness with landscape diversity in each of our study sites at all six scales and compared the resulting correlation coefficients. Correlation coefficients peaked at 750 m for abundance and 1000 m for bee genus richness (see Appendix S1: Table S4). Due to the strong correlation between landscape diversity at 750 and 1000 m (Spearman's rank correlation; $r_s = 0{\cdot}98$, $P < 0{\cdot}001$), for subsequent landscape-scale analyses, we chose the 750-m radius. This scale is biologically realistic since it is within the upper limit of the foraging range of many pollinator species (Gathmann & Tscharntke 2002; Greenleaf *et al.* 2007). To examine the effects of anthropogenic land use on plant and flower visitor communities as well as their interactions, we summed the proportion of land use classes belonging to urban or agricultural in each site and calculated a land use index, ranging from pure agricultural (−1) to pure urban (+1), based on the proportional area of each land class within a 750-m radius (see Appendix S1: Tables S1 and S3).

EXPERIMENTAL PLANT COMMUNITIES

To estimate pollination service provision at each of our nine sites during each round of sampling, we used two experimental plant communities ('pollinometers') of self-incompatible, insect-pollinated wild plant species, naturally widespread in the region (Frankel & Galun 1977; de Nettancourt 2001). The first community comprised borage (*Borago officinalis* L.) and white mustard (*Sinapis alba* L.) and was exposed at the sites for all 4 days of the first round of sampling in mid-summer (July 2013). Two plant species with an extended flowering period, red clover (*Trifolium pratense* L.) and white clover (*Trifolium repens* L.), constituted the second community and were exposed to flower visitors at each site for all 4 days of the second round of sampling in late summer (August 2013).

Seeds of these experimental plant species were obtained by a local seed provider (Rieger-Hofmann GmbH, Blaufelden-Roldshausen, Germany) and were germinated and grown for 2 months in an insect-free glasshouse before placement at study sites. Five potted plants per species with already open flowers marked with coloured tape were placed at each field site during the flying insect sampling dates, facing south to reduce effects of differential shading. Plants in each community were randomly ordered within 1 m distance of each other along a transect of 10 × 1 m within the 25 × 25 m site plot.

At each site, we monitored all flying insects visiting the experimental plants for 1 of the 4 days on which they were exposed in order to identify their main flower visitors. Individual plants were observed twice per site (20 min per individual plant in the morning and 20 min per individual plant in the afternoon), for a total of 200 min observation time per focal plant species per site. Visitor identity (morphogroup: Coleoptera; hoverfly; other Diptera; Lepidoptera; bees of the families Andrenidae, Colletidae, Halictidae or Megachilidae; *Bombus* spp.; honeybee) was recorded. During the 4 days of the experiment for each sampling round at a site, all experimental plants were regularly watered and subsequently returned to the glasshouse until seed production. Seeds from marked flowers were counted at the level of the floral display unit and used as a measure of pollination service provision. These data on seed set have been used by Theodorou *et al.* (2016) to explore the relationship between pollinator parasitism and pollination.

Dependency of all four focal plant species on insect-mediated pollination was tested in an additional glasshouse experiment. Five plants per species were kept during their entire flowering period in an insect-free glasshouse chamber. Flowers were marked and seed set was assessed in the same way as in field experimental plants.

LOCAL FLOWER VISITOR NETWORKS

Local flower visitor interactions at each site were quantified in July and August using 30-min transect walks (250-m long), performed on the same 4 days that the experimental plant community was exposed at each site. We carried out two transect walks per site in July (mid-summer community with *B. officinalis* and *S. alba*) and two in August (late summer community with *T. pratense*

and *T. repens*), one in the morning (09.00–12.00) and one in the afternoon (14.00–17.00). Our focal experimental plant communities were part of the transect walks and all four experimental plant species were also found naturally in or near the transect walks at one or more sites. All flower visiting insects were recorded to one of 10 groups (as above) and the identity of the visited plant species was recorded to genus using identification keys for local flora (Bäßler, Jäger & Werner 1999; Jäger *et al.* 2013).

It would have been ideal to identify flower visitors to the species level. However, great challenges in identifying flying insects under field conditions prompted us to identify flower visitors to morphogroup level. We defined an interaction to be when an insect touched the reproductive parts of a flower.

STATISTICAL ANALYSIS

Prior to statistical analysis of the data to test our hypotheses, we used Mantel tests and spline correlograms (R package 'ade4', Dray & Dufour 2007; package 'ncf', Bjornstad 2013) to check for potential spatial autocorrelation in our data set. There was no significant spatial autocorrelation for flying insect abundance, local flower richness or seed set ($P > 0{\cdot}05$; see Appendix S1: Table S5).

To reduce any effect of multi-collinearity and to derive comparable estimates, we standardised all quantitative predictors to a mean of zero and standard deviation of one. Prior to each analysis, we used variance inflation factors to check for collinearity among our explanatory variables. Collinearity was assessed with a cut-off value of 3 (Zuur *et al.* 2009).

Pooled flower visitation data (derived from transect walks) from both sampling rounds were used for network analysis. We represented each of the nine networks (one per site) as an incidence matrix with plants in n rows and flower visitors in m columns. For each matrix, we calculated common weighted quantitative network- and group-level indices to examine network complexity, generalisation and specialisation levels across our land use gradient. We calculated: linkage density, H_2' (network-level specialisation), flower visitor generality and specialisation (d') using the R package 'bipartite'v.2.05 (Dormann *et al.* 2009). Linkage density was calculated as the mean number of links per insect morphogroup/plant genus weighted by the number of interactions. H_2' describes network-level specialisation; it ranges between 0 (no specialisation) and 1 (complete specialisation). Flower visitor generality is defined as the mean effective number of visited plant genera per flower visitor morphogroup, weighted by their relative abundance. Individual-level specialisation (d') measures how specialised a given flower visitor morphogroup is with respect to available resources, and ranges from 0 for more generalised to 1 for more specialised (Blüthgen, Menzel & Blüthgen 2006). Mean d' was calculated for each flying visitor morphogroup per network.

We used structural equation modelling (SEM) to analyse the effects of land use and local nesting resources for ground-nesting bees (all species of Andrenidae and most Colletidae and Halictidae) on our quantitative network properties (i.e. linkage density, H_2', flower visitor generality and flower visitor d'), acting either directly or via changes in local plant and pollinator community structure (richness, abundance and composition) (Fig. 1). We use SEM because it allows specific, hypothetically causal links to be incorporated into a logical chain or series of relationships (Kline 2011), whereas other methods, for example, multiple regression, test all links among all pairs of variables, whether logically plausible or not. Richness, abundance and composition were used to describe the structure of the local plant and pollinator communities. Richness for each site is represented by local flower richness (derived from quadrats). Abundance is defined as the total number of flying insect individuals collected in pan traps across all sampling periods at each site. Composition was estimated from community composition of pan-trapped bees. We used non-metric multi-dimensional scaling (Bray–Curtis distance) and the first axis scores (Axis 1: $R^2 = 0{\cdot}86$) to represent bee community composition.

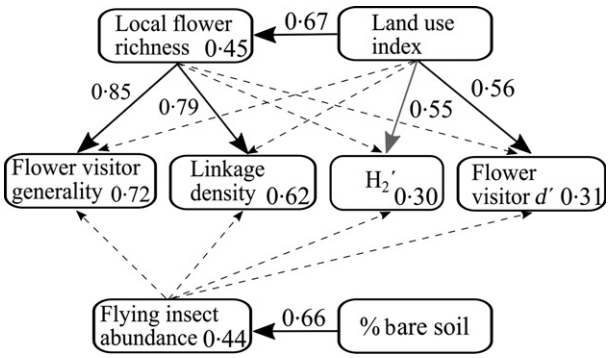

Fig. 1. Path model of land use and local habitat factors and their hypothesised effects on plant–pollinator network properties (flower visitor generality, linkage density, H_2' and flower visitor d'). Black arrows show significant effects derived from structural equation modelling analysis, grey arrows show retained but non-significant effects and dashed arrows show hypothesised effects that were not retained in the final model. Standardised path coefficients are reported next to the bold arrows and R^2 values are reported in the lower right corner of all response variables (see Results for details).

From an overall SEM based on *a priori* knowledge of interactions with all hypothesised effects, we performed stepwise model selection; we evaluated the fit of each model of the effects of land use and local nesting resources on quantitative network properties and selected the best model using the BIC criterion with the specification search function. The final model was assessed using 10 000 bootstrap samples. To further assess the validity of our models, we used the Bollen-Stine bootstrapped χ^2 test (Bollen & Stine 1992). SEM analysis and bootstrapping were performed in AMOS v. 7.0 (Arbuckle 2006).

To test if our observed network properties differed from random expectations, we constructed random interaction networks for each site, based on the observed row and column total (Dormann *et al.* 2009). Characteristics of simulated ($N = 1000$) and observed networks were compared using a Welch t-test. As linkage density and generality are partly dependent on network size (sum of plant genera and flower visitor morphogroups) (Dormann *et al.* 2009; see Appendix S1: Table S6), we standardised these network metrics relative to a null expectation in order to directly compare networks of different dimensions. Relative linkage density and generality were calculated for each network as $(N-\bar{N}_r)/\sigma_{Nr}$, where N is the observed value of linkage density or generality and $\bar{N}_r$ and σ_{Nr} are the mean and standard deviation, respectively, for the 1000 replicated randomised networks (e.g. Dormann *et al.* 2009; Dormann & Strauss 2014).

To study the effects of flying insect community structure (derived from pan trap material), local habitat (derived from quadrats), network complexity and specialisation and flying insect generality on pollination service provision (seed set), we performed generalised linear mixed models with Poisson error structure for each experimental plant species separately. Individuals of the same plant species nested within site were treated as a random factor. We performed all mixed models using the package 'lme4' v. 1.0-4 (Bates *et al.* 2015). If overdispersion was detected, we used an observation-level random effect (Harrison 2014).

Model selection and averaging were conducted using the R package 'MuMIn' (Bartoń 2013). All candidate models, with up to two variables to avoid over-fitting, were ranked based on AICc

values. We used a cut-off ΔAICc value of 2 (Burnham & Anderson 2002) and, if more than one model was retained, we used model averaging to determine the relative importance of each fixed effect factor on pollination. We performed all statistical analyses in R v. 3.0.2 (R Core Team 2013).

Results

During 864 h of pan trapping at nine sites, we collected a total of 5256 flying insect individuals. From those individuals, 938 (18%) were bees, 418 (8%) were syrphids, 291 (6%) were Lepidoptera, 3075 (59%) were other Diptera, 235 (4%) were other Hymenoptera and 176 (3%) were Coleoptera. The 938 bee individuals belonged to 20 genera. The main bee genera sampled were *Lasioglossum* at 40% (377 individuals), *Halictus* at 23% (215 individuals), *Andrena* at 8% (79 individuals), *Bombus* at 8% (71 individuals) and the honeybee *Apis mellifera* at 4% (33 individuals). Increasing bee genus richness (derived from pan traps) was associated with increasing urbanisation in the surrounding landscape ($t = 3{\cdot}86$, $P = 0{\cdot}006$, $R^2 = 0{\cdot}63$; Fig. 2a) and it was correlated with local flower richness (Spearman's rank correlation; $r_s = 0{\cdot}70$, $P = 0{\cdot}03$; Fig. 2b).

Overall from all 1080 min of transect sampling, we observed a total of 1408 interactions (N_{int}) between flying insects (10 morphogroups) and local flowering plants across all nine sites and sampling periods. Bumblebees were involved in 22% of these interactions ($N_{int} = 316$), syrphids in 21% ($N_{int} = 298$), Lepidoptera in 19% ($N_{int} = 264$), halictid bees in 9% ($N_{int} = 129$), other Diptera in 9% ($N_{int} = 123$), andrenid bees in 5% ($N_{int} = 75$), *A. mellifera* in 5% ($N_{int} = 66$), Coleoptera in 4% ($N_{int} = 62$), colletid bees in 3% ($N_{int} = 39$) and megachilid bees in 3% ($N_{int} = 36$) (for overall characteristics and estimated network parameters, see Appendix S1: Table S7a and b).

Based on direct observations of our experimental plant communities, *B. officinalis* plants were mainly visited by honeybees (41%, 48 interactions), halictid bees (17%, 21 interactions) and bumblebees (15%, 18 interactions). *Sinapis alba* plants were mainly visited by hoverflies (75%, 135 interactions) and halictid bees (15%, 28 interactions). *Trifolium pratense* plants were mainly visited by bumblebees (53%, 46 interactions) and butterflies (41%, 36 interactions). *Trifolium repens* plants were mainly visited by bumblebees (38%, 15 interactions), butterflies (18%, 7 interactions) and halictid bees (15%, 6 interactions) (see Appendix S1: Table S8). Overall visitation rates to our experimental plants increased with increasing flower richness ($z = 2{\cdot}223$, $P = 0{\cdot}026$, $R^2 = 0{\cdot}41$). Furthermore, bumblebee visitation rates increased with increasing urban cover ($z = 5{\cdot}089$, $P < 0{\cdot}001$, $R^2 = 0{\cdot}87$).

FLOWER VISITATION NETWORKS

The model selection process yielded one final path model relating the observed network metrics to local and landscape variables, with stable fit to our data (Bollen-Stine bootstrap, $P = 0{\cdot}111$; Fig. 1). The final SEM did not include bee community composition due to substantial reduction in model fit.

In the final model, local flower richness was positively related with the degree of urbanisation ($R^2 = 0{\cdot}44$, $P = 0{\cdot}011$; Figs 1 and 2c; see Appendix S1: Table S9a and b) while the percentage of bare soil was positively related to flying insect abundance ($R^2 = 0{\cdot}44$, $P = 0{\cdot}013$; Figs 1 and 2d, see Appendix S1: Tables S9a and b). Local flower

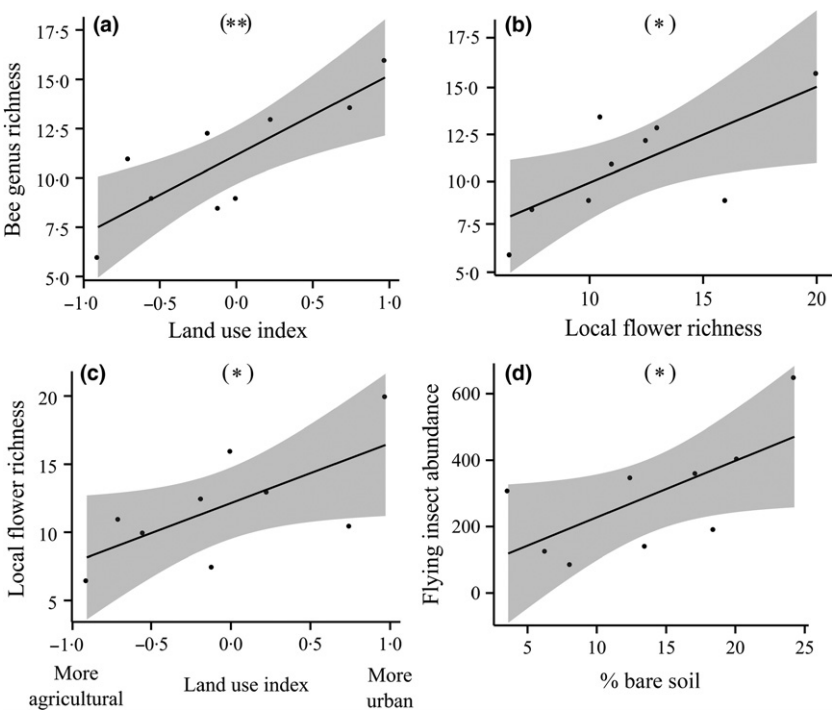

Fig. 2. Relationships between (a) bee genus richness and (agricultural to urban) land use, (b) bee genus richness and local flower richness, (c) local flower richness and (agricultural to urban) land use and (d) flying insect abundance and percentage of bare soil (as a surrogate of insect ground-nesting resources). Plotted lines show the predicted relationship and shaded areas indicate the 95% confidence intervals: $*P < 0{\cdot}05$; $**P < 0{\cdot}01$.

richness was also significantly positively related to network metrics, for example, linkage density ($R^2 = 0{\cdot}62$, $P < 0{\cdot}001$, Fig. 1, see Appendix S1: Table S9a and b) and flower visitor generalisation ($R^2 = 0{\cdot}72$, $P < 0{\cdot}001$; Fig. 1, see Appendix S1: Table S9a and b). The degree of urbanisation was positively associated with network specialisation, though the relationship was not significant ($R^2 = 0{\cdot}30$, $P = 0{\cdot}065$; Fig. 1, see Appendix S1: Table S9a and b). The degree of urbanisation positively affected flower visitor specialisation ($R^2 = 0{\cdot}31$, $P = 0{\cdot}05$; Fig. 1; see Appendix S1: Table S9a and b). The degree of urbanisation also had a positive, though indirect, relationship, mediated through local flowering plant richness, with two network metrics: increasing linkage density and flower visitor generality ($P < 0{\cdot}05$; Fig. 1, see Appendix S1: Table S9c and d).

The null model analysis showed significant differences between all properties of the observed and the random interaction networks, supporting the view that our results are not mere sampling artefacts (Welch *t*-test, $P < 0{\cdot}05$). Both the null model analysis and SEM showed no direct effect of the degree of urbanisation on observed and relative linkage density and flower visitor generality (see Appendix S1: Figs 1 and S2). Also, urbanisation affected linkage density and flower visitor generality only indirectly through local availability of floral resources.

POLLINATION

All plants in our experimental communities produced more seeds per flower unit in the open pollination treatment (*B. officinalis,* 3 ± 0; *S. alba,* 3 ± 0; *T. pratense,* 30 ± 3; *T. repens,* 26 ± 4) compared with the control plants in the glasshouse (*B. officinalis,* 0 ± 0; *S. alba,* 0 ± 0; *T. pratense,* no seeds; *T. repens,* no seeds; Mann–Whitney U test, $P < 0{\cdot}05$), demonstrating their need for insect visitation to set seed.

Model selection based on AICc gave five equally good models which explained *B. officinalis* seed set (Table 1a). These five models explained on average 47% of the variation in pollination (Table 1a). *Borago officinalis* seed set was positively associated with the degree of urbanisation (Table 2a; Fig. 3a).

Three equally good models explaining *S. alba* seed set were identified (Table 1b). These three models explained on average 43% of the variation in pollination (Table 1a). With increasing urban cover in the surrounding landscape, *S. alba* plants produced more seeds (Table 2b; Fig. 3b).

Two equally good models explaining *T. pratense* and *T. repens* seed set were identified (Table 1c and d). For *T. pratense*, these two models explained on average 13% and for *T. repens*, 60% of the variation in pollination (Table 1c and d). With increasing bee genus richness, both *T. pratense* and *T. repens* plants produced more seeds (Table 2c and d). With increasing urban cover in the surrounding landscape, *T. pratense* plants produced more seeds (Table 2c, Fig. 3c); the relationship for *T. repens*, though positive, was not statistically significant (Fig. 3d). However, flying insect abundance positively affected seed set of *T. repens* (Table 2d).

After model selection based on AICc, we found that network-level metrics and flower visitor generality were poorly related to pollination success of our four experimental plant species. Network specialisation and flower visitor generality were only in 16·6% ($n = 2$ each) of the top model sets across our experimental flowering plant species and were never the top-weighted variable for an individual analysis (Tables 1 and 2).

Table 1. Model selection statistics of the relationships between local (including insect abundance) and landscape factors and plant–visitor network properties of the four experimental flowering plants: (a) *Borago officinalis*, (b) *Sinapis alba*, (c) *Trifolium pratense* and (d) *Trifolium repens* (network metrics 'linkage density' and 'flower visitor *d*' did not enter any best-fit model)

Response (model)	d.f.	AICc	ΔAICc	Weight	R^2		Land use index	Bee genus richness	Flying insect abundance	Local flower richness	Flower visitor generality	H'_2
					R^2_m	R^2_c						
(a) *B. officinalis*												
	4	393·23	0·00	0·26	0·39	0·47	+					
	5	393·87	0·64	0·19	0·43	0·47	+					+
	5	394·14	0·91	0·16	0·43	0·48	+	+				
	5	394·45	1·22	0·14	0·42	0·47	+				+	
	5	394·85	1·59	0·12	0·41	0·47	+			+		
(b) *S. alba*												
	4	122·08	0·00	0·29	0·42	0·42	+					
	5	123·72	1·63	0·13	0·44	0·44	+					+
	5	123·82	1·74	0·12	0·45	0·45	+				+	
(c) *T. pratense*												
	4	475·57	0·00	0·60	0·15	0·15	+					
	4	477·53	1·96	0·22	0·12	0·12		+				
(d) *T. repens*												
	4	474·36	0·00	0·40	0·28	0·61		+				
	4	474·68	0·31	0·35	0·30	0·60			+			

Table 2. Model-averaged coefficients and relative variable importance of flower visitor network properties, local and landscape factors as well as insect abundance for seed set of (a) *Borago officinalis*, (b) *Sinapis alba*, (c) *Trifolium pratense* and (d) *Trifolium repens*

Response (model)	Estimate	Std. error	*z* value	*P*-value	Relative variable importance
(a) *B. officinalis*					
(Intercept)	3·919	0·071	52·774		
Land use index	0·374	0·095	3·706	<0·001***	0·87
Bee genus richness	−0·154	0·117	1·276	0·201	0·16
Local flower richness	−0·091	0·089	0·989	0·322	0·12
Flower visitor generality	−0·089	0·073	1·180	0·238	0·14
H'_2	−0·118	0·080	1·415	0·157	0·19
(b) *S. alba*					
(Intercept)	2·675	0·214	11·943		
Land use index	1·049	0·267	3·789	<0·001***	0·54
H'_2	0·378	0·275	1·317	0·187	0·13
Flower visitor generality	−0·338	0·179	1·398	0·162	0·12
(c) *T. pratense*					
(Intercept)	3·240	0·084	37·246		
Land use index	0·250	0·085	2·850	0·004**	0·60
Bee genus richness	0·219	0·087	2·439	0·01*	0·22
(d) *T. repens*					
(Intercept)	2·178	0·431	4·887		
Bee genus richness	1·075	0·437	2·380	0·01*	0·35
Flying insect abundance	1·074	0·426	2·531	0·01*	0·40

All estimates are based on standardised values. Relative variable importance of each parameter in the average model is calculated by summing the AICc for each model that includes that parameter.
*$P < 0·05$.
**$P < 0·01$.
***$P < 0·001$.

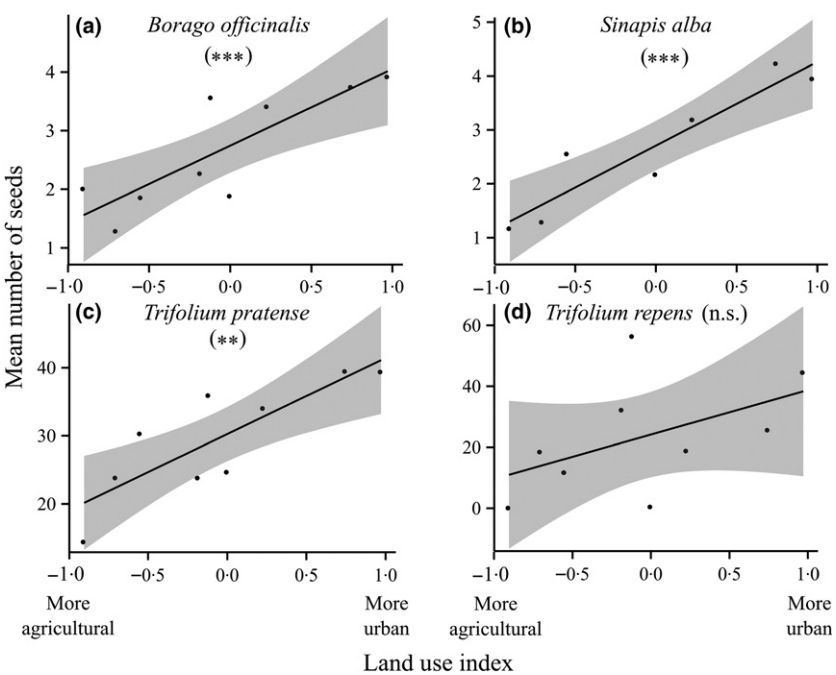

Fig. 3. The effects of (agricultural to urban) land use on the mean number of seeds per flower unit produced by (a) *Borago officinalis*, (b) *Sinapis alba*, (c) *Trifolium pratense* and (d) *Trifolium repens*. Plotted lines show the predicted relationship and shaded areas indicate the 95% confidence intervals: n.s., not significant; **$P < 0·01$; ***$P < 0·001$.

Discussion

In this study, we simultaneously assessed how local habitat and surrounding land use can affect plant–flower visitor communities and their interaction networks. We further explored how these multiple factors influence pollination of pollinator-dependent plants. We found that both bare soil and agricultural-urban land use independently influenced local plant and flying insect community structure, and that land use affected interaction networks and pollination. Network-level metrics and flower visitor generality were not, however, related to pollination *per se*.

FLOWER VISITOR NETWORKS

Mutualistic network architecture results from plant–pollinator community structure and is driven by both random interactions (interaction neutrality) and trait matching (Vázquez *et al.* 2009). Consistent with a recent study in the UK (Baldock, Goddard & Hicks 2015), we observed higher flower visitor generality in urban compared to agricultural areas, likely due to the higher availability of floral resources in urban areas. Furthermore, in our study, we found an increase in flower visitor specialisation in urban sites. Thus, urban pollinators observed in our study were more generalistic in their diet (higher generalisation) but visited proportionally less plant species (higher specialisation). Consequently, we also observed higher network-level specialisation in urban compared to agricultural areas. Bee composition did not change across our land use gradient and was not related to any of our network or group-based metrics, suggesting that the greater generalisation of flower visitors across our sites was mainly driven by changes in their foraging behaviour in flower-rich (i.e. urban) communities.

As expected, our empirical data showed an association between network linkage density and flower richness (Dormann *et al.* 2009). Increased linkage density characterises more complex biotic interaction networks that could also lead to higher network robustness, preventing species extinctions (e.g. Naeem 1998) and potentially leading to more consistent pollination (Blüthgen & Klein 2011).

POLLINATION

Seed set of pollinator-dependent plants could be affected directly by a lack of compatible pollen donor plants in the vicinity and by the absence of pollinators (pollinator visit 'quality' and quantity), and indirectly by local flower richness and abundance, which in turn influence pollinator visitation rates. In our field experiments with two plant communities, we found that increased abundance of flying insects and/or richness of local bee communities were significantly associated with increased seed set in two of our four plants, namely in the two *Trifolium* species. This indicates not only the importance of the availability and diversity of pollinators in the vicinity to ensure pollination but also points to a potential role of the quality of those interactions in terms of the number of compatible, viable pollen grains deposited on stigmas (Ballantyne, Baldock & Willmer 2015). Our focal plants were mainly visited by bees, and bee richness was found to be higher in urbanised compared to rural areas, as seen by others (Fortel *et al.* 2014; Baldock, Goddard & Hicks 2015). The increase in bee richness could reflect the abundant and diverse supply of food and availability of diverse nesting locations (e.g. exposed soil, dead wood, cavities in walls) for pollinators in urban areas (Fetridge, Ascher & Langellotto 2008; Neame, Griswold & Elle 2013). Increasing ground-nesting resources (bare soil for many bee species in the genera Andrenidae, Colletidae and Halictidae) and flower richness were associated with higher abundance of flying insects, bee genus richness and increased overall visitation rates to our 'pollinometers', further emphasising the importance of local habitat quality for pollinator communities.

Flower visitor generality also increased along our urbanisation gradient. Consequently, urban flower visitors could be less effective pollinators (Geslin *et al.* 2013; Baldock, Goddard & Hicks 2015), depositing more heterospecific pollen per visit due to increased diet breadth. Higher loads of heterospecific pollen physically and chemically interfere with conspecific pollen performance and could potentially reduce seed production (Ashman & Arceo-Gómez 2013). Yet, all experimental plants showed increasing reproductive success along the gradient from more agricultural to more urbanised areas. Indeed, we found positive effects of surrounding urban land cover for seed set, suggesting potential facilitative effects for pollination success of wild plants in moderately urbanised areas despite the possibility for more heterospecific pollen transfer from urban flower visitors.

Multiple studies have attempted to relate habitat loss and urbanisation with the architecture of plant–pollinator interaction networks (Geslin *et al.* 2013; Spiesman & Inouye 2013; Baldock, Goddard & Hicks 2015). However, we still lack studies linking community network topology to ecosystem function (but see Gómez, Perfectti & Jordano 2011; Gómez & Perfectti 2012; Tur, Castro-Urgal & Traveset 2013). In our study, we did not find significant associations between our network metrics and seed set of our four focal plant species. Future studies constructing more informative community networks, that is, distinguishing between mere flower visitors and effective pollinators (e.g. Ballantyne, Baldock & Willmer 2015), over longer periods of time and using a wider range of experimental plant species, are needed to further explore the extent to which network metrics are associated with ecosystem function, and specifically how flower visitor networks relate to pollination.

Conclusions

Our findings show that, in moderately urbanised areas providing rich floral resources, both positive effects on bee richness and plant reproduction can be observed. From a theoretical perspective, it is noteworthy that we did not find a relationship between flower visitor network metrics and pollination of four experimental plant species. From an applied perspective, as cities expand world-wide, the strong effects of local habitat on pollinator communities further emphasise the potential for local management as a tool for biodiversity conservation in urbanised areas.

Authors' contributions

P.T. participated in the design of the study, collected field data, undertook data analysis and drafted the manuscript; K.A. and R.R. collected field

data; J.S. and O.S. assisted in data interpretation; T.E.M. and R.J.P. participated in study design and data interpretation. All authors assisted in drafting the manuscript and gave final approval for publication.

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Data accessibility

The data sets used in analyses are available as Supporting Information.

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Study area, land cover, local scale factors, summary statistics and output tables from SEM.

Fig. S1. Study area.

Fig. S2. Relationships between land use and observed and relative linkage density and generality.

Table S1. Coordinates of field sites and land use index.

Table S2. Plant richness per site and mean percentage (%) of bare soil per quadrat.

Table S3. Mean percentage of each land cover type across sites.

Table S4. Relationship between flying insect community and landscape diversity.

Table S5. Summary results of Mantel tests.

Table S6. Relationship between network size, interactions, links and network metrics.

Table S7. Overall characteristics and estimated parameters of flower visitor networks.

Table S8. Number of visits per pollinator morphogroup recorded on our experimental plants.

Table S9. Table of path coefficients, squared multiple correlations and indirect effects from the best-fit SEM.