Flower-visitor and pollen transport networks in a large city: structure and properties

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Received: 20 June 2012 / Accepted: 23 August 2013 / Published online: 12 September 2013
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Abstract Plant species and their pollinators are linked by their mutualistic interactions, which form the basis of pollination networks. The use of a network approach allows one to take into account all interactions between a group of plants and its animal pollinators, and to reveal the structure of these connections. We analysed pollination interactions for urban habitat fragments located within the Warsaw city environment. We compared two similar, ruderal communities (phytosociological order *Onopordetalia acanthii*) located in distant parts of the city of Warsaw (Poland) that differed with the surrounding ecosystems. The aim of this study was to define the structures and properties of flower-visitor (visitation) and pollen transport networks (based on analysis of pollen loads carried by insects) and to assess the differences between the studied sites. Although the sites differed in insect relative abundance (Diptera dominated one study site, whereas Hymenoptera dominated the other), network size and structure were similar for both communities. In both cases, networks contained moderately specialized species (based on H_2' index); however, networks were dominated by apparently ecologically generalized insect taxa as well as those represented by a single specimen. Networks based on pollen transport indicated greater generality of insect species (more links) than those based on our samples of visitation. The most highly linked plant species represented were either the most abundant (Fabaceae) or phenotypically generalized taxa (*Daucus carota*). We conclude that plant–

pollinator interactions in such highly disturbed and isolated habitats are composed mostly of ecologically generalised species. Moreover, we stress the usefulness of pollen load analysis in the development and verification of visitation data.

Keywords Flowering plants · Food web · Insects · Modularity · Mutualism · Pollen loads · Pollination · Warsaw

Introduction

Despite over two centuries of systematic research into plant–pollinator interactions and numerous case studies, we are still far from fully understanding the actual biological mechanisms underlying the evolution of flower–insect mutualisms (Mayer et al. 2011). Although the number of papers dealing with pollination biology is growing steadily (Zych and Jakubiec 2008), most of these refer to a single plant species and interacting pollinators, without reference to other species present in the same community. This may impoverish our understanding of the ecological and evolutionary processes acting on the level of the ecosystem (Memmott 1999; Jordano et al. 2003; Olesen et al. 2012). This community-wide assessment may help us to assess the actual interactions, e.g., in the case of invasive species, for the purpose of restoration of rare taxa or responses of the whole communities to climate change and habitat loss (Elle et al. 2012), but has long posed difficulties owing to methodological constraints. For several years, however, the application of novel analytical techniques based on graph theory has greatly facilitated research not only into plant–animal pollination networks, but also other ecological and biological networks (see e.g., Proulx et al. 2005; Jordano

Handling Editor: Neal Williams.

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et al. 2006; Bascompte and Jordano 2007). Studies of pollination networks in particular, carried out in different parts of the world, revealed some common properties of such assemblages, namely: (1) low connectance, as there is rather a small fraction of realized links in the interaction matrix when compared with all the possible links that can be established between interacting partners (plants and animal pollinators), (2) the probability distribution of link number (node degree) follows power law or truncated power law, (3) the matrices of interactions are nested, which means that there are few highly connected species (generalists) that interact with other generalists and also with specialists (weakly connected species) and, conversely, there are many specialists that interact solely with generalists and (4) most of the studied networks have a modular structure, with some species acting as system hubs binding the whole network together (for general review of biological network properties see, e.g., Jordano et al. 2006; Bascompte and Jordano 2007; Vazquez et al. 2009; Olesen et al. 2010, 2012; Tylianakis et al. 2010). However, most of the network analyses conducted so far rely on insect visits as a measure of mutualism (Alarcon 2010; Popic et al. 2013), whereas visitation patterns are, in fact, only one of the components of animal quality as pollinators (Johnson and Steiner 2000; Pellmyr 2002; Willmer 2011), and sometimes a misleading one, since plants seem to be pollinated by fewer pollinators than assumed from visit observations (Ollerton 1996). This is especially pronounced of generalist plants. For example, 30–50 % of flower-visiting taxa to umbelliferous plants (Apiaceae), such as *Angelica sylvestris* L. and *Heracleum sphondylium* L., do not carry conspecific pollen (Zych 2007; Niemirski and Zych 2011). Quite a high proportion of “cheating” floral visitors is also observed in ecosystem-wide analyses, ranging from 18 % in British hay meadows (Forup and Memmott 2005) to 25–34 % in montane communities in California (Alarcon 2010). In such cases, pollen analyses may add a valuable perspective to our knowledge of plant–animal networks (Forup and Memmott 2005; Gibson et al. 2006; Forup et al. 2008; Bosch et al. 2009; Alarcon 2010; Devoto et al. 2011; Popic et al. 2013). Also, some traditionally used metrics for studying network properties, especially connectance, are said to be strongly dependent on sampling effort (Nielsen and Bascompte 2007; Vazquez et al. 2009; Blüthgen et al. 2006, 2008; Blüthgen 2010; Dorado et al. 2011), and adequate sampling of interaction diversity is labour intensive, so networks published to date may be largely undersampled (Chacoff et al. 2012) and may not necessarily be ecologically meaningful (Ulrich 2009; Blüthgen 2010). Therefore, in purely technical terms, applying pollen datasets could enhance the resolution of the results as they allow us to record “past flower visitation” (Forup and Memmott 2005), and hence discover

some existing links that usually go undetected, compensating, in some cases, lower sampling effort (Blüthgen 2010).

An estimated 87.5 % of all flowering plant species rely on pollinators for their sexual reproduction (Ollerton et al. 2011); hence, pollination is an important ecosystem service (Kearns et al. 1998; Potts et al. 2010), and studies of pollination networks may, for instance, help in understanding how various anthropogenic disturbances affect plant–pollinator communities (Elle et al. 2012). However, concerning pollination networks from various habitats, most of the published studies were conducted in natural or semi-natural landscapes, and virtually no works to date address the structure of pollinator–plant networks in greatly altered habitats, such as urban environments. With the effect of increasing human pressure on natural habitats, e.g., via land reclamation and urbanization, this kind of habitat becomes prevalent in some landscapes (see, e.g., Grimm et al. 2008; Seto et al. 2011) and, sometimes, surprisingly, supports greater biological diversity than the surrounding habitats (Goddard et al. 2010; Faeth et al. 2011; Kowarik 2011). For example, large city gardens and green areas may host numerous rare invertebrates from many taxonomic groups (see, e.g., Kowalczyk et al. 2004; Talley et al. 2007; Matteson et al. 2008; Bąkowski et al. 2010; Koperski 2010). In coupling information relating to the increasing importance of urban areas in sustaining biodiversity (Grimm et al. 2008; Goddard et al. 2010; Kowarik 2011) with the widely reported decline in pollinators and the disruption of mutualistic networks (Kearns et al. 1998; Biesmeijer et al. 2006; Vamosi et al. 2006; Potts et al. 2010), one should be aware that understanding the structure of human-altered communities becomes an increasingly important aspect of biodiversity conservation, especially when failure to consider the ecosystem-wide context of biodiversity loss can lead to wastage of conservation resources and counterproductive management measures (Tylianakis et al. 2010). For some species, such anthropogenic habitats may be the only option to survive, therefore assessing, understanding and enhancing urban biodiversity may be of great importance for conservation reasons. Observations and analyses of the fluctuations in species number and communities’ composition are desirable for understanding their response to urbanization pressure (Kowarik 2011). While conservationists usually tend to prioritize natural ecosystems or native taxa, urban areas also offer the opportunity to study completely novel (“emerging”) ecological systems with new combinations and abundances of taxa, and their persistence (Hobbs et al. 2006). Last but not least, when social perspective is considered, studies of urban biodiversity and related conservation efforts may positively influence human well-being, public health and allow more people to “experience

nature”, thereby raising citizens’ environmental awareness (Kowarik 2011, and lit. cited).

In the present study, we aim to (1) identify the structure and properties of flower-visitor and pollen transport networks in two small, ruderal communities in a large city and (2) verify the usefulness of data based on pollen loads carried by flower visitors, in contrast to simple visitation data.

Materials and methods

Study area

Warsaw, the capital of Poland, is the largest city in the country and is situated in central Poland, covering 517.2 km², with a population of approx. 1.7 million people (based on 2008 data; Czerwińska-Jędrusiak 2009). The present study was conducted for two patches of ruderal plant communities situated within the city agglomeration. The two sites (hereafter called Ochota, O, and Kabaty, K) differed in their surrounding vegetation, but were similar with regard to plant species assemblages. Both sites can be assigned to the phytosociological order *Onopordetalia acanthii* with its only alliance *Onopordion acantii*, which represents thermophilous plant communities with highly drought-resistant perennials and a small number of therophytes (Matuszkiewicz 2001).

Ochota (O) is a community located in the city centre (the new Life Sciences campus of the University of Warsaw) and surrounded by an urban landscape—streets and buildings, with no direct connection to any large green areas. The area of the whole patch does not exceed 1,000 m². The plants were not mowed during the study period.

Kabaty (K) is a community located near the city border (southern Warsaw) and surrounded by an urban landscape from the north and open, post-rural wastelands from the south, in close proximity to the Kabacki Forest—one of the major forested areas adjacent to the urban agglomeration. The area of the whole community is much greater (around 8,000 m²) than that of Ochota. In late summer, the areas were mowed twice during the study period; this, however, did not coincide with sampling work.

In the middle of each site, we marked a single 400 m² plot. Each plot was then divided into eight equal parts, each having an area of 50 m².

Plant species and floral abundance

We collected, preserved as herbarium specimens, and identified individuals representing all entomophilous plant species growing on both plots together with other species growing in close proximity. Herbarium material was also

used for the preparation of a pollen reference collection: from each plant species represented in the plots, we collected pollen grains directly from the anthers and prepared semi-permanent microscope slides, stained and fixed using the gelatine-fuchsine method (Dafni et al. 2005). The reference collection was later used for identification of pollen grains found on the bodies of flower visitors.

For simplification of field surveys, species of similar appearance (usually from the same genus) were clustered together. This applied to species of the genera *Erigeron* L., *Potentilla* L. and *Cerastium* L. Moreover, *Matricaria maritima* subsp. *inodora* (L.) Dostál and *Chamomilla recutita* (L.) Rauschert were pooled into one group named CHAM/MAT.

For each of the eight designated parts of the two plots, we estimated flower abundance based on counts of all flower units (as defined in Gibson et al. 2006) found on one randomly chosen 1 m² square. This was done during insect capture (June and July 2008 and May 2009).

Flower-visitor sampling

For the same randomly chosen square (1 m²), we sampled, for 15 min, all insect visitors to flowers. This procedure was repeated another seven times, once for each 50 m² section of the plot. The order of the sections was randomised. All insects were captured with an entomological net or exhaustor, killed with ethyl acetate in a separate vial to avoid contamination with external pollen, and pinned for further identification and pollen load analysis. We discarded any ants caught (Formicidae), because their inefficiency as pollinators is well documented (Puterbaugh 1998; Beattie and Hughes 2002). Insect sampling was done between 1100 and 1500 h, only on sunny days with a gentle breeze. It was repeated three times over the years 2008–2009 to cover all phenological phases of the community: early summer (6–13 June) and late summer (19–26 July) in 2008, and spring in 2009 (25 May–8 June; owing to the high spring temperature in 2008, the spring bloom period was very short in that year, and therefore, we could not sample some plants). In total, our work resulted in 6 h of insect sampling per community (12 h in total for both communities). Specimens were determined to the lowest possible taxon: in most cases to species or family/order.

Pollen analysis

For pollen analysis, we used all insect individuals captured during field sampling (see above; sample sizes for individual taxa are included in the pollen matrices in Appendix 2). The pollen load carried by an insect was sampled in the same way as for pollen grains for the reference collection (above): using fine forceps and a small cube (ca. 3–4 mm³)

of gelatine-fuchsin jelly (Dafni et al. 2005), we cleaned the insect body surface under a stereomicroscope of adhering pollen grains (in the case of bees, prior to the above procedure, we removed corbicular pollen loads so that they could not contaminate the sample). The jelly was subsequently transferred to a microscope slide, a coverslip applied and the slide gently warmed over a flame to make a semi-permanent preparation. The slides were later checked for the presence of pollen grains that were identified by comparing with our reference collection.

Pollen grain morphology is often similar for closely related species and precise identification of species solely based on pollen morphology is impossible for some genera and even families (Faegri and Iversen 1989). Using light microscopy and working with a large number of samples (also hundreds of pollen grains in one sample), we generally could not identify a particular pollen grain to species level and thus decided to cluster pollen grains into eight categories (easily recognised pollen species), each containing pollen grains of similar morphology: Apiaceae (*Daucus carota*, *Pastinaca sativa*), Asteraceae I (*Achillea millefolium*, *C. recutita*, *Erigeron* sp., *M. maritima* subsp. *inodora*), Asteraceae II (*Cichorium intybus*, *Lenotodon autumnalis*, *Taraxacum* sp.), Caryophyllaceae (*Cerastium* sp.), Brassicaceae (*Berteroa incana*), Fabaceae (all Fabaceae), Rosaceae I (*Potentilla argentea*), Rosaceae II (*Potentilla supina*).

Data analysis

Our observations were organized separately for O and K in binary adjacency matrices showing interacting species $p \times v$, where p = plant species (taxon) and v = floral-visitor species (taxon). There were four variants of the matrix:

- (1) A full-year matrix based on data from flower visits for the whole flowering season (visitation matrix, O_V and K_V , respectively),
- (2) A full-year matrix as in (1) but excluding singletons (multiple visit matrix, O_M and K_M , respectively),
- (3) A full-year matrix based on pollen analysis (pollen matrix, O_P and K_P , respectively), which is equivalent to the “pollen transport web” of Forup and Memmott (2005).
- (4) Since pollen data does not allow for identification of the actual plant species (see *Pollen analysis* above), in order to compare matrices (1) and (3), a variant of visitation matrix was created where plant nodes were clustered into eight categories corresponding to nodes in pollen matrix, that is to pollen species, as described above (clustered matrix, O_C and K_C , respectively).

For each of the above matrices, we calculated basic network metrics: connectance (the overall fraction of realized links to all those possible in the network), average node

degree for plants (p) and their visitors (v), the rate of singly caught visitors and nestedness using Aninhado Bangu 3.0 version (Guimaraes and Guimaraes 2006), and Nestedness Temperature Calculator (NTC) (Atmar and Patterson 1993). Following Bascompte et al. (2003), the matrix temperature T was converted to N —the nestedness index, which is calculated from the equation: $N = (100 - T)/100$. To test the reliability of the nestedness level obtained with Aninhado, random matrices were generated to compare with the actual results (Gotelli and Graves 1996). Two model types were used: ER (the occurrence of a connection (1) is attributed to random matrix cells) and CE [the probability of a cell a_{pv} being a 1 (an interaction between species p and v) is described by an equation $[(P_p / C) + (P_v / R)] \times 2^{-1}$, where P_p = the number of 1 s (interactions) in a row; P_v = the number of 1 s in a column; C = the number of columns; R = the number of rows (Guimaraes and Guimaraes 2006)]. For the CE model, the probability of a given plant and insect is a function of their specialization (Bascompte et al. 2003; Guimaraes and Guimaraes 2006). As connectance may be prone to sampling bias (Nielsen and Bascompte 2007; Vazquez et al. 2009; Blüthgen et al. 2006; 2008; Blüthgen 2010; Dorado et al. 2011), for assessing specialization of our visitation networks based on quantitative data (i.e., interaction frequencies), we calculated frequency-based indices H_2 and its standardized version H_2' , which relies on $H_{2\max}$ and $H_{2\min}$ values calculated from random interaction matrices. H_2' ranges between 0 and 1.0, and characterizes the degree of network specialization, respectively, from extreme generalization to perfect specialization (Blüthgen et al. 2006).

For all matrices, we performed a modularity analysis using Netcarto (Guimerà et al. 2007) with the following parameters: random number seed = 7, iteration factor (f) = 1, and cooling factor (c) = 0.995, as advised by the authors. From this analysis, we excluded K_m and O_m matrices, as the number of interacting species in both cases was $\ll 50$, which according to Olesen et al. (2007a) marked a borderline for modular networks. The results of the modularity analysis were tested against 100 randomly obtained networks with the same node degree distribution. Following Olesen et al. (2007a), the species were assigned to four different network roles (peripherals, connectors, module hubs and network hubs) depending on their z (within-module degree) and c (among-module connectivity) scores. According to these authors, peripheral species establish only one few links mostly within their own module (they have low $z \leq 2.5$ and low $c \leq 0.62$), connector species have many links to other modules (low $z \leq 2.5$ and high $c > 0.62$), module hubs develop many links within their own modules (high $z > 2.5$ and low $c \leq 0.62$) and network hub species have many links both within their own module and to other modules (high $z > 2.5$ and high $c > 0.62$).

Results

During the observations, we listed 11 zoogamous plants on O and 17 on K, and sampled 89 individual insects on O and 80 on K (Appendix 1). The most frequent floral visitors were insects of the orders Hymenoptera, Diptera and Coleoptera. In both plots, individuals of these orders jointly constituted approx. 90 % of all sampled insects (Fig. 1). The relative proportion within each order, however, differed for each of the investigated communities: in O, 55 % of visits were performed by hymenopterans, compared with only 34 % in K, where dipterans were more abundant (56 %). Hemiptera were exclusively observed in O, where Lepidoptera were seldom caught (only 1 % visits). They, in turn, were more abundant in K (7.5 %). The most frequently observed species in O were solitary bees of the genera *Evylaeus/Seladonia*, *Apis mellifera*, as well as *Cordylepherus viridis* (Coleoptera). Each of these accounted for 7 % of captures. In K, bumblebees (*Bombus*) accounted for 14 % of visits, *Sphaerophoria scripta* (Syrphidae) for 14 % and hoverflies of the genus *Syrphus* for 9 %. In both plots, the majority of the captured individuals (over 67 % in O and 57.5 % in K) belonged to rare taxa (one-time captures, Table 1), resulting in a large proportion of single-link floral visitors.

Both communities were very similar with regard to the size and properties of networks: they had the same number of plant species (11; in K, six plant species out of 17 received no insect visits during observations, and therefore, we excluded them from the K_V and K_M matrices) and a similar number of insect taxa (48 in O vs. 40 in K), and they could be characterized by similar network parameters: connectance and average link number (node degree) for plant and insect (visitor) taxon (Table 1). The number of insect taxa was approximately four times greater than that for plants. Both communities were similar in terms of plant species (Sørensen index $QS = 0.73$) and rather dissimilar in terms of animal species (Sørensen

index $QS = 0.29$; overall similarity 0.38). Although the estimated plant abundance was almost two times greater for K (1,300 vs. 817 floral units per 1 m²), the visitation and pollen networks for O were larger (more insect taxa and interactions).

In terms of relative floral abundance, species of the family Fabaceae were the most abundant for both plots (64 % floral units in O and 56 % in K). In visitation matrices (Appendix 1), representatives of this family also occurred among the most connected species—on O, *Trifolium repens* (15 connections) and *Medicago varia* (9) were followed by an umbellifer, *D. carota* (8), and in K, *Medicago falcata* (13) followed by *D. carota* (10). Also in pollen matrices (Appendix 2), Fabaceae established the largest number of links—37 in O and 30 in K. Four species on K and 5 on O had short bloom period and were in flower only during one of the sampling seasons. However, except for *D. carota* that for both study sites flowered only in late summer, for all the most connected species (*M. falcata*, *M. varia*, *T. repens*), their flowering period extended over all three sampling seasons (two in the case of *M. varia* on O; Fig. 2).

In both communities, plant node degree in visitation matrices was positively correlated with floral abundance, but only for O was this relationship statistically significant (Ochota $r = 0.79$, $df = 9$, $t = 3.9245$, $p < 0.01$; Kabaty $r = 0.40$, $df = 9$, $t = 1.3134$; $p = 0.22$; Fig. 3).

When quantitative data were considered for both sites, H_2 indices were significantly smaller than those for random matrices (for K $H_{2K} = 3.946$, $H_{2ran} = 4.163 \pm 0.044$ (mean $\pm$ SD); for O $H_{2O} = 3.960$, $H_{2ran} = 4.268 \pm 0.042$; for both matrices $p < 0.0001$), indicating that they are significantly more specialized than random ones, and the value of H_2' indices was 0.428 and 0.567, respectively, for K and O. The exclusion of singletons significantly reduced the fraction of apparent specialist visitors.

As expected, for both sites, clustering plants according to pollen morphology caused a decline in the number of plant

Fig. 1 Relative abundance (%) of insects from various taxonomic orders observed for the studied communities of Ochota (city centre) and Kabaty (city margin); based on captured individuals, data pooled over the whole study period

Table 1 Four versions of the plant–insect interaction network for Ochota and Kabaty sites

	O _V	O _M	O _P	O _C	K _V	K _M	K _P	K _C
No of plant species (<i>p</i>)	11	10	6	4	11 ^a	9	7	5
No of visitor species (<i>v</i>)	48	16	46 ^b	48	40	17	35 ^b	40
No of interactions (<i>i</i>)	63	34	100	55	58	31	78	47
Connectance ($i/[p \times v]$)	0.12	0.21	0.36	0.28	0.13	0.20	0.32	0.24
Average number of links (node degree) <i>p</i>	5.8	3.4	16.7	13.8	5.3	3.4	11.1	9.4
Average number of links (node degree) <i>v</i>	1.3	2.1	2.2	1.2	1.5	1.8	2.2	1.2
Single-link <i>v</i> [%]	79.6	18.8	37.0	89.1	67.5	41.1	17.1	85.0

O_V/K_V—networks based on data for flower visits during the whole flowering season (visitation network); O_M/K_M—network excluding singly caught insects—singletons (multiple visit network); O_P/K_P—network based on pollen analysis (pollen network); O_C/K_C—a variant of O_V/K_V matrix, where plant nodes were clustered into eight categories corresponding to nodes in “pollen” matrix, that is to pollen species as described in “Materials and methods” (clustered network). Single-link *v*—specialist visitors, interacting with a single plant species

^a There were 17 zoogamous plant species present in the surveyed transect in K, but only 11 of these were visited by anthophilous insects during the surveys (see Appendix 1)

^b Counted were only visitor species that included individuals actually carrying any pollen grains on their bodies

nodes in pollen matrices and in clustered matrices. Also, the number of visitor nodes in pollen matrices was smaller, because some insects carried no pollen grains of a particular plant, and consequently were not considered to be effective pollinators. Conversely, our pollen analysis revealed that insects also carried pollen of other plants that were not recorded during insect observations and were thus not taken into consideration in the visitation matrices (Appendix 2), e.g., *Myatropa florea* in O and *Syricta pipiens* in K. During the sampling period, both species visited only one plant species, but pollen analysis revealed that each of them established at least three more links within the community. When compared with clustered matrices, pollen matrices for both sites had higher connectance and revealed more interactions (82 % more in O and 66 % in K) with a smaller proportion of specialized visitors (Table 1).

Irrespective of the measure of nestedness applied (NODF vs. NTC) and zero model, pollen network matrices for both sites (O_P and K_P) were always significantly nested, whereas in the case of visitation network, the results of the analysis were less clear because NODF showed no significant nestedness for either site, while, according to NTC, the matrices were significantly nested, except for K_V and Ce model (Table 2).

Visitation and pollen networks differed in modularity. Visitation matrices for both sites showed significant modularity: $M_{OV} = 0.676$ ($p < 0.05$) and $M_{KV} = 0.623$ ($p < 0.05$), respectively, for O and K. In both cases, the analysis resulted in seven detected modules. They were, however, formed by different species: 1 or 2 plant species (except a module on K formed by three plant species), together with a varying number of animal taxa (1–11 in O, 1–8 in K). We found two generalist insect species (connector nodes) in O: *Cordylepherus viridis* and *Seladonia confusa*, whereas the K network contained three such species: *Andrena ovatula*, *Bombus pascuorum* and *Polyommatus icarus*. The same

species were also the most connected animal nodes in the visitation networks. Of the plant species, *M. varia*, *M. lupulina*, *D. carota* and *T. repens* played the role of the module hub in O, whereas the remaining four modules had no such hub nodes. In K, the role of module hubs was also played by *M. falcata* and *D. carota*. No network hubs were detected for either of the two studied visitation networks. Pollen networks were non-modular for both sites ($M_{OP} = 0.280$ vs. $M_{ran} = 0.292 \pm 0.009$ for the random network and $M_{KP} = 0.291$ vs. $M_{ran} = 0.318 \pm 0.012$, respectively, for O and K).

Contrary to non-modular pollen networks, significant modularity was also detected for both clustered matrices ($M_O = 0.492$ and $M_K = 0.498$, for both $p < 0.05$), but the number of modules decreased to five in K and three in O. In both sites, modules usually included a single pollen taxon (except one module in O that included two taxa) and few-to-several interacting insect taxa. Most of the taxa established 1–2 links and only some plants played the role of module hubs (Apiaceae and Fabaceae in both sites, and additionally Caryophyllaceae in O), indicating their generalist character in the network. The only animal taxon that played the role of a connector was *P. icarus* in K.

Discussion

Our comparison of visitation and pollen (transfer) networks for highly anthropogenic urban conditions show that the latter indicate greater generality of insect species (more links) than those based on our samples of visitation. This general trend was constant in both our study sites, which were selected based on their similar vegetation characters and composed mostly of perennial and biennial plant species commonly found on wastelands and disturbed sites. Although these kinds of regularly disturbed areas may also

Fig. 2 Average floral abundance (number of floral units $\times m^{-2}$) in two urban communities Ochota and Kabaty recorded during insect sampling in spring (black), early summer (grey) and late summer (white). Shown are only plant species that received at least one recorded visit. For definition of the floral unit see Gibson et al. (2006). Cham/Mat = *Chamomilla recutita* and *Matricaria maritima* ssp. *inodora*, Cerast = *Cerastium* spp., D.car = *Daucus carota*, Erig = *Erigeron* spp., M.alba = *Melilotus alba*, M.fal = *Medicago falcata*, M.lup = *Medicago lupulina*, M.off = *Melilotus officinalis*, M.var = *Medicago varia*, Poten = *Potentilla* spp., T.arv = *Trifolium arvense*, T.prat = *Trifolium pratense*, T.rep = *Trifolium repens*

be inhabited by therophytes (annuals), it is the biennial and perennial plants (hemicryptophytes) that make the site more attractive to at least some pollinator groups, e.g., syrphid flies or parasitic hymenopterans (Ellis and Ellis-Adam 1995). In fact, all zoogamous plants in our study sites represented more or less functionally generalised species (sensu Ollerton et al. 2007). However, the most abundant perennials, namely *T. repens* (in O) and *Medicago* spp. (in O and K) had also the longest blooming time and were able to attract pollinators throughout the whole study period, which probably was the reason that for both recorded visitation networks, they were the hubs forming the core of their modules. In the fallow land network studied by Junker et al. (2013), spatiotemporal co-occurrence of flowers and animals (phenology) was one of the most important floral traits influencing pollinators'

Fig. 3 Plant node degree in relation to flower abundance for a given plant species (no. of floral units) in two urban communities: city-centre site Ochota (O) and city-margin site Kabaty (K); solid line is a regression line and dotted line shows 95 % confidence limits. Only for Ochota (O) is the correlation statistically significant, $r^2 = 0.6312$; $r = 0.7945$; $p < 0.01$

behaviour. In our study site, later in the season, plants of the Fabaceae family were accompanied also by the highly linked biennial generalist umbellifer *D. carota*. This seems to be consistent with the results of Stang et al. (2006), who demonstrated for the thermophilous Mediterranean community that flower abundance and simple morphological constraints of flowers may explain much of the variation in the number of insect visitors. In our study, the relationship between floral abundance and the number of established links was especially pronounced in the city-centre site Ochota, whereas in city margin Kabaty, floral abundance was relatively unimportant. Given the similar floristic composition of both sites, this difference can perhaps be explained by the effect of the surrounding landscape matrix and insect foraging mode. Our observation transect in Kabaty was a small fragment of a larger area of similar character, and insects (mostly opportunistic flies) could unrestrictedly search for other plants or floral patches, whereas Ochota transect was surrounded by an otherwise hostile environment, and pollinators (mostly bees that usually show floral constancy) could only forage within the actual site which largely restricted their choice.

In both study sites, the most connected plants belonged to families Fabaceae and Apiaceae and these are known to be visited by a vast range of floral visitors (Ellis and Ellis-Adam 1993; Proctor et al. 1996; Willmer 2011), the former being especially attractive to bees because of its protein-rich pollen (Goulson et al. 2005; Hanley et al. 2008; for contrasting opinion see, however, Roulston et al. 2000), whereas the latter are typical phenotypical generalists with open, easily accessible flowers (Olesen et al. 2007b; Ollerton et al. 2007) and are known to be visited by a taxonomically diverse array of generalist insects, especially flies (see e.g., Zych 2004; Zych et al. 2007). Also, the insect species recorded in our study

Table 2 Nestedness of the obtained matrices depending on the algorithm used (NODF vs. NTC, see [Materials and methods](#))

		O _V	O _M	O _P	O _C	K _V	K _M	K _P	K _C
NODF	Nestedness	10.62	22.68	59.82	13.85	13.66	18.19	58.62	20.82
	NODF(Er)	12.78	22.12	38.19	27.42	14.34	23.30	34.12	23.35
	p(Er)	0.83	0.43	0.00	1.00	0.60	0.85	0.00	0.85
	NODF(Ce)	13.80	23.76	44.72	30.35	15.88	24.89	40.63	26.51
	p(Ce)	0.91	0.56	0.00	1.00	0.79	0.91	0.00	0.85
NTC	N	0.73	0.54	0.86	0.59	0.71	0.67	0.84	0.73
	N(Er)	0.52	0.55	0.38	0.28	0.53	0.56	0.40	0.32
	p(Er)	0.00	0.52	0.00	0.00	0.00	0.12	0.00	0.00
	N(Ce)	0.59	0.57	0.58	0.56	0.60	0.58	0.59	0.62
	p(Ce)	0.02	0.63	0.00	0.40	0.06	0.17	0.00	0.13

O_V and K_V—visitation matrices; O_M/K_M—network excluding singly caught insects (multiple visit network); O_P and K_P matrices constructed based on insect pollen loads; and O_C/K_C—a variant of O_V/K_V matrix, where plant nodes were clustered into eight categories corresponding to nodes in “pollen” matrix, that is to pollen species as described in [“Materials and methods”](#) (clustered network). ER/CE are zero models used for generation of random matrices for comparisons with actual results (see [Materials and methods](#)), where p stands for the probability that the model-generated matrix is equally or more nested than is the actual one. Boldface indicates statistically significant results when both zero models were significantly less nested at $p < 0.05$

networks were largely generalists. Of the bees, most species at both study sites represented polylectic taxa (Pawlikowski 1996; Beil et al. 2008; Banaszak-Cibicka and Żmihorski 2011). Even *A. ovatula* observed in the Kabaty site, regarded as oligolectic by some authors (e.g., Banaszak-Cibicka and Żmihorski 2011), was observed visiting many floral resources with preference towards Fabaceae plants (Beil et al. 2008). In our study sites dominated by Fabaceae, however, individuals of this species visited only Fabaceae, and we found no other pollen on their bodies. Interestingly, in the visitation matrices, this species played the role of a connector species, linking several species of Fabaceae. In pollen and clustered matrices, however, this function disappeared because all Fabaceae were clustered into one pollen taxon. The prevalence of generalists is consistent with the results of Banaszak-Cibicka and Żmihorski (2011), who in a study of bee diversity conducted in similar anthropogenic habitats in another large city in Poland (Poznań) reported insect assemblages composed mostly of opportunistic taxa. In our study also, visitors from other taxonomic groups belonged to the generalist species and included very common (e.g., *Gonepteryx rhamni* or *Pieris brassicae*) and/or highly migratory species (e.g., *Episyrphus balteatus*, *S. scripta*). These observations strongly agree with those of Aizen et al. (2012), who showed that a decrease in the size of the habitat produces a larger proportion of generalists in the network, but this somewhat contradicts some network metrics obtained for our study systems. For example, the complementary specialization index H_2' (Blüthgen et al. 2006), based on quantitative visitation data showed that they are moderately specialized, which would place them well within ranges of many other pollination networks (Blüthgen et al. 2007). As shown by Aizen et al. (2012), the persistence of specialists in highly fragmented habitats is also possible if they interact with

locally resilient generalists, but in our study, this was due to a significant proportion of our pollinator assemblages being composed of rare, one-visit insect species (singletons), which, especially in qualitative data metrics (e.g., connectance) are regarded as specialists. In our study, the ratio of singletons was greater than in other studies of similar habitats (usually 20–30 % for bees; e.g., Banaszak-Cibicka and Żmihorski 2011; Tonietto et al. 2011), possibly because of undersampling. Undoubtedly, not all of them represent real specialists. This is reflected in our O_M and K_M matrices and is consistent with the results of Petanidou et al. (2008), who showed that in observations over short periods of time, the specialization of species may be overestimated due to the great temporal plasticity in interaction identities. When we removed singletons from the analysis, the number of apparent food specialists (visitors to a single plant species) dropped considerably from 80 to 19 % in O and from 68 to 41 % in K. The greater reduction in the city centre (Ochota), when compared with the city outskirts, may show a more general trend in which generalist insects occupy more urbanized parts of the city (Banaszak-Cibicka and Żmihorski 2011, and lit. cited). This pattern is consistent with greater sensitivity of specialists to disturbance (Williams et al. 2010).

Both our study networks were similar in size (11 × 49 and 11 × 40 interacting species in visitation networks, and 6 × 46 and 5 × 35 in pollen networks, respectively, for Ochota and Kabaty), but this similarity, however, was not reflected in the insect assemblages present. The city centre network (Ochota) was dominated by bees, whereas flies were prevalent in the city border network (Kabaty). This taxonomic shift can probably be attributed to the effect of the surrounding landscape matrix and urbanization. The negative effects of urbanization on species diversity and visitation have been observed for many

important insect pollinator groups, e.g., bees (Bates et al. 2011; Hennig and Ghazoul 2012; Toniello et al. 2011), hoverflies (Bates et al. 2011), sarcophagid flies (Mulieri et al. 2011) or butterflies (Dallimer et al. 2012; Soga and Koike 2013), all recorded also in our study. Their response, however, may be highly variable and depend on many factors. For instance, the abundance of bee species in urban conditions is positively correlated with floral abundance and diversity (Wojcik 2011), as well as resource distribution (e.g., nesting or egg-laying sites; Hennig and Ghazoul 2012). As shown by the latter authors, diversity and visitation by syrphids in urban conditions can also be related to the presence of a green area. Furthermore, for many species, the important factor may be the availability of egg-laying sites since, e.g., for calliphorid flies, hoverflies and butterflies, this means access to relatively rare resources in urban habitats, i.e., carrion or appropriate host animals, water reservoirs, specific host plants, respectively. Most of the above-mentioned resources, though scarce in Ochota, were more readily available in Kabaty; hence, generally, resource availability may perhaps best explain our findings for flies and butterflies, which seem especially sensitive to the availability of egg-laying sites. Conversely, our city-centre site, surrounded by ruderal vegetation, probably still offers relatively many nesting sites for ground-nesting bees and bumblebees that made up most of the bee visits in our study and prevailed in the Ochota site. This seems to contradict the results of Matteson et al. (2008) for New York, where soil-nesting species were relatively rare, but the large meta-analysis by Williams et al. (2010) showed that subterranean nesters are generally less sensitive to disturbance.

Possibly, both main pollinators groups, namely, flies and bees, have a threshold response to urbanization, and their reaction to urban conditions is highly species-specific, with some taxa responding positively to an increasing urbanization gradient, despite the general trend. This has been demonstrated for bees (Williams et al. 2010) and butterflies (Bergerot et al. 2011) and may be due to the fact that, in some cases, the urban surrounding may offer more appropriate conditions for these insects when compared with adjacent agricultural lands that are greatly impoverished due to agrotechnical activities (Bates et al. 2011). Several authors have shown that some suburban or garden environments may even be useful to agriculture by providing a source of pollinators (Goulson et al. 2002, 2010; Samnegard et al. 2011).

As expected, the pollen networks seemed to better describe the existing systems. They were different from the networks constructed using visitation data (to retain the same plant species number and reliably compare visitation and pollen matrices, we used O_C and K_C matrices, i.e., networks with plant species clustered according to pollen morphology) in that they revealed much more interactions (82 % more in O and 66 % in K) between insect visitors and plants, with both player groups having higher node degrees. In network metrics,

this translated to significant nestedness, higher connectance and lack of modularity in pollen matrices when compared with clustered visitation matrices, suggesting greater generalization of the former. Of course, an increase in connectance of our pollen matrices, in part, could also result from methodological issues and represent a simple mathematical artefact as clustered pollen taxa retained most of their links which resulted in “denser” and more nested networks. This effect could be strengthened by the relatively low sampling effort when compared to other network studies, with many observations being singletons. However, pollen analysis revealed “past flower visitation” (Forup and Memmott 2005) of these individuals, indicating their more generalist floral visitation pattern. Increase in generalization of pollen transport networks was also reported by Forup and Memmott (2005) and Gibson et al. (2006) for other anthropogenic ecosystems, hay meadows and arable fields, respectively. It is likely that this can be observed in many other pollination networks, since many of them are probably largely undersampled (Blüthgen et al. 2008; Blüthgen 2010; Chacoff et al. 2012), and using pollen data in fact extends the sampling period by taking into account previous visits to other plant species. In our study, this was, for example, observed for Asteraceae II and Brassicaceae, which were not seen to be visited in K, but their pollen grains were noted on several insect species (in fact we noted pollen grains of a similar morphology also in O, although there were no corresponding plants on site). Pollen analyses are also more useful in detecting the real identity of the observed interactions, because in most network studies, flower visits are treated interchangeably with pollinations, but this is not necessarily true (see e.g., Schemske and Horvitz 1984; Fumero-Cabán and Meléndez-Ackerman 2007; Zych 2007; Watts et al. 2012). In our systems, the proportion of taxa that carried no pollen whatsoever was relatively small, 4 and 13 %, respectively, for Ochota and Kabaty, but this number may be higher for other ecosystems (Forup and Memmott 2005; Alarcon 2010). Body pollen loads are one of the necessary prerequisites of pollination (Johnson and Steiner 2000; Pellmyr 2002), but they still do not provide much information on the real importance of visitor taxa (see e.g., Zych et al. 2013) and hence do not offer the ultimate solution to our efforts of studying real pollination networks, as opposed to flower-visitor networks. Pollen transport networks seem, however, an important step towards better understanding the complex relationships that exist between plants and their pollinators on an ecosystemic scale (Popic et al. 2013).

In conclusion, our study revealed that even small patches of ruderal vegetation in highly urbanized areas may harbour considerable pollinator diversity. However, our urban networks were composed mostly of generalist species, which was in contrast to the results of most network metric analyses performed on visitation data, indicating the rather specialized character of the observed systems. This may indicate

undersampling (emphasized by the high proportion of singletons in our study), but also that some indices are of little value in studies of ephemeral and disturbed habitats such as these. This problem of ecologically meaningful reasoning based on some network metrics has already been pointed out by several authors (Blüthgen et al. 2008; Ulrich 2009; Blüthgen 2010). In our case, more coherent results were obtained using pollen data, which revealed many more interactions within the studied communities. Difficulties in pollen identification, however, make comparisons with visitation matrices more problematic, as some changes in pollen network metrics have purely mathematical explanations. Our solution was to restructure visitation matrices so that they contained the same pollen species, but this, in turn, resulted in some information being lost. In spite of some methodological constraints, this approach nonetheless seems a promising tool for interpreting mutualistic relationships, since in many cases,

in our study system, inferring the function of species solely from visitation networks could be misleading.

Acknowledgments We thank Agnieszka Draber-Mońko, Jan Goldstein, Piotr Tykarski and Grzegorz Świerżewski for arthropod identification. Martina Stang, Neal Williams and two anonymous reviewers made invaluable comments that greatly improved earlier versions of the manuscript. During preparation of the paper, MZ was supported by Grant No. N304 367938 from the Polish Ministry of Science and Higher Education.

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Appendix 1

See Table 3.

Table 3 Visitation matrices for Ochota and Kabaty sites (O_V and K_V, respectively)

Ochota												
	N	Trifolium repens D	Medicago varia B	Daucus carota F	Medicago lupulina E	Potentilla sp. C	Erigeron sp. C	Trifolium pratense G	CHAMMAT E	Melilotus alba G	Melilotus officinalis A	Trifolium arvense B
Cordylepherus viridis	E 8											
Seladonia confusa	B 5											
Cerceris rybyensis	G 3											
Eupeodes corollae	E 2											
Helophilus hybridus	C 2											
Evylaeus fulvicornis	F 2											
Lindeni albilabris	E 2											
Miridae 1	C 5											
Polistes gallicus	B 3											
Sphaerophoria scripta	F 6											
Ichneumonidea 2	G 1											
Ichneumonidea 3	C 1											
Andrena minutula	E 3											
Proanthidium oblongatum	D 3											
Apis mellifera	D 7											
Bombus pascuorum	D 1											
Bombus lapidarius	D 1											
Bombus terrestris	D 1											
Coccinella septempunctata	F 1											
Coccinula quatuordecimpustulata	F 1											
Curculionidae	G 1											
Eristalis tenax	B 2											
Eucera longicornis	B 1											
Eumeninae	E 1											
Eupeodes latifasciatus	C 1											
Evylaeus laticeps	F 1											
Evylaeus morio	B 2											
Seladonia subaurata	G 1											
Hemipenthes morio	D 1											
Heriades truncorum	A 1											
Holopyga fastuosa	D 1											
Evylaeus minutissimus	E 1											
Lasioglossum sp.	C 1											
Evylaeus rufitarsis	D 1											
Megachile rotundata	D 1											
Melitta sp.	B 1											
Miridae 2	D 2											
Myathropa florea	F 1											
Odynerus sp.	G 1											
Pentatomidae	C 1											
Philanthus triangulum	G 1											
Pieris brassicae	B 1											
Sarcophaga subgen. Heteronychia	D 1											
Sarcophaga nigriventris	C 1											
Sphecodes puncticeps	E 1											
Syritta pipiens	C 1											
Trichopsomyia flavitarsis	F 1											
Tytthaspis sedecimpunctata	E 1											
89												

Kabaty												
	N	Medicago falcata Z	Daucus carota T	Trifolium pratense S	Medicago lupulina W	Trifolium repens U	Melilotus officinalis U	Potentilla sp. W	Medicago varia X	Cerastium sp. W	Erigeron sp. T	CHAMMAT Y
Andrena ovata	S 3											
Bombus lapidarius	U 5											
Bombus pascuorum	X 5											
Polyommatus icarus	X 4											
Sphaerophoria scripta	T 11											
Andrena dorsata	U 2											
Apis mellifera	U 3											
Chloromyia formosa	S 2											
Seladonia subaurata	W 2											
Paragus sp.	W 2											
Pollenia rudis	W 3											
Syrphus ribesii	Z 6											
Systoechus ctenopterus	S 2											
Acaplytrata	Y 1											
Ichneumonidea 1	Z 1											
Ancistrocerus claripennis	S 1											
Bombus terrestris	X 1											
Bombylius canescens	S 1											
Brachicomia devia	T 1											
Chrysotoxum festivum	T 1											
Coccinella quinquepunctata	Z 1											
Dinera griseocens	Z 1											
Empididae	W 1											
Episyrphus balteatus	T 1											
Eristalis tenax	T 1											
Gonepteryx rhamni	Z 1											
Seladonia confusa	W 1											
Seladonia tumulorum	W 1											
Sarcophaga melanura	Z 1											
Lucilia sp.	T 2											
Megachile circumcincta	Z 1											
Mordellidae	W 1											
Muscidae	U 1											
Odynerus melanocephalus	U 1											
Pieris brassicae	S 1											
Sarcophaga nigriventris	Z 1											
Sarcophila latifrons	T 2											
Syritta pipiens	T 2											
Syrphus torvus	Z 1											
Trichopsomyia flavitarsis	T 1											
80												

Black box indicates that at least one individual of a given insect taxon visited flowers of a given plant. Taxa are arranged in decreasing order of links. Insect species names are given according to Bogdanowicz et al. (2004, 2007). For Kabaty, six plant species (*Achillea millefolium*, *Berteroa incana*, *Cichorium intibus*, *Leontodon autumnalis*, *Vicia villosa*, *Trifolium dubium*) were excluded from the matrix as we recorded no insect visits to their flowers. CHAM/MAT = *Matricaria maritima* ssp. *inodora* and *Chamomilla recutita*. Letters A–G for Ochota and S–Z for Kabaty indicate that, according to modularity analysis (Guimerà et al. 2007), species with the same letter were assigned to the same module

Appendix 2

See Table 4.

Table 4 Pollen matrices for Kabaty and Ochota sites (K_P and O_P , respectively)

Ochota							Kabaty									
	N	Fabaceae	Asteraceae I	Apiaceae	Asteraceae II	Rosaceae I	Brassicaceae		N	Fabaceae	Asteraceae I	Apiaceae	Asteraceae II	Caryophyllaceae	Rosaceae I	Brassicaceae
Sphaerophoria scripta	6							Sphaerophoria scripta	11							
Helophilus hybridus	2							Odynerus melanocephalus	1							
Myathropa florea	1							Syritta pipiens	2							
Evylaeus fulvicornis	2							Syrphus ribesii	6							
Polistes gallicus	3							Seladonia tumulorum	1							
Cerceris rybyensis	3							Apis mellifera	3							
Cordylepherus viridis	8							Eristalis tenax	1							
Proanthidium oblongatum	3							Seladonia subaurata	2							
Bombus terrestris	1							Lucilia sp.	2							
Eristalis tenax	2							Episyrphus balteatus	1							
Eupeodes latifasciatus	1							Pieris brassicae	1							
Heriades truncorum	1							Paragus sp.	2							
Pieris brassicae	1							Systoechus ctenopterus	2							
Eupeodes corollae	2							Andrena dorsata	2							
Lindenus albilabris	2							Bombus lapidarius	5							
Seladonia confusa	5							Bombus pascuorum	5							
Ichneumonoidea 2	1							Bombus terrestris	1							
Ichneumonoidea 3	1							Chrysotoxum festivum	1							
Bombus pascuorum	1							Trichopsomyia flavitarsis	1							
Bombus lapidarius	1							Bombylius canescens	1							
Coccinula quatuordecimpustulata	1							Brachicoma devia	1							
Eumeninae	1							Chloromyia formosa	2							
Evylaeus laticeps	1							Polennia rudis	3							
Seladonia subaurata	1							Polyommatus icarus	4							
Hemipenthes morio	1							Dinera grisescens	1							
Megachile rotundata	1							Acaplyprata	1							
Odynerus sp.	1							Ichneumonoidea 1	1							
Philanthus tringulum	1							Empididae	1							
Syritta pipiens	1							Sarcophaga melanura	1							
Andrena minutula	3							Sarcophila latifrons	2							
Apis mellifera	7							Ancistrocerus claripennis	1							
Coccinella septempunctata	1							Andrena ovatula	3							
Curculionidae	1							Megachile circumcincta	1							
Eucera longicornis	1							Seladonia confusa	1							
Holopyga fastuosa	1							Syrphus torvus	1							
Evylaeus minutissimus	1															
Evylaeus morio	2															
Evylaeus rufitarsis	1															
Melitta sp.	1															
Miridae 2	2															
Sarcophaga subgen. Heteronychia	1															
Sarcophaga nigriventris	1															
Sphecodes puncticeps	1															
Trichopsomyia flavitarsis	1															
Tytthaspis sedecimpunctata	1															
Miridae 1	5															
	87								75							

Black box indicates that at least one individual of a given insect taxon carried pollen grains of a given plant. Taxa are arranged in decreasing order of links, N indicates sample size, i.e., the number of individual insects analysed for body pollen loads. Insect species names are given according to Bogdanowicz et al. (2004, 2007)

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