Non-native plant species integrate well into plant-pollinator networks in a diverse man-made flowering plant community

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Abstract

Urban green areas offer diverse flower resources for pollinators. Yet, the role of non-native plant species in local plant-pollinator networks is understudied. We explored the effects of plant origin, nationwide distribution, flower color and type on flower visitation by wild bees and honey bees as well as the structure of a plant-pollinator network in a botanical garden in Hungary. Honey bee preferred North American plants over Europeans; it had the highest degree and topological centrality value. The network had similar compactness with its simulated removal from the network model. The species richness and abundance of flower-visiting wild bees did not differ among the plants of different origins and flower color and type. Plant species of different origin, nationwide distribution, and flower color and type had the highest number of direct and indirect links. Our results suggest that non-native plant species can integrate well in diverse botanical gardens and wild bees can adopt these new foraging resources.

Keywords Flower color · Flower type · Honey bee · Plant origin · Wild bees

Introduction

Biodiversity has shown a steep decline worldwide (IPBES 2019). Recently, several studies have suggested that terrestrial insect populations have decreased in both managed and protected areas over the last decades (Hallmann et al. 2017; Sánchez-Bayo and Wyckhuys 2019), and almost 10% decline is expected every ten years (van Klink et al. 2020). Besides general land-use conversion and intensive agricultural management, including usage of agrochemicals, urbanization is one of the major drivers behind insect population losses (van Klink et al. 2020). The rapid expansion of urban areas decreases the area of semi-natural habitats and creates a new environment, with often uncertain effects on wildlife (Wenzel et al. 2020).

Pollinator species, including wild bees (Hymenoptera: Apiformes), are one of the most threatened groups of insects (IPBES 2016; Sánchez-Bayo and Wyckhuys 2019). Nine percent of the European bee species are threatened, and populations are declining for 37% of the species (Nieto et al. 2014), while fruit production of 87.5% of flowering plant species depends on animal pollination to some extent (Ollerton et al. 2011). Wild bee decline is associated mostly with land-use change, intensive agricultural habitat management, and the consequent loss of floral and nesting resources in the landscape (Kennedy et al. 2013). However, urban and suburban habitats might be beneficial for wild bees if they can provide suitable nesting and foraging resources (Baldock et al. 2015, 2019; Wenzel et al. 2020). Urban green areas such as parks, private gardens, botanical gardens, or even balconies may offer a wide variety of flower resources for pollinators and serve as important refuges for wild bees (Fortel et al. 2014; Choate et al. 2018). The higher number of plant species may also lead to more complex and specialized plant-pollinator interactions than non-urban habitats (Baldock et al. 2015). In urban settings, the alien, ornamental species might integrate well into the pollination networks (Marquardt et al. 2021), where most pollinators might tend to show generalist tendencies (Lowenstein et al. 2019). However, the value of urban and suburban green areas in pollinator conservation significantly relies on how the different plant species can be utilized

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by the local pollinators (Larson et al. 2014; MacIvor et al. 2015; Masierowska et al. 2018).

The flora of gardens and parks is not merely composed of native, common flowering herb, shrub, and tree species. New, introduced plant species become available in the pollinators' diet through wide-scale international trade involving new garden or ornamental plants (Smart et al. 2006). These planted flowers are attractive to the human eyes; however, they might vary greatly in their level of attractiveness to insects (Garbuzov and Ratnieks 2014). Some planted ornamental or non-native, exotic plant species might be easily pollinated by local pollinators, while others might appear less attractive due to their flower morphology and phenology. The suitability of different plant species in such human-made environments is an essential question in pollinator conservation and is increasingly studied (Gunnarsson and Federsel 2014; Banaszak-Cibicka et al. 2018; Choate et al. 2018; Sikora et al. 2020; Tasker et al. 2020). Recent studies have found either lower (Frankie et al. 2005; for diversity, Rollings and Goulson 2019) or similar (Wenzel et al. 2020; for abundance, Rollings and Goulson 2019) flower visitation by bees on non-native, exotic ornamental plant species in urban green areas compared to native species. Whereas there is evidence on the importance of native plant species to maintain pollinator communities in urban areas (Pardee and Philpott 2014), the role of the introduced plant species in local plant-pollinator networks is still less known (but see Lowenstein et al. 2019).

The topology of pollinator networks is determined by the morphology and phenology of all the flowering plants and pollinators present. Pollinators can prefer certain flowers based on their type, morphology, or even color (Sikora and Kelm 2012; Reverté et al. 2016; Bauer et al. 2017; Rollings and Goulson 2019; Wenzel et al. 2020). They can also show different resource exploitation strategies: both generalists such as western honey bee (*Apis mellifera*) and rather specialist wild bee species can be present (Hung et al. 2018; Kovács-Hostyánszki et al. 2019). Studying plant and pollinator trait filtering is vital to understanding plant-pollinator interactions and flower visitation networks in urban and suburban green areas (Harrison and Winfree 2015; Sikora et al. 2020).

Our study aimed to explore the structure of a plant-pollinator network in a man-made environment with a diverse set of native and non-native plant species. We conducted our research in a botanical garden that presented an excellent opportunity for comparative analysis on plant-pollinator relationships. Besides native plants, a high number of exotic species represented a broad spectrum of traits. First, we explored whether flower visitation by the honey bee and wild bees on plant species can be explained by the plants' broad geographical origin, nationwide distribution, and flower traits. Second, we analyzed how the importance and specialization of plants and pollinators in this flower visitation network relate to these species-specific plant traits. Third, we identified the most central sets of plant and pollinator species in the network. We hypothesized that alien plant species integrate into local pollinator networks by interacting with rather specialist wild bee species, not only with generalist pollinators such as the honey bee.

Material and methods

Study site

We assessed flower visitation of plant species in the National Botanical Garden in the city of Vácrátót, near Budapest, Hungary (https://botanikuskert.hu). Its total area is about 27 hectares, and it contains more than 3000 different plant species, including herbs, shrubs, trees, and ornamental plants of different origins. Flowering plant species were chosen randomly from 19 April to 25 July, observing 13 species in April, the highest number of species observed during May (59), and a further 30 species in June and 28 in July. Our sampling covered the overall flowering period in the garden, and we observed each plant species at its peak flowering. The observed plant species were chosen spatially randomly, distributed across the whole garden in various habitat types (open meadows, flower beds, shrubby areas, and forest-like habitat patches) but chosen only in the open-air areas (i.e., no observations were made in the greenhouses). Although, to sample independent bee communities would require spatial separation of hundreds of meters (in the case of wild bees) to several kilometers (in the case of honeybees), we made efforts to make observations from the different plant species as independent as possible within the botanical garden. They were not grouped spatially according to the native region or according to phylogeny in the garden.

Bee sampling

To assess flower visitation of different plant species, we conducted a direct observation of blooming plants during spring and summer under favorable weather conditions (in sunny hours, at 20–30 °C, and up to moderate wind speed (< 15 km/h)). We observed bees on 130 flowering plant species in total, using each plant species in one census only. For each plant species, we chose 25 flower units and divided them into five groups. In the case of trees and shrubs (the species of which were often represented by only one individual in the garden) with multiple flowers, it mostly meant flower groups on one individual plant. In contrast, in herb species with individual flowers, we chose groups of flowering individuals next to each other. We observed each group for 3 min, with a total of fifteen-minute censuses, and summed the observations at plant species level. Obser-

vations were made between 9.30 and 17.00, and plant species were observed in a random order over the course of a day. Honey bee and some other common species (e.g., *Bombus* spp.) were identified in the field, while all other wild bees were collected by hand-netting and preserved in ethyl-alcohol until identification at species level was performed. Based on the flower visitation data, we calculated the number of honey bee visits, the number of wild bee visits, and the number of visiting wild bee species for each observed plant species. There were no honey bee colonies within or adjacent to the garden, but beekeeper activity was probable in the region (exact data are unknown).

Plant species characterization

We characterized all plant species included in the direct flower visitation observation according to their geographic origin, nationwide distribution, and flower color and type. *Origin*: We assigned all plant species to the continent of their native distribution (Europe, North America, or Asia). *Nationwide distribution*: we checked the distribution of each plant species within Hungary based on the grid-cell system of the Vascular Plants of Hungary Online Database to express the number of occurrences according to field observations and museum records (Bartha et al. 2020; https://floraatlasz.uni-sopron.hu/). *Flower color*: We grouped the plant species of various flower colors into four flower color categories: white, yellow, red (purple, pink, red), and blue (violet, blue). *Flower type* was classified after Kugler, applying his suggested ten main flower type categories (bell, brush, disk, flag, funnel, head, lip, pollen flower, stalk disk, trap) (Kugler 1970). We used the Biolflor (Klotz et al. 2002), Plants for A Future (PFAF 2021) and Plants of the World Online (POWO 2021) databases to guide flower characterization based on field observation data, and Plants of the World Online and Encyclopedia of Life (EOL 2021) databases to gather information about the plants' origin.

Based on the available flowering plant species in the study period, we sampled 75 European and 55 non-European species (29 Asian and 26 North American). Observations of the native and non-native plant species were distributed relatively evenly across the study months: 7:6 in April, 38:21 in May, 15:15 in June, 15:13 native and non-native plant species, respectively. Almost half of the species occurred in the wild in Hungary to some extent (60 species), while the other 70 species had no such occurrence data. We had quite an even distribution of plant species according to their flower color, sampling 26 species with blue, 35 with red, 25 with white, and 44 with yellow flowers. A quarter of the species had disk flowers (36), another quarter head flowers (33), while the other species were shared among the other flower morphol-

ogy categories: bell – 12, brush – 1, flag – 13, funnel – 6, lip – 22, pollen flower – 4, stalk disk – 2, trap – 1 species.

Analysis of flower visits

We analyzed the flower visits for each plant species using phylogenetic comparative methods (Garamszegi 2014). To analyze the number of honey bee and wild bee visits as well as wild bee species richness, we used Phylogenetic Generalized Least Squares (PGLS) models with normal distribution and identity link (Symonds and Blomberg 2014). For the honey bee presence, we used Phylogenetic Generalized Linear Models (PGLM) with binomial distribution and logit-link (Ives and Garland 2014). We used the following explanatory variables in all initial models: **Origin** – nominal variable (factor) with three levels: Europe (reference), Asia, and North America; **flower color** – nominal variable (factor) with three levels: blue (reference), red, white, yellow; **occurrence in Hungary** – binary nominal variable, whether the given plant species occurs wild in Hungary; **flower type** – nominal variable (factor) with 10 levels: bell (reference), brush, disk, flag, funnel, head, lip, pollen flower, stalk disk, trap. We parameterized the initial models and all their subsets as effects models with respect to the given reference categories (see above). We considered the effects of all explanatory variables to be additive; no interactions were defined in the models. We used an AIC-based approach (Faraway 2002) for model selection. We removed explanatory variables from our initial models one by one, and we chose the candidate model with the lowest AIC value. After the exclusion of a variable, we repeated this until we reached an optimal model fit. If there were multiple models with AIC scores differing by 2 or less, we chose the simplest one. The final binomial model describing honey bee presence contained only a single explanatory variable. As contrast calculations and post-hoc procedures were not available in the phylolm 2.6.2 R package (Ho and Ane 2014), we used a "cell means model" modelling approach to get direct point and confidence interval estimates for each group of the Origin variable. This can be achieved by reparametrizing the final model by removing the intercept term (Quinn and Keough 2002). We transformed these estimates (b_i) from the logit scale to the probability scale with the inverse-logit function: $e^{b_i}/\left(1 + e^{b_i}\right)$. For hypothesis testing, we used Wald-type p-values for the model coefficients available in the model's output (Ho and Ane 2014). The null hypothesis of the test claims that there is no difference between the reference and the given factor level (the coefficient is zero, $H_0 : \beta_i = 0$). We adjusted for multiple comparisons using the Holm–Bonferroni method (Holm 1979). We extracted phylogenetic relationships from Smith and Brown (2018) phylogenetic tree (version 0.1; Smith and Brown 2018). We removed 11 species (six Euro-

pean, three Asian, and two North American) from these analyses, as they were not included in the phylogenetic tree.

Network structure

We studied both the global and local properties of the plant-pollinator flower visitation network using various indices. We used the following global indices to describe the network: number of plant (N_P) and pollinator species (N_A), their ratio (N_P/N_A), and connectance (C):

$$C = \frac{L}{N_P \times N_A},$$

where L is the observed number of plant-pollinator interactions.

Since western honey bee often tends to dominate plant-pollinator networks (Hung et al. 2018; Kovács-Hostyánszki et al. 2019), we also recalculated the connectance without it, focusing only on wild bees as pollinators. Although we are aware that the actual network was formed under the effect of honey bee and its simulated removal from the network does not completely eliminate its effects on the plant-pollinator networks, we believe that such a simulated removal model has the potential to assess the network of wild bees and plants without the honey bee in a more focused manner.

To describe the importance of the species in the network, we used the number of their partners (degree) and the weighted topological importance index (WI2) with interaction ranges up to two (a measure of the species' direct and indirect relationships). To measure the interaction specialization of the species, we used the specialization index d', which describes the level of plant selectiveness for pollinators and pollinators' selectiveness for plants as departing from an expected visitation frequency based exclusively on species abundances.

We used R 4.0.3 (R Core Team 2020) and the ape 5.4-1 (Paradis and Schliep 2019), arm 1.11-2 (Gelman and Su 2020), bipartite 2.15 (Dormann et al. 2008, 2009), car 3.0-10 (Fox and Weisberg 2019), flextable 0.6.3 (Gohel 2021), ggplot2 3.3.3 (Wilke 2020), nlme 3.1-151 (Pinheiro et al. 2020), openxlsx 4.2.3 (Schauberger and Walker 2020),

phylolm 2.6.2 (Ho and Ane 2014), RcmdrMisc 2.7-1 (Fox 2020), readxl 1.3.1 (Wickham and Bryan 2019), and the reshape 1.4.4 (Wickham 2007) packages for analyzing and preparing the figures.

Keyplayers

We used the keyplayer approach (Parca et al. 2020) to find sets of species that can together reach the most species in the network. We looked for keyplayers based on reachability (m-reach). This method counts the number of reachable nodes by a set k of nodes in m links (here, two) or less. We looked for $N = 1 - 2$ keyplayer sets using the brute-force method (exact), and $N = 3 - 6$ sets were using the "greedy" algorithm of Pyntacle (Parca et al. 2020). The algorithm was independently started 20 times for each k. If the results differed, the set or sets with the highest coverage were chosen. We also recalculated the keyplayers without the honey bee, focusing only on the wild bees as pollinators.

Results

Flower visitation patterns

We observed 1363 individuals of 162 wild bee species (Table S1) and 411 honey bees on the 130 plant species in total (Table S2). When we analyzed the number of wild bee visits and species richness of flower-visiting wild bees, we could not find models with an appropriate fit using the aforementioned explanatory variables (see Table S3 for details). For the honey bee presence, we chose subset model number 10 (see Table S3 for more details), as it demonstrated the best fit based on the models' AIC values. This model had only one explanatory variable in it: origin. See Table 1 for the model estimates on logit scale, their standard errors (S.E.), the corresponding Wald statistics, and p-values. We discovered that plant species of North American origin had a significantly higher chance of being visited by honey bees ($p = 0.0414$) compared to Europeans (Table S4). According to our model, honey bees visited European species with a probability of 0.37 (95% C.I.: 0.26–0.48) compared to the 0.67 (95% C.I.: 0.46–0.84) probability of the North American species (Fig. 1; Table S4).

Table 1 Results of the final model describing honey bee presence with the single remaining explanatory variable: the origin of plants. The model had three parameters: the logit of presence on European plants (intercept), the difference in logit-presence between European and Asian, and the logit-presence between European and North American plants. The table shows the estimates on logit scale, their standard errors (S.E.), and the corresponding Wald statistics and adjusted p-values

Parameter	Estimate (logit)	S.E.	Wald statistic	Adjusted p-values
Europe	–0.53	0.25	–2.13	0.0668
Asia – Europe	0.70	0.46	1.53	0.1254
North America – Europe	1.28	0.52	2.46	0.0414

Network structure

Our network contained $N_{P} = 130$ plant and $N_A = 163$ bee species (including honey bees), with a $N_P / N_A = 0.7975$ (Tables S1 and S2; Fig. S1). The connectance of the whole network was $C = 0.039$. The simulated removal of honey bees broke the network in two: a large and a small compartment. The small compartment consisted of a single plant species, *Berberis x ottawensis*, and two wild bee species, *Andrena jacobi* and *Andrena rufula*. The connectance of the larger network component was barely smaller than in the whole network (0.037).

The highest degrees among the observed plant species were found in the case of *Apocynum cannabinum* (d = 16), *Salvia nemorosa* (d = 16), and *Laserpitium siler* (d = 15) (Table S2). Among pollinator bee species, honey bees had the highest degree, with 61 visited plant species. The second highest degree (d = 32) was found in the case of *Bombus pascuorum*, while all the other wild bee species had a degree lower than 25 (Table S1).

L. siler, *A. cannabinum*, and *S. nemorosa* hold the highest WI2 values among plant species (Table S2). Honey bees had the highest and almost four times higher WI2 value than any wild bee species in the network. *B. pascuorum*, *Heriades truncorum*, *Lasioglossum,* and *Hylaeus* species had the highest weighted topological importance among wild bees (Table S1).

The specialization index (d') was the highest in the case of *Doronicum grandiflorum*, *Centaurea transcaucasica,* and *Gypsophila fastigiata* among plants (Table S2), and in the case of *Andrena subopaca*, *A. minutula* among bees (Table S1).

We found similar values of degree, WI2, and d' among plant species groups of different origin, nationwide distribution, and flower color and type (Figs. 2, S2, and S3).

Keyplayers

The honey bee was a keyplayer in the network, reaching alone 62% of the plant and pollinator species in two steps or less. Together with *S. nemorosa* and *Origanum vulgare* as plants and *Lasioglossum pauxillum* and *L. politum* as pollinators, these five keyplayers reached 90% of all species (Table 2). Without the honey bee, *L. pauxillum*, *Bombus humilis*, *Hylaeus brevicornis*, *Megachile centuncularis* were keyplayer bees, and *Pycnanthemum*

Fig. 1 The probabilities of plant species visited by honey bees (*Apis mellifera*) originated from different continents. The 95% confidence intervals are estimated by Phylogenetic Generalized Linear Models (PGLM). This probability was significantly ($p = 0.0414$; Wald test, adjusted for multiple comparisons) higher for North American ($N = 24$), but not for Asian species ($N = 26$) compared to the Europeans ($N = 69$)
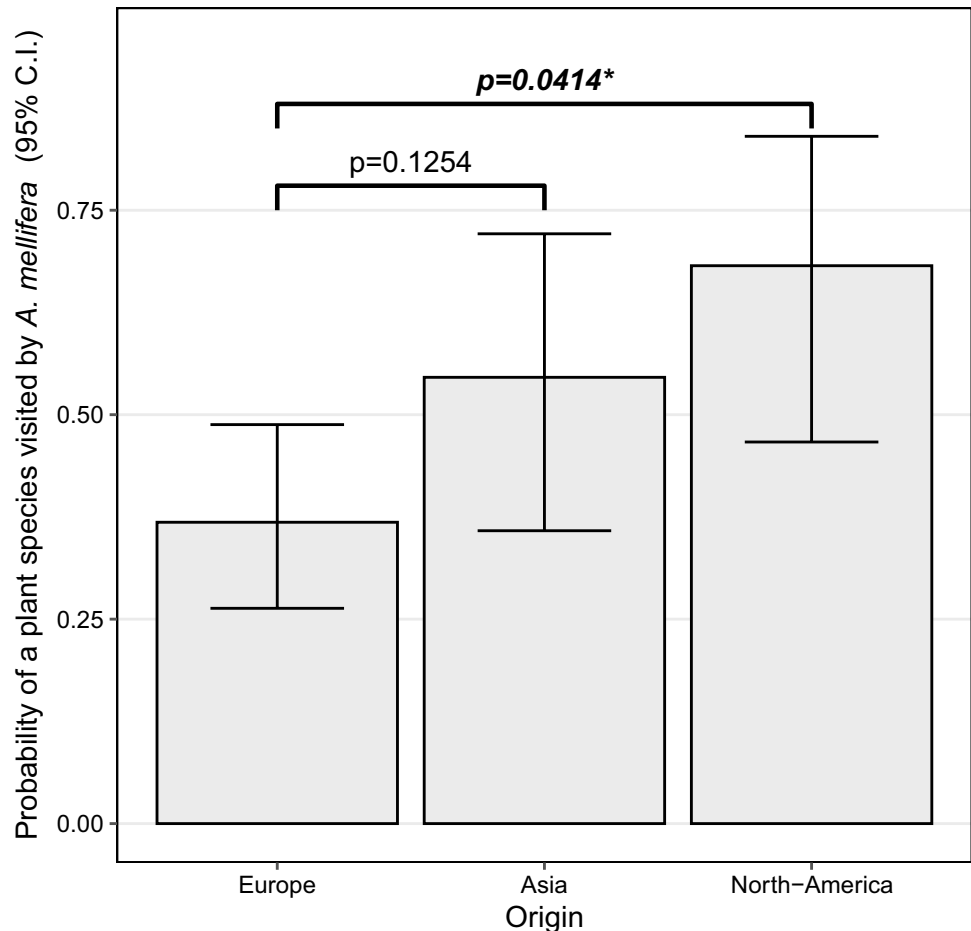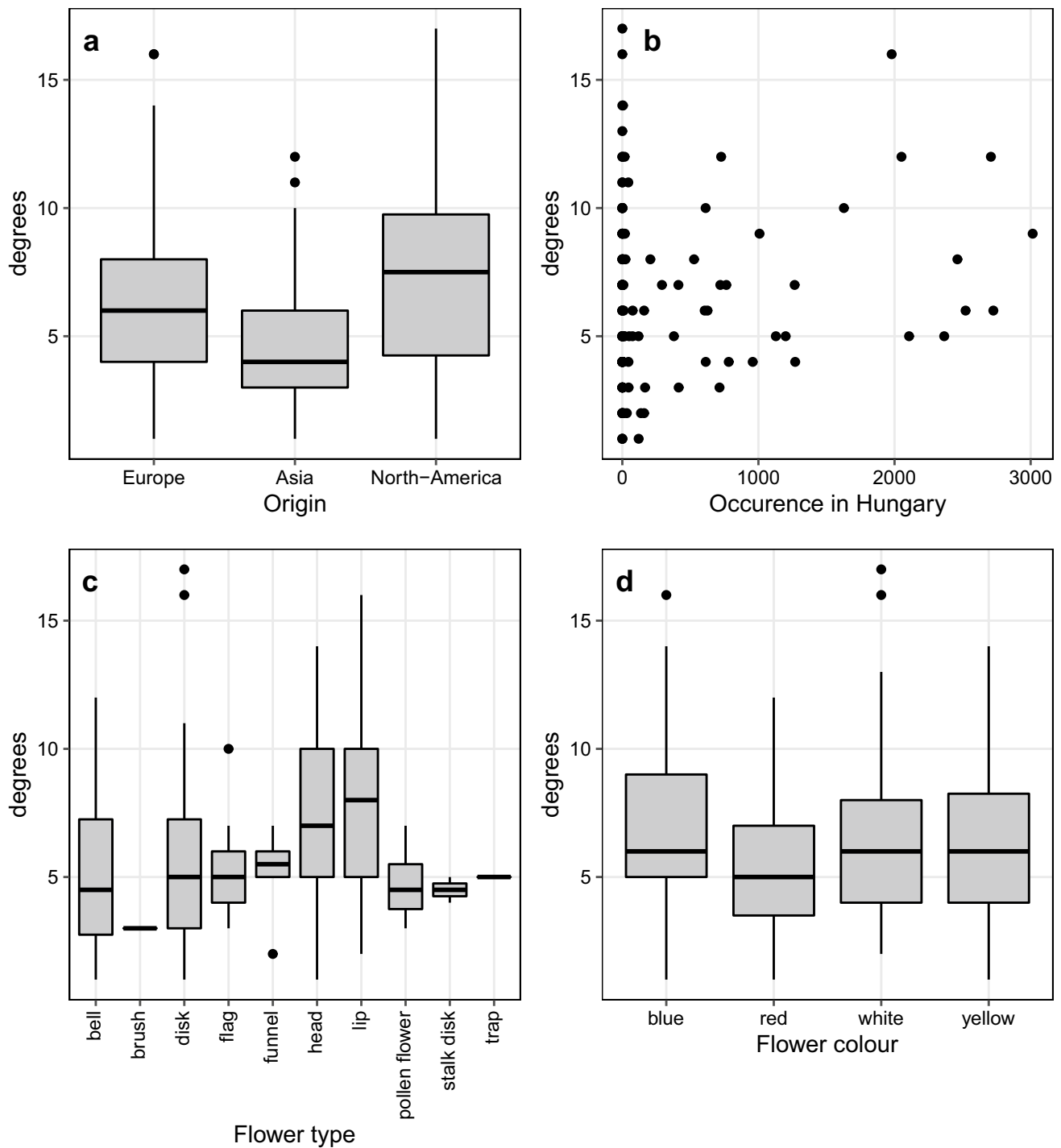
Fig. 2 Number of pollinating wild bee species (degrees) by various plant characteristics: (**a**) **continent of origin** (Europe: $N = 75$, Asia: $N = 29$, North-America: $N = 26$); (**b**) **nationwide distribution** (does not occur wild in Hungary – 0: $N = 70$, occurs wild in Hungary – ≥ 1: $N = 60$); (**c**) **flower type** (bell: $N = 12$, brush: $N = 1$, disk: $N = 36$, flag: $N = 13$, funnel: $N = 6$, head: $N = 33$, lip: $N = 22$, pollen flower: $N = 4$, stalk disk: $N = 2$, trap: $N = 1$) and (**d**) **flower color** (blue: $N = 26$, red: $N = 35$, white: $N = 25$, yellow: $N = 44$)

virginianum and *Salvia officinalis* were keyplayer plant species, reaching together 87% of all members of the network (Table 3). The simulated removal of honey bees

from the pollinator network affected the species composition of the keyplayer sets and lowered their coverage (see Tables 2 and 3).

Table 2 Keyplayer sets with keeping honey bee (*Apis mellifera*) in the network. Multiple optimal solutions exist for sizes N = 5 and N = 6. Abbreviated species names are as follows: Apimel = *Apis mellifera*; Salnem = *Salvia nemorosa*; Laspau = *Lasioglossum pauxillum*; Pycvir = *Pycnanthemum virginianum*; Andbic = *Andrena bicolor*; Laspol = *Lasioglossum politum*; Hylbre = *Hylaeus brevicornis*; Orivul = *Origanum vulgare*

n	metric	value	coverage	Apimel (Poll)	Salnem (Plant)	Laspau (Poll)	Pycvir (Plant)	Andbic (Poll)	Laspol (Poll)	Hylbre (Poll)	Orivul (Plant)
1	m-reach	181	62%	X							
2	m-reach	230	78%	X	X						
3	m-reach	246	84%	X	X	X					
4	m-reach	257	88%	X	X	X	X				
4	m-reach	257	88%	X	X	X			X		
5	m-reach	264	90%	X	X	X		X	X		
5	m-reach	264	90%	X	X	X	X	X			
6	m-reach	270	92%	X	X	X	X	X		X	
6	m-reach	270	92%	X	X	X	X	X			X

Discussion

Botanical gardens host a variety of plant species from all around the world. As flowers' morphological and phenological spectrum is especially wide, they can be essential habitats and refuges for pollinators. We found a high diversity of wild bees in the studied botanical garden with 162 species, constituting almost a quarter of the Hungarian bee fauna (Józan 2011). Despite the different origin, nationwide distribution, and flower color and type, we found no difference in the species richness and abundance of flower visitor wild bees. In contrast, honey bees were more likely to visit North American plant species than Europeans. The key positions within the plant-pollinator networks were held by both native and non-native plant species. This suggests that non-native plant species integrated successfully into the local flower visitation networks in a diverse man-made environment.

Flower visitation

Previous results on the potential differences in flower visitation of native and non-native plant species were inconclusive. Some studies found a higher species richness and/or abundance of flower visitors on native species (Frankie et al. 2005; Pardee and Philpott 2014; Rollings and Goulson 2019). They argued that the introduced alien plants could be less attractive. Therefore, replacing the native vegetation with non-native, ornamental species was considered to potentially negatively affect floral specialists in urban environments (Frankie et al. 2005; Hernandez et al. 2009; Rollings and Goulson 2019). Others suggested that exotic species and even ornamental varieties are as attractive as the native ones (Garbuzov and Ratnieks 2014; Rollings and Goulson 2019; Wenzel et al. 2020). Our study seems to favor the second theory, as the species richness and abundance of flower-visitor wild bees did not differ significantly among plant species of European, Asian, or North American origin. Biogeographical regions partly overlap on these continents, which could smoothen out such differences in associated interaction patterns. Our results seem to disagree with Razanajatovo et al. (2015). They found fewer flower visitors on the non-naturalized alien species than on native and naturalized alien species. Additionally, they found a more diverse set of pollinators on naturalized species, with a larger distribution range at a country scale. We suggest that plant species in a man-made botanical garden with high pollinator diversity might integrate faster into the plant-pollinator networks, and wild bees might adapt to these new foraging resources comparatively easier than in a more natural environment. Furthermore, plant origin might not be the sole or even the most determinant driver of flower visitation in each case (Dibble et al. 2020).

Table 3 Keyplayer sets after simulated removal of honey bees (*Apis mellifera*) from the network. Multiple optimal solutions exist for size n = 5. Abbreviated species names are as follows: Laspau = *Lasioglossum pauxillum*; Bomhum = *Bombus humilis*; Hylbre = *Hylaeus brevicornis*; Bompas = *Bombus pascuorum*; Pycvir = *Pycnanthemum virginianum*; Saloff = *Salvia officinalis*; Megcen = *Megachile centuncularis*; Orivul = *Origanum vulgare*; Plagra = *Platycodon grandiflorus*; Salnem = *Salvia nemorosa*; Teuhir = *Teucrium hircanicum*

n	metric	value	coverage	Laspau (Poll)	Bomhum (Poll)	Hylbre (Poll)	Bompas (Poll)	Pycvir (Plant)	Saloff (Plant)	Megcen (Poll)	Orivul (Plant)	Plagra (Plant)	Salnem (Plant)	Teuhir (Plant)
1	m-reach	115	39%				X							
2	m-reach	176	60%				X	X						
3	m-reach	209	72%	X			X	X						
4	m-reach	229	78%	X	X	X								
5	m-reach	244	84%	X	X	X						X		
5	m-reach	244	84%	X	X	X			X		X		X	
6	m-reach	255	87%	X	X	X		X	X	X				X

Indeed, the attractiveness of plants for pollinators can strongly depend on flower morphology and color, which might be more important determinants of flower visitation than the origin of the particular species (Stang et al. 2007; Sikora and Kelm 2012; Schiestl and Johnson 2013; Garbuzov and Ratnieks 2014). However, we found no difference in wild bees' species richness and abundance on flowers of different types and colors. These results do not confirm the findings of the abovementioned studies. On the one hand, they might be explained by the high diversity of flower visitor wild bees. The 162 wild bee species of 30 genera show widely different morphological and phenological characteristics (Michez et al. 2019). However, their individual preferences altogether add a much broader spectrum that includes all types of flowers found in the garden. On the other hand, it had to be acknowledged that our categorization of flower types can alter from other studies, and some of the flower type categories were underrepresented in our study compared to others. Moreover, cultivars of the different ornamental plant species can attract different pollinator species in different numbers (Marquardt et al. 2021), while we could test only one cultivar per ornamental plant species in our study, and could not take this effect into account.

The flower choice of honey bees was seemingly not determined by the studied flower properties, which is in line with the generally broad foraging diet of this supergeneralist species (Hung et al. 2018). Interestingly, honey bees seemed to prefer North American plant species over European ones. The wide selection of flower choices by honey bees often includes introduced species (Dibble et al. 2020). Honey bees also show a broad seasonal presence; therefore, we suppose that North American plants supplied a more or less continuous foraging resource for them together with other blooming plants.

Importance of plants and pollinators in the network related to certain species-specific traits

The number of direct pollinator partners (degree) and the strength of indirect relationships (weighted topological importance) of plant species did not differ among plant species of different origins and nationwide distribution. We identified three key plant species that ranked highly on topological metrics (degree and WI2) and had the highest number of direct and indirect links in the network accordingly. These three species were flowering and thus sampled in the second part of May, when many wild bee species were around. But their central position probably cannot be explained so simply. These three species were different in terms of origin, nationwide distribution, and flower type and color. Yet, all were visited by a wide range of wild bee species. *Apocynum cannabinum* grows throughout much of North America and does not occur in the wild in Hungary.

It has disk flowers with large five-lobed white corollas that moths and butterflies pollinate in its original distribution area. According to our results, it seems to be often visited by bees too. *Salvia nemorosa* is native to Central Europe and Western Asia and has a broad distribution in Hungary. Its lip flowers range in color from violet to violet-blue, rosy pink, and even white. *Laserpitium siler* can be found in mountainous areas of central and southern Europe, but it does not occur wild in Hungary. Its white disk flowers seemed to be attractive for the wild bee species. In agreement with the conclusions by Harrison and Winfree (2015) we suggest that plant species can be central in a flower visitation network independently from their origin and nationwide distribution in the studied community.

Among bees, the honey bee had the highest degree with 61 visited plant species and had the highest and almost four times higher WI2 value than any wild bee species in the network. The western honey bee is an important supergeneralist pollinator of both commercial crops (Abrol 2012) and wild plant communities (Hung et al. 2018). Our results indicate that less than half of the plant species were visited by honey bees in the studied diverse, man-made community. Nevertheless, it played a key role in the flower visitation network, reaching alone 62% of the plant and pollinator species in two steps or less. The network showed basically the same compactness without this species in its simulated removal from the network model. This confirms that networks with a high plant-to-pollinator ratio are relatively stable against the loss of honey bees (Kovács-Hostyánszki et al. 2019).

Bombus pascuorum was a key wild bee species in the botanical garden regarding degree and WI2 indices. Bumblebees usually show a preference for a wide range of plant species and flower forms, but primarily for lip flowers, e.g., the Lamiaceae family (Sikora and Kelm 2012). We found it on 32 plant species of various origins, nationwide distributions, and flower colors and types, reflecting this species' rather generalist flower preferences. *Heriades truncorum* also had a relatively high number of direct and indirect links in our network (degree=2, WI2=4.46) and visited flowers mainly from the Asteraceae family. Interestingly, it visited only North American and European plants, mostly with yellow head flowers. This suggests that species with narrower foraging spectrums can also hold many direct and indirect links in the flower-visitation networks.

Honey bee with *Lasioglossum pauxillum* and *L. politum* as pollinators and *Salvia nemorosa* and *Origanum vulgare* as plants already reached 90% of all species in two steps or less. Both of *Lasioglossum* species are polylectic, generalist, and widespread in Europe (Michez et al. 2019). They visited 20 and 23 plant species of various origins, flower color, and morphology, primarily rare or non-native to Hungary. Not surprisingly, polylectic species can make more accessible use of non-native plant species and play a key role in such a flower visitation network (Harrison and Winfree 2015). However,

both key plant species were native and widespread in the country. In another common garden study, *O. vulgare* was found to be one of the most attractive plant species for pollinators (Dibble et al. 2020). This shows the importance of plants with long bloom periods and with small, densely arranged flowers. *S. nemorosa* – like other Lamiaceae species – is one of the most visited plant species by bumblebees (Sikora and Kelm 2012; Hülsmann et al. 2015). In our study, it was also visited by nine other wild bee genera.

After the simulated removal of honey bees from the network, *Pycnanthemum virginianum* and *Salvia officinalis* became the keyplayer plant species. These species of the Lamiaceae family do not occur or are rare in the country. We cannot clearly explain why these plant species stepped forward and became keyplayers in this simulation. Possibly, their flower rewards make them highly attractive to a broad set of wild bee species. Flower rewards in such sense seem to be more important for wild bee visitation than the origin of the visited plant species. This suggests the adaptability of wild bees to introduced plants and the good integration potential of alien plants to plant-pollinator networks (Lowenstein et al. 2019). We cannot recommend specific plant species that were keyplayers for conservation efforts in such urban areas. However, we argue that a careful selection of ornamental plants, taking into consideration their flower morphology, might enhance local pollinator communities.

The specialization index (d') was highest in the case of *Doronicum grandiflorum*, *Centaurea transcaucasica,* and *Gypsophila fastigiata* among plants, and in the case of *Andrena subopaca*, *A. minutula* among bees. These three plant species have different flower colors and types and little to zero nationwide distribution. Surprisingly, both bee species are polylectic, usually visiting a range of different plant species and occuring in various habitat types (https://www.bwars.com/). Our study found both species in low numbers that might suggest unfavorable conditions for these species or bad timing compared to their flight period. *A. minutula* was primarily found on species that do not occur in Hungary and have red flowers. However, it also visited a common Hungarian plant with yellow flowers (*Potentilla arenaria*). *A. subopaca* visited only the European *D. grandiflorum* that does not occur in Hungary. These findings might suggest some tendencies, namely higher selectiveness of pollinators for plant species that do not occur in the native flora, but further research would be needed to strengthen this hypothesis.

Conclusions

We conclude that non-native plants can be just as important as natives for local pollinators in man-made environments. Plant species of different origins, nationwide distributions,

and flower colors and types had many direct and indirect links. Wild bee species showed a wide range of foraging preferences regarding flower color and type, plant species origin, or national distribution. As a highly generalist species, honey bee played an essential role in urban pollination networks, with several introduced species in its diet. Our results suggest that non-native plant species can integrate well into local pollination networks in man-made environments such as botanical gardens. As increasing urbanization makes wild bee conservation more crucial than ever, our results potentially offer new conservation tools in such environments. Yet, we must acknowledge that our results are based on observations made in a single botanical garden. Nonetheless, the high number of species and flower observation data we gathered serve as a robust flower visitation network worthy of further investigation.

Availability of data and material Data will be made available on reasonable request.

Declarations

Ethics approval Not applicable.

Consent to participate The work is all original research carried out by the authors.

Consent for publication All authors agree with the contents of the manuscript and its submission to the journal.

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