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Research

Red and white clover provide food resources for honeybees and wild bees in urban environments

Laura Kanduth, Marion Chartier, Jürg Schönenberger and Agnes S. Dellinger

L. Kanduth (https://orcid.org/0000-0001-5638-4072), M. Chartier (https://orcid.org/0000-0001-6757-4760), J. Schönenberger (https://orcid.org/0000-0001-6791-2731) and A. S. Dellinger (https://orcid.org/0000-0003-1394-3414) ✉ (agnes.dellinger@univie.ac.at), Dept of Botany and Biodiversity Research, Univ. of Vienna, Vienna, Austria.

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Pollination is a key ecological process both in wild plant species and in economically important crops. Global land use change and urbanization are known to alter plant–pollinator interactions, but our understanding of how the local (i.e. size of green area, food resource availability) and landscape (surrounding green area) context affect pollinators in urban landscapes remains understudied. We selected two co-occurring clover species, *Trifolium pratense* and *T. repens* to assess whether mixed stands of common wildflowers provide resources for a diverse pollinator assemblage by supporting differently adapted/specialized pollinator species. We further wanted to test how environmental factors (flower diversity, resource availability, size and percentage of green area) alter plant–pollinator interactions in urban environments.

We studied the pollinator assemblage and visitation rate of pollinators in 1-m^2 plots in 21 green areas of different sizes in the city of Vienna (Austria). In addition, we assessed the surrounding landscape context by estimating the percentage of green area in perimeters of 100, 500 and 1000 m around each study plot and measured local flower resource availability.

We found that proportions of pollinator taxa differed significantly between white and red clover, with *T. repens* mainly pollinated by *Apis mellifera*, and *T. pratense* primarily pollinated by different bumblebee species. Visitation frequency was positively correlated to local resource availability (number of anthetic *Trifolium* inflorescences in each plot), but independent of the surrounding landscape context (i.e. percentage of green area).

We conclude that the establishment and maintenance even of small patches of different common wildflowers help maintain a diverse bee community in urban environments. Particularly large-flowered species may be important for supporting long-tongued, late emerging pollinators such as certain bumblebee species.

Keywords: *Apis mellifera*, *Bombus*, green area size, pollinator community, urban ecology, visitation frequency

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Introduction

Pollination, the successful transfer of conspecific pollen, is an essential process in the sexual reproductive cycle of plants (Tommasi et al. 2004). Around 90% of all angiosperms, including many of the most important agricultural crops, rely on pollen transfer by animal vectors (Klein et al. 2007, Ollerton et al. 2011). Bees (ca 20 000 species; Sann et al. 2018) visit flowers to primarily forage for pollen and nectar, and are of particular importance as pollinating agents both in natural and urban environments (Bates et al. 2011, Hagenstein and Neumayer 2015, Matias et al. 2017, Theodorou et al. 2017). Against the longstanding view that honeybees are the most important pollinators of many agricultural crops, recent studies have highlighted the enormous economic value of pollination services provided by wild bees (Klein et al. 2007, Potts et al. 2010). In particular, wild bees may substitute pollination services of honeybees when honeybee abundances are reduced, i.e. due to cold weather, diseases, pests, pesticides, decline of beekeeping activity (Klein et al. 2007, Winfree et al. 2007, Garibaldi et al. 2013). Hence, the preservation of diverse and abundant wild bee communities is of primary importance, not only for the preservation of wild plant communities, but also to secure human food supply.

The recent dramatic decline of wild bee populations demands for urgent action in the conservation of bees (Biesmeijer et al. 2006, Brown and Paxton 2009, Potts et al. 2010, Dupont et al. 2011, Goulson et al. 2015, EU Pollinators Initiative). Global land use changes, which go along with rapidly increasing urbanization, resulting in habitat loss and fragmentation, have been identified as primary cause of the loss of diverse pollinator (e.g. bee) communities (Ahrné et al. 2009, Andrieu et al. 2009, Winfree et al. 2009, Potts et al. 2010, Harrison and Winfree 2015, Matias et al. 2017, Theodorou et al. 2020, Wenzel et al. 2020). The link between urbanization and pollinator decline is not straightforward, and studies report both positive and negative effects of urbanization on pollinator diversity (Gunnarsson and Federsel 2014, Theodorou et al. 2017, Bennett and Lovell 2019, Wenzel et al. 2020; note that these effects were always negative for non-bee pollinators, Theodorou et al. 2020). Generally, an urban area can be characterized as a complex mosaic of impervious surfaces and built-up patches, intermingled with variable amounts of green areas (vegetated habitats or uncultivated land; Machlis et al. 1997, Alberti 2005). While pollinator diversity declines in dense urban areas (i.e. densely built-up areas with more than 50% impervious surface and only small green habitats), moderate levels of urbanization (i.e. city margins with large green habitats) may sustain even higher bee–pollinator diversity than modern agricultural landscapes (Lanner et al. 2020, Wenzel et al. 2020).

At the local scale, the availability of food and nesting resources determines wild bee–pollinator abundance and diversity (Ahrné et al. 2009, Blackmore and Goulson 2014). Highly diverse and abundant bee communities have been found in urban habitats characterized by abundant and diverse (both wild and ornamental) flowering resources, as well as large patches of green areas offering a diversity of nesting sites (Fründ et al. 2010, Hennig and Ghazoul 2012, Gunnarsson and Federsel 2014, Lanner et al. 2020, Wenzel et al. 2020). A reduction in green area size or flowering resources, as well as a decline in connectivity between such habitat patches, resulted in species loss of both plants and pollinators (Collinge 1996, Alberti 2005, Andrieu et al. 2009, Wenzel et al. 2020). Fruit and seed set of plants decreased accordingly, demonstrating direct detrimental effects of urbanization on the ecosystem service pollination (Wenzel et al. 2020).

To date, few studies have attempted to disentangle the relative impact of landscape features (i.e. percentage of green area) and local conditions (i.e. food and nesting site availability) on pollination in urban environments (Verboven et al. 2014, Quistberg et al. 2016). The little evidence we have indicates that pollinator-friendly local conditions may outweigh or at least counter-balance the negative landscape-scale effects of urbanization (Wenzel et al. 2020). In other words, maintaining even small green habitat patches with diverse and abundant flowering resources in the urban matrix seems to be an effective and low cost key conservation measure.

In this study, we investigate how local conditions (e.g. resource availability, resource diversity) and the landscape context (proportions of sealed and green areas) in urban environments affect plant–pollinator interactions. We chose two common, co-flowering European plant species, *Trifolium repens* L. (white clover) and *Trifolium pratense* L. (red clover), to investigate how common wildflowers contribute to maintaining bee–pollinator diversity. We compare pollinator community composition, pollinator abundance and fruit set, in 21 green areas of different sizes in the city of Vienna (Austria). In particular, we hypothesize 1) that the two *Trifolium* species, differing in flower colour and size, attract distinct pollinator taxa, 2) that pollinator communities are more diverse in continuous urban green areas of larger size and 3) that visitation frequency of the pollinators is higher in continuous urban green areas of larger size (resulting in higher seed set in these areas) and increases with higher food resource availability and percentage of surrounding green area.

Material and methods

Unless specified otherwise, all statistical analyses were conducted using the software R ver. 3.5.3 (<www.r-project.org>). Functions are referred to in the following format: *function name*{*package name*}.

Study sites

Our study was conducted in the city of Vienna, Austria, in June and July 2018. We selected a total of 21 sites (Supporting information), each composed of mostly continuous vegetation, mainly grass. To investigate the effect of green area size on pollinator compositions and frequency, we studied three categories of sites: small patches (< 5000 m^2, n = 8), intermediate parks (10 000–250 000 m^2, n = 7) and large green areas (> 400 000 m^2, n = 6), referred to as 'study site categories' from here onwards. The percentage of green area in and around each site was further described (sections on 'Landscape context' below). Site locations were selected to achieve a balanced design of sites located close to the city centre, with higher percentage of sealed surfaces and at the outskirts of the city (Fig. 1).

In each site, we selected a plot of 1 m^2 for pollinator observations, including at least eight blooming inflorescences of both *Trifolium repens* and *T. pratense*. We recorded the respective number of anthetic and withering inflorescences of both study species for further analyses on pollinator visitation frequency and seed set. We recorded the GPS coordinates of the observation plots on a smartphone using the application 'My GPS coordinates' (TappiApps for Android ver. 1.74 released February 2017).

Study species

Trifolium repens and *T. pratense* (Fabaceae) are two perennial, self-incompatible species that are frequently encountered on lawns in urban and rural areas (Hegi et al. 1975). Both species are pollinated by bees, particularly nectar collecting honeybees and bumblebees (Hegi et al. 1975, Free 1993). Like other Fabaceae, *Trifolium* moreover offers pollen with a high

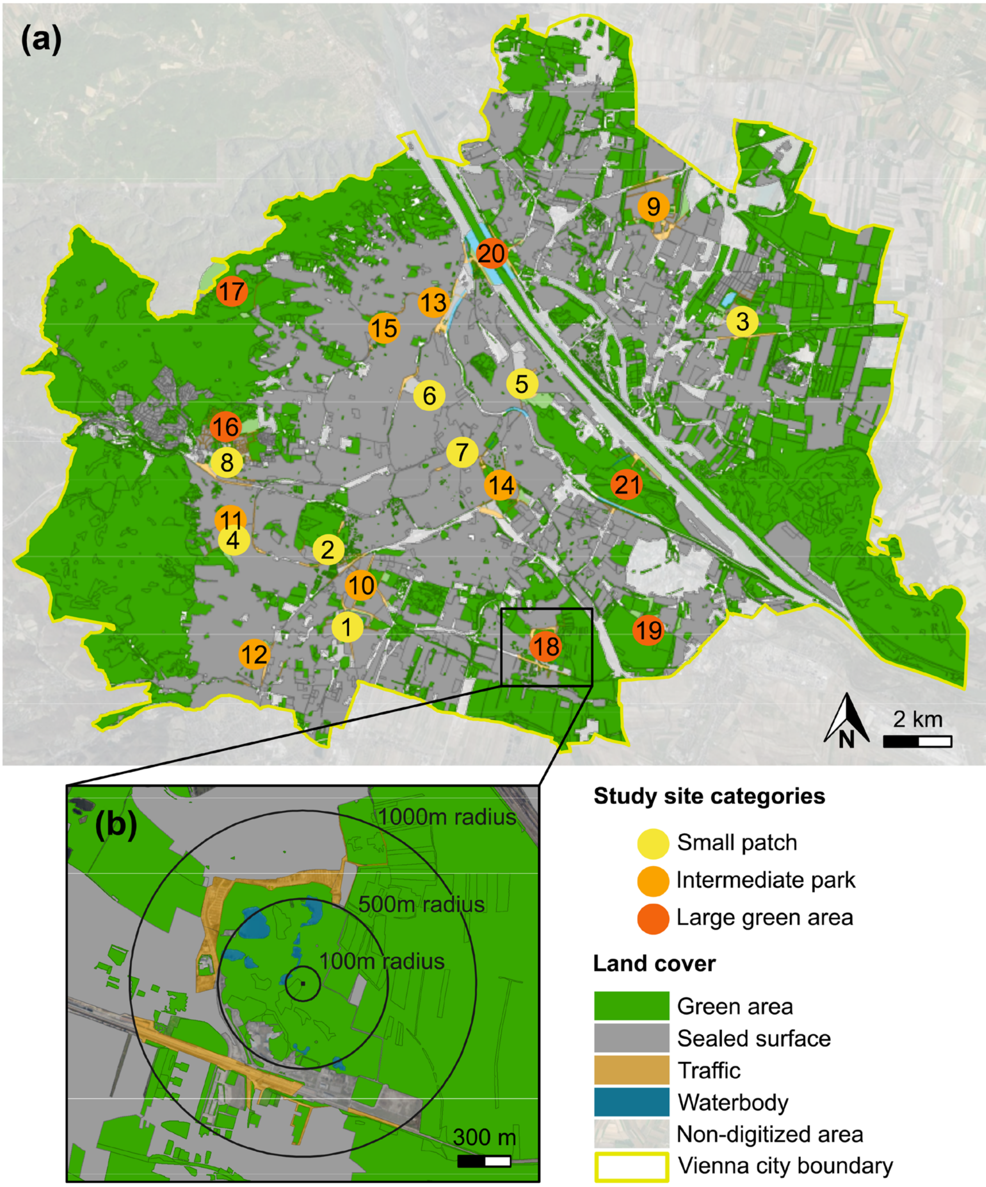

Figure 1. Distribution of the study sites in the city of Vienna and assessment of the landscape context. (a) Map of Vienna showing the distribution of the 21 study sites. (b) Exemplary plot (number 9) and the surrounding landscape context over radii of 100, 500 and 1000 m. The main types of land cover are indicated in the legend.

protein content, which is collected especially by social bees to feed their offspring/larvae (Free 1993). The chosen study species have a long flowering period (approximately May–September/October) and hence provide food also for wild bees emerging later in the season (Free 1993, Goulson et al. 2005). Both *Trifolium* species have similar globular inflorescences composed of densely packed small papillionaceous flowers. In the genus *Trifolium*, pollination happens via a simple 'foldaway' mechanism (one of the four pollination-mechanisms described for Fabaceae by F. Delpino (1868)): a pollinating insect lands on the keel and holds on to the connected wings. The keel is pushed down while the flag opens to the top. During this movement, the anthers and the stigma become exposed and touch the pollinator (Hegi et al. 1975). The flowers of *T. repens* are whitish with short (3 mm) corolla tubes whereas the flowers of *T. pratense* are pinkish with longer (8–10 mm) corolla tubes (Hegi et al. 1975, Free 1993, Fischer et al. 2008).

Pollinator observations and collection

We conducted pollinator observations between 7 June and 17 July 2018. Each plot was visited on a single day between 10 a.m. and 04 p.m. under good weather conditions (sunny, no permanent cloud cover, minimum temperature 18°C). Once per hour, we additionally recorded cloud cover (proportion of sky covered by clouds, estimated in eighths). We alternated observations between study site categories to minimize effects of phenological turnover in pollinator community composition on our analyses of the impact of green area size (Supporting information). Please note that visitation of each site only once does not allow for assessing potential differences in pollinator assemblages between sampling days, but was our method of choice in order to provide comparable and accurate data despite frequent and unpredictable mowing.

During observations, of both *Trifolium* species at the same time, one or two observers sat near the plot and recorded pollinators for 15 min per hour, for six hours, resulting in a total observation time of 1½ h per plot. We recorded each insect that visited an inflorescence and counted the number of inflorescences it visited in the plot. Based on the insects' behaviour, we differentiated visitors, which only landed or crawled on the inflorescence, from pollinators, probing flowers by inserting their head into the corolla and thereby contacting the reproductive parts of the flowers. Subsequently, for the statistical analyses we only looked at the potential pollinators. Pollinators showed high flower constancy so that we did not count shifts between the two *Trifolium* species. We took pictures of all visitors and pollinators and classified them into morpho-species for later identification.

To identify pollinator morpho-species, we added a 15-min collection round after each 15-min observation round. In each observation plot, we collected a maximum of five specimens per pollinator morpho-species. We caught the insects in small plastic tubes while they probed *Trifolium* flowers and immediately put them on ice in an insulation box. At the end of each observation day, we froze pollinators at −18°C in the laboratory of the Department of Botany and Biodiversity Research (University of Vienna), and later mounted them for identification. We identified bumblebees using Gokcezade et al. (2017) and other bees with the help of specialists (Florian Etl and Martin Streinzer). When possible, we identified the pollinators to species level, otherwise to genus level or above. We chose to circumscribe pollinator taxa broadly (i.e. *Bombus* cf *lapidarius*) since we would have had to capture and kill all visiting insects for reliable identification. Given the decline of many insect taxa in urban environments, and the nature conservation aspect of our work, we refrained from the collection of all insects.

Pollinator frequency and total visitation frequency of the two *Trifolium* species

For each *Trifolium* species, we calculated pollinator frequency as the number of visits of a potential pollinator taxon per inflorescence per hour. We further calculated the total visitation frequency for each *Trifolium* species as the total number of pollinating insects visiting each species per inflorescence per hour. From here onwards, we use the term 'pollinator frequency' when referring to single insect taxa, and 'total visitation frequency' when comparing frequencies summed across all pollinators for each *Trifolium* species.

Assessing differences within the pollinator community

We divided all observed pollinators into six taxonomic groups: *Apis mellifera*, *Bombus* cf. *lapidarius*, *Bombus* cf. *pascuorum*, *Bombus* sp., 'other Apoidea' and 'other insects'. The group '*Bombus* sp.' included different *Bombus* species observed in lower abundances (e.g. *B.* cf. *hortorum*, *B.* cf. *terrestris*, *B.* cf. *humilis*) and may have also included additional individuals of *B.* cf. *pascuorum* and *B.* cf. *lapidarius*, which could not be identified with certainty, as well as other or unidentified individuals of the genus *Bombus*. The group 'other Apoidea' includes individuals of the superfamily Apoidea (e.g. genera: *Hylaeus*, *Andrena*) or individuals of the family Halictidae (e.g. genera: *Halictus*, *Lasioglossum*). The group 'other insects' includes infrequent insect pollinators, including Lepidoptera, Coleoptera and Syrphidae as well as other unidentified Hymenoptera. To assess differences in pollinator frequencies, we conducted a perMANOVA using *adonis*{*vegan*} (Oksanen and Stevens 2019). We tested for the influence of *Trifolium* species, study site categories and the interaction of these two variables. We used a Wilcoxon–Mann–Whitney test with *wilcox.test*{*stats*} to examine significant differences. We visualized differences in pollinator frequencies for the two *Trifolium* species using principal component analyses (PCA) with *dudi.pca*{*ade4*} (Chessel and Dufour 2004).

Seed set

Our one-day pollinator observations only give a snapshot idea of potential differences in pollinator frequencies at each site and may be influenced by current conditions such as recent mowing or weather. Since each *Trifolium* plant produces many flowers per inflorescence and flowers for several days, we also assessed seed set to obtain a second measure of pollinator performance in the different sites. On the same day as when performing the pollinator observations, we harvested and dried a total of three, at least ⅔ withered, inflorescences per *Trifolium* species and site. Whenever enough withered inflorescences where available, we took them from the 1-m^2 plot, otherwise collected them in the immediate surrounding. We randomly chose 10 withered flowers per inflorescence (n = 630 flowers per species) and removed the seeds from the ovaries by gently grinding each withered flower between the fingers. We then examined them under a stereomicroscope to differentiate aborted from developing seeds, and calculated the average number of initiated seeds per flower. We further counted the number of flowers per inflorescence and extrapolated the averaged seed set to the inflorescence level. This way we obtained an averaged seed set per inflorescence for the respective plot.

Local scale: recording flower resource availability and diversity

To assess local flower resource availability, we recorded the number of anthetic and withered *Trifolium* inflorescences of both study species in each observation plot (Supporting information). To further characterize flowering resources in the immediate surroundings of each observation plot, we recorded flower diversity along 5-m transects starting at the four edges of each plot and extending in the four cardinal directions. We included all plant species flowering on the day of observations and potentially offering pollinator rewards, thereby excluding wind-pollinated graminoids. We counted all inflorescences in a 10 cm wide strip along these transects. From these data, we calculated the Shannon diversity index (Shannon and Weaver 1949) of each plot as an estimate of resource diversity (Supporting information).

Landscape context: recording the percentage of surrounding green area

To quantify the urban aspects of the landscape context, we used the OpenStreetMap data with land-use information for Vienna (GeofabrikGmbH and OpenStreetMap Contributors 2018, Stadt Wien 2014) as data basis in ArcGIS 10.5 (ESRI 2016). We loaded the GPS-points of our observation plots into the map. Around each observation plot, we conducted a buffer-analysis to characterize the relative amounts of different land cover types, using the geoprocessing tool 'Buffer'. We characterized the types of land cover in perimeters of 100, 500 and 1000 m around each observation plot (Fig. 1B). We distinguished green areas (vegetated surfaces like gardens, parks, grass areas along roads, sport courts) from other landcover types (i.e. sealed surface, traffic and waterbodies). We then calculated the percentage of green area in the given perimeter around each observation plot (Fig. 1B, Supporting information). All data files are in the projected coordinate system MGI_Austria_GK_M34.

Assessing the effect of the landscape context and resource availability

We used generalized linear models (GLM, *glm {stats}*) to assess the impact of local flower resource availability (Shannon diversity index of flowering plants, number of anthetic inflorescences of the respective *Trifolium* species in the plot), the percentage of green area surrounding observation plots, and study site category on the response variables 'number of visitors/day/plot' or 'seed set' of the respective *Trifolium* species per plot (four datasets: total visitation frequency of *T. repens* and *T. pratense*; seed set of *T. repens* and *T. pratense*; n = 21 per dataset). We also included cloud cover in the models on visitation frequency in order to rule out bias from weather conditions, and the number of withered *Trifolium* inflorescences in the models on seed set. Before model construction, we checked for collinearity between all explanatory variables specified above using pairwise scatterplots and correlation coefficients (Supporting information). The variables 'study site category' and the landscape-scale percentages of green area in 100 m and 500 m radii showed high correlation. We hence built three separate models for each of the four datasets: M100 included the resource variables, percentage of green area in radii of 100 m and cloud cover or number of withered *Trifolium* inflorescences; M500 included the resource variables, percentage of green area in radii of 500 m and cloud cover or number of withered *Trifolium* inflorescences; M1000 included the resource variables, study site category, percentage of green area in radii of 1000 m and cloud cover or number of withered *Trifolium* inflorescences. All four data sets showed overdispersion, so we chose GLMs with a quasi-Poisson distribution.

We first constructed full models (including all variables specified above) and compared their fit to models of reduced complexity with single variables removed (*drop1 {stats}*). We selected the models including the remaining significant explanatory variable(s) and having smaller residual deviance. We validated model fit by calculating Pearson residuals (scaled for overdispersion) and plotting Pearson residuals against the fitted values and all explanatory variables included in the initial models (Supporting information, Zuur et al. 2009). Although not significant, we included percentage of green area in 100 m radius and number of withered *T. pratense* inflorescences in the model of seed set for *T. pratense* since there were clear patterns in plots of residuals and the inclusion of these terms reduced residual deviance of the model.

Results

Pollinator taxa composition of the two *Trifolium* species in relation to study site category

Apis mellifera, *Bombus* cf. *lapidarius* and *Bombus* cf. *pascuorum* were the main pollinators in the studied plots (Fig. 2).

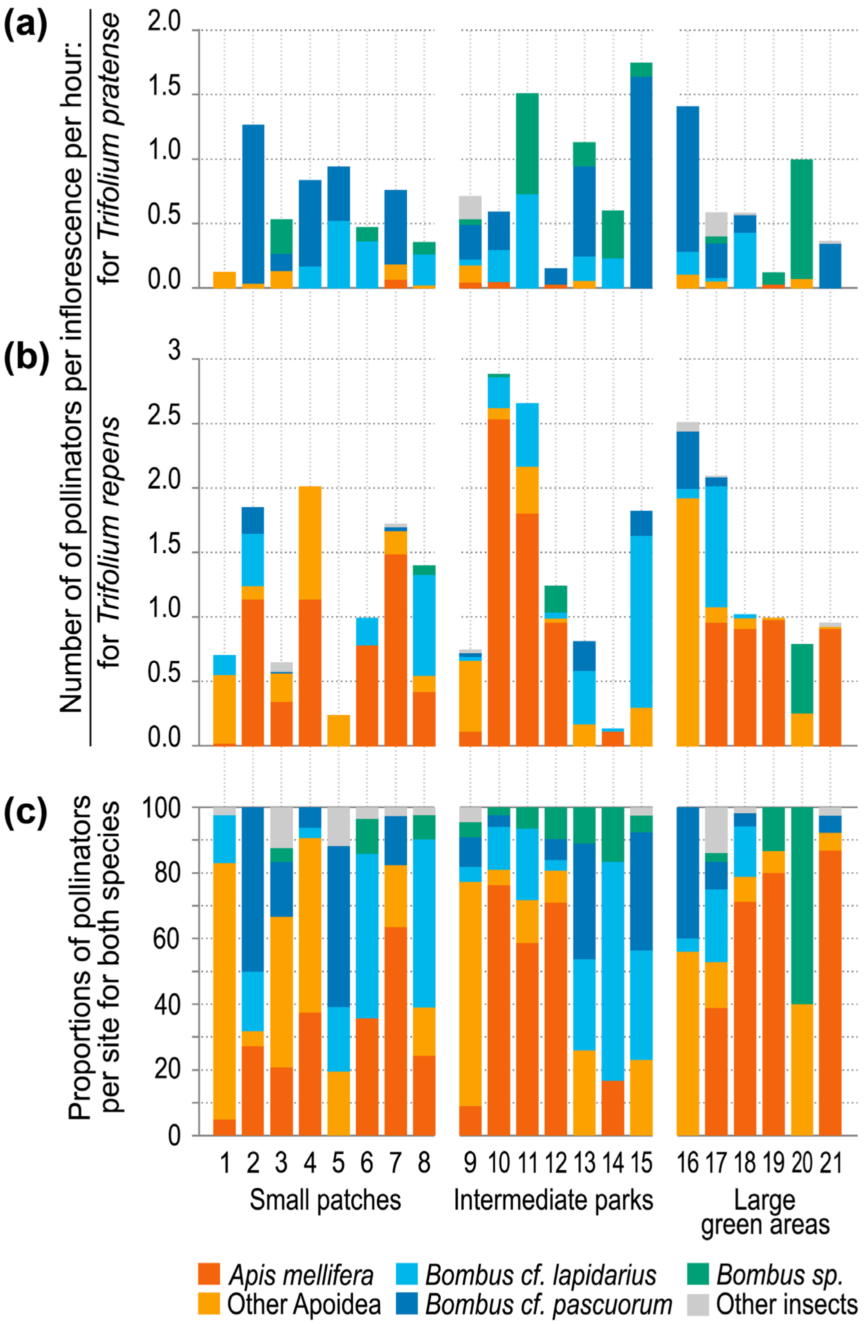

Figure 2. Pollinator diversity and visitation frequency in green areas of different sizes in the city of Vienna. (a) Number of pollinators per inflorescence per hour for *Trifolium repens* in each study site, (b) number of pollinators per inflorescence per hour for *Trifolium pratense* in each study site, (c) proportions of pollinators pooled for both *Trifolium* species in each study site. Numbers below the bars represent each study site; study sites are ordered per increasing size (Supporting information).

We also observed other wild bee species, additional *Bombus* species and, in low abundances, Lepidoptera, Coleoptera and Syrphidae (Fig. 2). *Apis mellifera* was the most frequent pollinator throughout the whole study (1105 visits on *Trifolium repens* inflorescences and 10 visits on *T. pratense* inflorescences), followed by wild bee species ('other Apoidea'; 352 visits on *T. repens* inflorescences and 40 visits on *T. pratense* inflorescences).

Pollinator taxa composition (measured through pollinator frequency) differed significantly between the two *Trifolium* species (perMANOVA: $F = 10.2$, $r^2 = 0.21$, $p < 0.01$, Fig. 2a–b, 3). The small-flowered *Trifolium repens* was visited significantly more often by *Apis mellifera* ($p < 0.01$) and 'other Apoidea' ($p < 0.01$) than *T. pratense*. With its longer corolla tubes, *Trifolium pratense* was visited significantly more often by larger pollinators such as *Bombus* cf. *pascuorum*

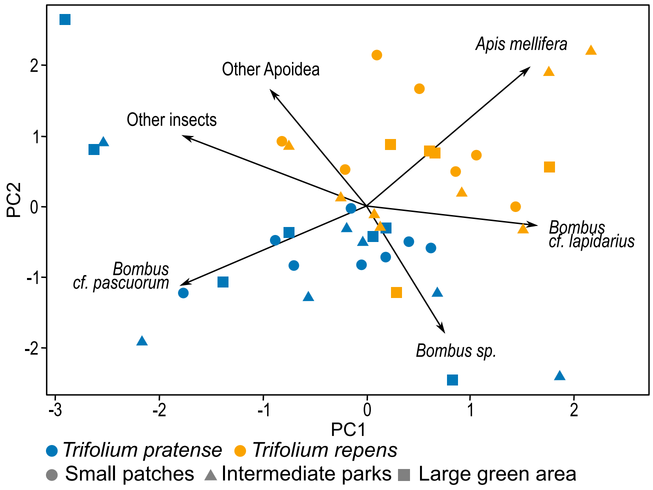

Figure 3. Principal component analysis showing a difference in proportions of pollinators for the two *Trifolium* species, but not among study site categories.

($p < 0.01$) and *Bombus* sp. ($p = 0.02$). *Bombus* cf. *lapidarius* ($p = 0.63$) and the group 'other insects' ($p = 0.53$) were equally frequent visitors of both *Trifolium* species (Fig. 2a–b). There was no significant difference in pollinator community across the three study site categories ('small patch', 'intermediate park', 'large green area'; $F = 0.7$, $r^2 = 0.03$, $p = 0.77$) or interaction between *Trifolium* species and study site category ($F = 0.14$, $r^2 = 0.01$, $p = 0.99$, Fig. 3).

Effect of resource availability and percentage of green area on visitor numbers and seed set

The total number of flower visitors per day per plot to either of the two *Trifolium* species increased significantly with higher availability of flowering inflorescences of the respective *Trifolium* species (food resource, Fig. 4a–b; for both *Trifolium* species, the best-fit models only included the number of anthetic inflorescences: *T. repens*: t-value 2.61, $p = 0.017$, residual deviance 606.38; *T. pratense*: t-value 3.76, $p = 0.001$, residual deviance 234.91, see the Supporting information for models including all explanatory variables, and for validation of final model). Visitor number was not significantly influenced by local flower resource diversity, study site category or percentage of surrounding green area (Supporting information). Temporary weather conditions (cloud cover) did not impact the number of flower visitors either and hence did not bias our results (Supporting information).

Seed set of *Trifolium repens* was not significantly influenced by any of the tested environmental variables (e.g. M1000: local flower resource diversity: t-value −0.202, $p = 0.843$; withered *T. repens*: t-value 0.665, $p = 0.517$; green area size: t-value −0.259, $p = 0.799$; Supporting information for all models and for model validation, Fig. 4c). Seed set of *T. pratense* showed a significant increase with local flower resource diversity (Fig. 4d, final model including flower diversity index, number of withered *T. pratense* inflorescences and percentage of green area in the 100 m radius buffer: t-value 2.741, $p = 0.014$, residual deviance 54.796, Supporting information for model validation).

Discussion

Our study demonstrates that common wildflowers such as red and white clover contribute to maintaining distinct pollinator communities even in small green habitat patches in urban environments. High local availability of red and white clover significantly increased total visitation frequency for both *Trifolium* species, while we did not find an effect of local floral diversity, the size of the study sites or the larger landscape context (i.e. percentage of surrounding green area up to 1000 m around from the study plots). In *T. pratense*, we found a significant increase in seed set with higher local flowering plant diversity. Our results are hence in line with recent findings highlighting the importance of abundant and diverse local floral food resources for pollinators in urban environments (Wenzel et al. 2020).

Different proportions of pollinator taxa on two co-flowering clover species

As expected, proportions of pollinator taxa differed significantly between *Trifolium repens* and *T. pratense*. Co-flowering plants may compete for flower visitors on the one hand, but resource competition among pollinators may also lead to pollinators preferentially visiting unexploited resources (Hennig and Ghazoul 2011, Hintermeier and Hintermeier 2017). The different proportions of pollinator taxa in our study may follow this pattern and are likely related to differences in floral size and reward accessibility. In the small flowers of *T. repens*, nectar and pollen are accessible to both short- and long-tongued pollinators. In our study, *T. repens* was preferentially visited by short-tongued pollinators (*Apis mellifera*, tongue-length: approx. 6–7 mm; Balfour et al. 2013, and different small wild bees). In the large-flowered *T. pratense*, short-tongued pollinators may not easily exploit floral rewards, leaving larger amounts of nectar and pollen to long-tongued pollinators. Accordingly, we observed long-tongued *Bombus* cf. *pascuorum* (tongue-length: 8.5 ± 0.6; Goulson et al. 2005) and *Bombus* sp. as more frequent visitors on *T. pratense* inflorescences, where foraging is likely more rewarding (Corbet et al. 1991). *Bombus* cf. *lapidarius*, which has an intermediate tongue-length (7.7 ± 0.4; Goulson et al. 2005), likely competes both with short-tongued and long-tongued bees and we observed it to forage on both *Trifolium* species equally often. Our study does not reveal, however, whether other traits (i.e. amino acid composition of nectar sugars, protein content of pollen) further influenced pollinator taxa composition (Hanley et al. 2008).

In recent years, an increase of generalist pollinators (such as honeybees), socially living insects and cavity nesters in urban environments has been reported (reviewed by Wenzel et al. 2020). As in previous studies on pollination in *Trifolium* in urban areas (Verboven et al. 2014), the main pollinator in

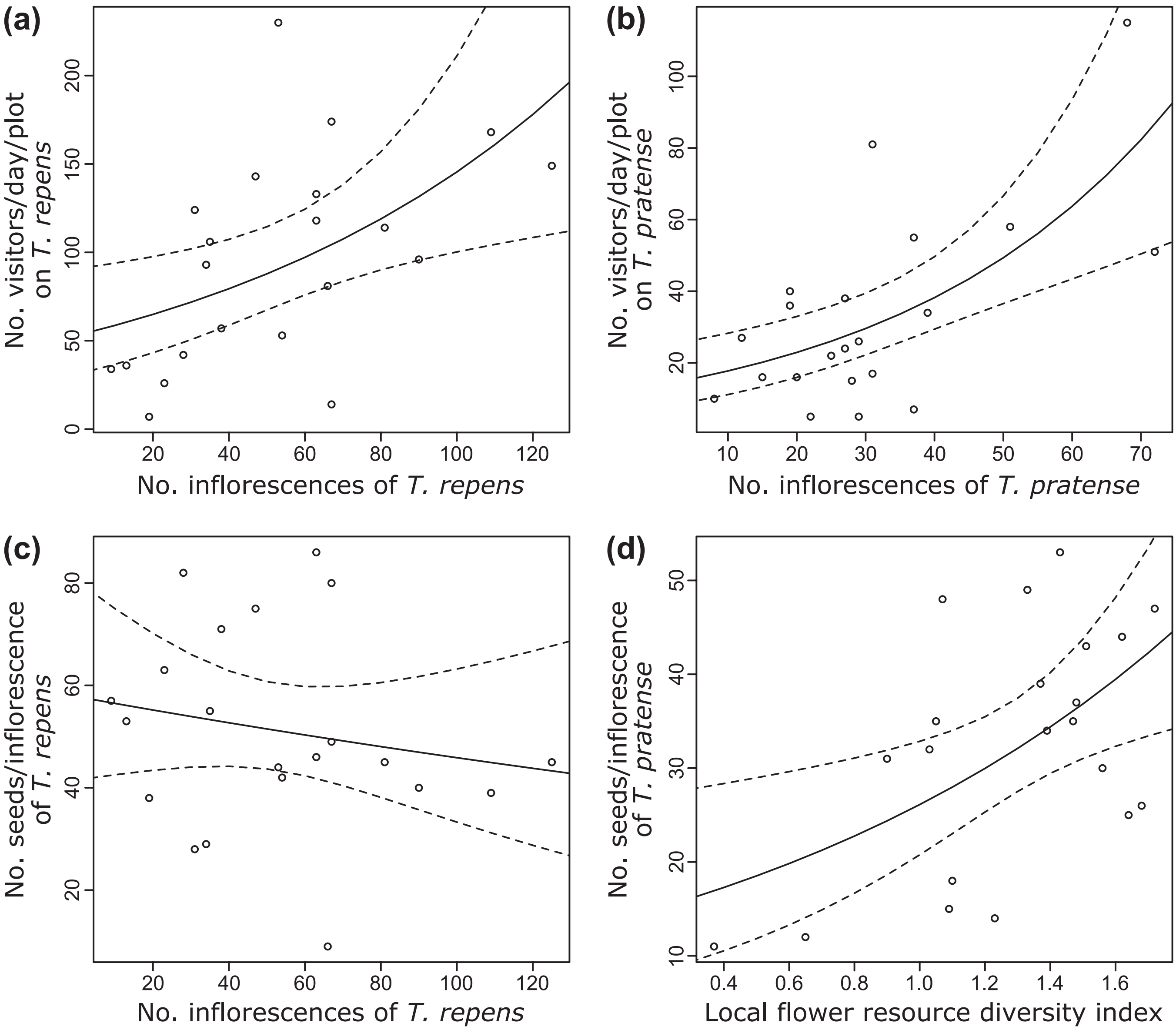

Figure 4. Local food resource availability significantly increases number of flower visitors in *T. repens* and *T. pratense* and seed set in *T. pratense*; fitted quasi-Poisson GLM curves (solid lines) with 95% confidence curves (dotted lines). (a) Number of flower visitors per plot per day increases significantly with the number of flowering *T. repens* inflorescences. (b) Number of flower visitors per plot per day increases significantly with the number of flowering *T. pratense* inflorescences. (c) Seed set was unaffected by local resource availability in *T. repens*; we plotted the relation with the number of flowering *T. repens* inflorescences since this variable had highest F-values when assessing model fit (Supporting information). (d) Seed set in *T. pratense* increased significantly with high local flower resource diversity.

our study also was the honeybee *Apis mellifera*. The trend in urban beekeeping very likely plays a prominent, and possibly negative role here (Ropars et al. 2019, Theodorou et al. 2020). Recent investigations have shown that high abundance of honeybee colonies negatively impact wild pollinators in urban environments (Ropars et al. 2019). With about 5000 honeybee colonies, bee hive abundance in Vienna is significantly higher than in rural areas in central Europe (Götzl and Sedy 2015). Since honeybees visit a large diversity of plant species, including non-native plants, they may easily outcompete more specialized flower visitors (Breed 2010, Bates et al. 2011, Threlfall et al. 2015, Koyama et al. 2018, Wenzel et al. 2020). Particularly in resource-poor urban areas, oligolectic wild bee species (specialized on a narrow niche of flowering resources), may be suppressed by polylectic foragers like honeybees (Kearns and Inouye 1997). Further, wild bees have been shown to avoid competition with honeybees by temporally or spatially adapting their foraging habits, or shifting to alternative floral resources (Zurbuchen and Müller 2012). The high abundance of honeybees on *T. repens* may thus also have impacted the distribution and foraging behaviour of wild bee species in our study. To further investigate effects of resource competition of high densities of honeybees on wild bees in urban environments, future studies may specifically select study sites differing in the density of surrounding honeybee hives (Wojcik et al. 2018, Ropars et al. 2019).

Local resource availability is more important than green area size

Against expectations, pollinator assemblages were not significantly more diverse in green areas of larger size. Also, pollinator frequency did not increase with larger study site categories (a measure of immediately connected green space) or with the percentage of green areas surrounding the study plots. This is in contrast to other studies reporting negative relationships between pollinator frequency and green area size in clover (Verboven et al. 2014). Overall, however, our results support a pattern also reported by other authors, specifically that local scale variables (i.e. local food resource availability) are more important predictors of pollinator frequency than landscape scale features (Gunnarsson and Federsel 2014, Verboven et al. 2014, Wenzel et al. 2020). We agree with those authors, however, that this pattern may be caused by strong habitat heterogeneity within study sites, rendering comparisons difficult (Wenzel et al. 2020). Furthermore, our estimation of surrounding green area size relies on the assumption that high percentages of green areas indicate a higher diversity of natural landscape, rich in food and nesting resources. However, it does not incorporate potential qualitative differences of green areas (i.e. structurally diverse gardens versus monotonous football pitch). Furthermore, even an urban area with high percentages of sealed surfaces may feature e.g. roof-top terraces with rich and abundant flowering resources, providing suitable habitats for cavity-nesting bee pollinators. Due to the complexity of urban environments, such large-scale estimations of landscape quality are hence likely less reliable predictors of pollination than local conditions (Wenzel et al. 2020).

In our study, as in others, the local availability of food resources directly influenced total pollination frequency of both *Trifolium* species (Hegland 2014, Theodorou et al. 2017). Studies in Germany, Belgium and California, USA, for example, found similar positive effects of high floral display on the activity and attraction of bee pollinators (Ebeling et al. 2008, Wojcik and McBride 2012, Verboven et al. 2014). Importantly, such effects also are scale-dependent, and positive relationships between floral density and pollinator visitation rate at the immediate scale (2.5 m radius) may turn into negative or neutral relationships already at a radius of more than 2.5 m (Hegland 2014). Further, besides diverse and abundant food resources (Beriatos and Brebbia 2011, Diaz-Forero et al. 2013), bees require sites with diverse nesting opportunities (e.g. hedges, gardens, gravel pits, stonewalls; Verboven et al. 2014, Hintermeier and Hintermeier 2017). In this context, monotonous lawns pose challenges to pollinators, because they provide poor food resources and make orientation towards good foraging and nesting patches difficult (Tommasi et al. 2004). To date, the extent to which such habitat properties affect bee species differently remains unclear. Larger bee species, for example, are expected to more easily navigate between isolated feeding patches than smaller species with smaller home ranges (Wenzel et al. 2020). On the other hand, larger pollinators require higher food resources and may thus be negatively impacted by small habitat patches with limited numbers of flowers (Wenzel et al. 2020). In our study, we found both larger (e.g. *Bombus*, *Apis*) and smaller (e.g. small wild bees in the families Halictidae and Andrenidae) bee pollinators across green areas of variable sizes, hence not indicating a relationship between pollinator size and green area size.

In summary, our results underline the high value of even small vegetated strips in urban environments as providing food resources for a variety of bee pollinators, and likely serving as stepping stones between habitats (Collinge 1996, Steffan-Dewenter 2003, Hennig and Ghazoul 2011). We propose that clover may represent a particularly important local food resource in the urban context given its frequent occurrence, fast regrowth after mowing, long flowering period and high-quality nectar and pollen food resource for (wild) bees (Roulston et al. 2000, Goulson et al. 2005, Larson et al. 2014). In the light of urban densification and continued increase in impervious surfaces, implications for suitable management strategies for the preservation of diverse pollinator communities may be drawn from these results and other studies. Even small, isolated patches of common wildflowers (Blackmore and Goulson 2014), contributing to the heterogeneity of the urban matrix, increase bee–pollinator diversity. It is crucial to conserve or establish continuous and diverse flower patches to provide sufficient resources for wild bees, particularly considering the over-abundance of honeybees in cities (Tommasi et al. 2004). Given the marked decline in native plant species, particularly long-tongued (bumble) bees with short foraging ranges and/or late emergence are negatively impacted (Goulson et al. 2005, Carvell et al. 2006, Dupont et al. 2011). Hence, in order to support both short-tongued and rare, long-tongued (bumble)bees, green areas with different autochthonous plant species (i.e. flowers of different sizes and shapes) and heterogeneity in flowering time throughout the season are required (Dupont et al. 2011, Hicks et al. 2016). Simple changes in urban green area management (i.e. reduced mowing intensity, following the 'lazy lawnmower' approach, Wenzel et al. 2020) are likely suitable to alleviate (some) negative effects of increasing urbanization.

Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.z34tmpgcf> (Kanduth et al. 2020).

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Author contributions

Laura Kanduth: Data curation (lead); Formal analysis (equal); Investigation (lead); Writing – original draft (lead). **Marion Chartier**: Conceptualization (lead); Formal analysis (supporting); Methodology (supporting); Supervision (equal); Validation (supporting); Visualization (lead); Writing – original draft (supporting); Writing – review and editing (supporting). **Jürg Schoenenberger**: Supervision (supporting); Writing – review and editing (supporting). **Agnes S. Dellinger**: Conceptualization (lead); Formal analysis (equal); Methodology (equal); Project administration (lead); Supervision (equal); Validation (lead); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (lead).

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