

Native and exotic plants play different roles in urban pollination networks across seasons

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Research Article

Keywords: greenspaces, nestedness, specialization, phenology, invasive species

Posted Date: April 4th, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1418244/v1>

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Version of Record: A version of this preprint was published at Oecologia on January 24th, 2023. See the published version at <https://doi.org/10.1007/s00442-023-05324-x>.

Abstract

Urban areas often host exotic plant species, whether managed or spontaneous. These plants are suspected of affecting pollinator diversity and the structure of pollination networks. However, in dense cityscapes, exotic plants also provide additional flower resources during periods of scarcity, and the consequences for the seasonal dynamics of networks still need to be investigated. For two consecutive years, we monitored monthly plant-pollinator networks in twelve greenspaces of Paris, France. We focused on seasonal variations in the availability and attractiveness of flower resources, comparing native and exotic plants at both the species and community levels. We also considered their respective contributions to networks properties over time (specialization and nestedness). Exotic plants provided more abundant and diverse flower resources than native plants, especially late in the season. However, native plants received more visits and attracted more pollinator species, both at the community and species levels. Exotic plants were involved in more generalist interactions, and this became more so as the season progressed. In addition, they contributed more to network nestedness than native plants. These results show that exotic plants are major components of plant-pollinator interactions in a dense urban landscape, even though they are less attractive to diverse pollinators. They constitute a core of generalist interactions that increase nestedness and can participate in the overall stability of the network. However, most exotic species were seldom visited by insects. Pollinator communities may benefit from including more native species, as well as entomophilous varieties of exotic plants, when managing urban greenspaces.

Introduction

Despite the negative impacts of urbanization on biodiversity, there is evidence that cities can sustain fairly rich pollinator communities, most notably regarding bees (Hall et al. 2017). In particular, Baldock et al. (2019) emphasize the major importance of private gardens and allotments in supporting pollinators, compared to parks and other public greenspaces. Nevertheless, in densely populated cities like Paris, private gardens and allotments are scarce, while parks cover larger areas (Shwartz et al. 2013). In such cities, public greenspace management practices are critical to maintaining pollinator biodiversity; and it is necessary to understand which ones best promote plant-pollinator interactions (Mata et al. 2021).

In private gardens and urban parks, much of the available flower resources are provided by ornamental plants, either native or exotic, that are highly variable in their attractiveness to pollinators (Garbuzov and Ratnieks 2014; Garbuzov et al. 2017; Erickson et al. 2019). The geographic origin of these garden plant species raises concerns since exotic plants can affect pollinator community composition (Pardee and Philpott 2014; Threlfall et al. 2015), whereas native plants are key elements to sustain rich and functionally diverse insect communities (Mata et al. 2021; Cecala and Wilson Rankin 2021). Yet, the relative contribution of native and exotic plants to urban pollinator communities remains debated (Majewska and Altizer 2020). Exotic flowering plants contribute substantially to the supply of nectar and pollen in urban landscapes (Tew et al. 2021; Casanelles-Abella et al. 2021), thus potentially supporting pollinator communities by increasing overall resources (Tasker et al. 2020; Staab et al. 2020). Indeed,

while at the plant community level natives might receive more visits, at the species level some exotics can be very attractive (Lowenstein et al. 2019; da Rocha-Filho et al. 2021). In addition, most of the mentioned studies were conducted in private gardens, allotments and nurseries; but seldom in public greenspaces within high density cityscapes. The relative attractiveness of exotics and natives to pollinators may depend on urbanization levels, due to possible effects of urban environmental stressors on pollinator foraging choices (Buchholz and Kowarik 2019). This issue has yet to be assessed in the context of public greenspaces in densely urbanized landscapes.

Furthermore, studies rarely explore how exotic garden plants integrate into pollination networks and affect their structure. Yet network structure is essential in maintaining stability against disturbance (Thebault and Fontaine 2010). By allowing to quantify single-species specialization levels (Blüthgen et al. 2006), network approaches can also help reconcile the contradictory levels of attractiveness observed at community and species levels for exotic plants. Such differences in plant specialization may rely on pollinator preferences (Salisbury et al. 2015), as exotic plants often fail to appeal to specialist pollinator species (Erickson et al. 2019). Looking at invasive plants, some studies have shown that these species often successfully integrate pollination networks, occupying a central place therein (Vilà et al. 2009; Thompson and Knight 2018). The consequences on insect communities vary greatly depending on the context (Stout and Tiedeken 2017; Davis et al. 2018). Invasive plants tend to attract more generalist pollinator species, while specialist pollinators are more strictly dependent on native plants (Parra-Tabla and Arceo-Gómez 2021). As a result, invasive plants display different species-level properties in networks compared to native plants (Arroyo-Correa et al. 2020). They have been found to generate less specialized pollination networks (Seitz et al. 2020) and create profound topological changes in interactions (Albrecht et al. 2014; Larson et al. 2016). Invasive plants act as super-generalists, notably raising network nestedness (Bartomeus et al. 2008; Russo et al. 2019). In an urban context, it is important to determine whether these results could be applied to exotic garden plants, and how that would affect the structure of pollination networks.

Recent works on plant and pollinator communities emphasize the importance of seasonal dynamics on pollination networks structure and species persistence (Guzman et al. 2021). Considering the respective phenologies of plants and pollinators, it is essential to examine interactions from a month-to-month perspective to assess short-term variations in network properties (CaraDonna and Waser 2020). Interestingly, the seasonal dynamics of exotic plants in pollination networks may be different from those of native plants (Larson et al. 2016; Arroyo-Correa et al. 2020; Seitz et al. 2020). Typically, exotic flora has been shown to complement native flora by providing late season resources for pollinators (Salisbury et al. 2015; Staab et al. 2020). While native floral cover fluctuates over time, exotic plants are often selected for their extended and complementary flowering, that can be kept constant by gardening practices (Erickson et al. 2019, 2021). However, these results still need to be confirmed in high-density city contexts where species phenologies can be broader and seasonality less marked than in natural landscapes (Uchida et al. 2018; Zaninotto et al. 2020). There, the seasonal dynamics of pollination networks and their impacts on pollinator diversity are still poorly understood.

Here we present the results of a two-year replicated monitoring of insect pollinator activity in the greenspaces of a densely urbanized landscape: the city of Paris (France). We investigated plant-pollinator interactions both at the plant species level and the plant community level. We examined pollination networks on a monthly basis from March to October, assessing the respective roles of the native and exotic floras. We addressed the following questions: **1)** How attractive are exotic and native floras to pollinators, both at the plant community and plant species level? Based on the literature, we hypothesize that native plants attract more pollinators in general, with wide variation among plant species. **2)** How does this attractiveness to pollinators vary over the seasons? We expect exotic plants, at the species and community level, to be visited more often in late season. **3)** How do these species fit into pollination networks and what are the implications for seasonal network dynamics? We expect exotic plants to be more generalist and contribute more to network nestedness than native plants, leading to more nested and generalist networks in the late season.

Methods

3.1. Site location

We operated on 12 sampling sites located in the city of Paris (France). We chose them to be dispersed across the city, at least 1 km apart from each other. Sampling sites were set in pesticide-free greenspaces of varying size (from 7,245 to 161,540 m²) and management practices, leading to distinct plant communities. In particular, intensively managed greenspaces hosted abundant and diverse garden plant species. In contrast, lightly managed areas contained a majority of spontaneous plants. More details on sampling sites can be found in Table S1 (Online Resource).

3.2. Insect sampling

Surveys were conducted in each site for two consecutive years (2019 and 2020), on a monthly basis from March through October (April 2020 was skipped due to the covid-19 crisis). All surveys were conducted by the same team, between the 1st and 15th of each month, in alternating order, covering two sites per day. Surveys were only done under conditions favorable to insects (no rain, low wind, temperature > 10°C), between 8:00 and 15:00 (local solar time).

Active sampling of foraging insect pollinators was conducted along 50 m transects in each site. Sampling was stratified across three habitats: shrubs, lawns, and flowerbeds, based on the respective proportions of these habitats in each greenspace. Transects were walked twice with a 10-minute interval in between, at a slow pace and with no time limit. All flowers within one meter on either side of the transect were examined for flower visitors. All flower visitors observed in contact with the fertile parts of a flower were collected with insect nets or plastic boxes, while visited plants were identified to species level. Unambiguously identifiable insects were recorded and released at the end of the survey. The others were euthanized with ethyl acetate vapors and then returned to the laboratory for collection. We identified them to genus level before sending them to several specialists for identification to species level. All the preserved specimens are now part of the iEES-Paris laboratory collection.

3.3. Plant inventories

We conducted monthly plant inventories during each survey, on five 1x1m quadrats evenly distributed over each transect. We identified all flowering plant species in these quadrats, and counted the floral units for each species (one floral unit = one individual flower, Apiaceae umbels and Asteraceae flower heads counting as one).

In urban settings, exotic plants encompass both planted garden species and spontaneous species. Depending on their population dynamics, the latter can be classified as subspontaneous, naturalized or invasive, although this varies over time and can be difficult to differentiate (Richardson et al. 2011). For this reason, we only considered the geographical origin of plant species, classifying them as either 'native' or 'exotic'. 'Native' plants comprised plants originating from the Ile-de-France bioregion, as well as anciently naturalized plants with stable populations (archaeophytes) (Jauzein and Nawrot 2011). 'Exotic' plant species included exotic garden plants, recently naturalized plants, but also horticultural varieties and species with regional invasive status (Wegnez 2018). In the end, most planted garden species (80%) were considered as exotic, whereas a majority of spontaneous and subspontaneous plants species (83%) were native.

3.4. Plant community- and species-level measurements

At the plant community level, we described flower availability separately for native and exotic plants in each site, using two indices. First, we calculated monthly values of flower density per m² to represent the amount of resources. Second, we determined flowering plant species richness per month as a proxy of floral diversity. We then assessed the attractiveness of these floral assemblages over time by looking at interactions with floral visitors at the community level, considering the number of interactions and the species richness of interacting pollinators.

At the plant species level, we also investigated the interactions with pollinators, accounting for flower density per plant species throughout seasons. For each site and each month, we calculated indices of network structure at the plant species level: the number of interactions, the number of interacting pollinator species (degree), Blüthgen's index of specialization d' (Blüthgen et al. 2006), and the species contribution to network nestedness (based on the NODF estimator, Almeida-Neto et al., 2008).

3.5. Statistical analysis

All data analyses were performed with R software version 4.0.5 (R Core Team 2021). At the community level, we constructed generalized linear mixed models (GLMM) of flower resources over time, with negative binomial error distributions. We successively modelled flower density (number of floral units per m²), and floral species richness (total number of plant species in bloom per site). Explanatory variables were the plant origin ('native' or 'exotic'), the day of the year (degree-2 polynomial) and their interaction. Additionally, we modelled the number of interactions and the number of pollinator species (degree) via GLMM with Quasi-Poisson error distributions. The explanatory variables were the same as above, also accounting for available flower resources: flower density (log-transformed) and floral species richness.

Besides, we investigated interaction networks at the community-level, using bipartite package (Dormann et al. 2008). We modelled the seasonal variations of the network-level nestedness (NODF) and specialization (H2', the network-level equivalent to d'), according to overall flower density, and the Day of the year (degree-two polynomial). We plotted networks aggregated over two months and all 12 sites, for visual clarity (Fig. 1).

At the plant species level, we used GLMM to study the seasonal variations of four network indices: the number of interactions, the degree, the specialization index (d'), and the contribution to nestedness. We used the following explanatory variables: the plant origin ('native' or 'exotic'), the Day of the year (degree-2 polynomial) and their interaction; as well as flower density per plant species and per month. The plant species was counted as a random effect. The number of interactions and the degree were modelled with Poisson error distributions. Meanwhile, the species contribution to nestedness (*nestedcontribution* function, bipartite package) followed a continuous distribution centered on zero (positive values representing positive contribution to nestedness) and was modelled with a gaussian error distribution. Finally, d' is comprised between 0 and 1 (*specieslevel* function, bipartite package; high values indicating high specialization), and was modelled with a beta-regression. A zero-one-inflated beta-distribution model achieved better normality of residues, but presented very similar results.

For all GLMMs, we integrated the year (2019 or 2020) as a fixed effect, and the site (n = 12) as a random effect. We selected the best models based on the second-order Akaike Information Criterion (AICc, Barton, 2020). We assessed the contributions of explanatory variables through analysis of deviance using Wald type-III chi-square tests (Fox and Weisberg 2019). Normality of residues and homoscedasticity were verified using DHARMA package (Hartig 2020).

Results

4.1. Overview of plant-pollinator interactions

Over the two years and across the 12 sites, we recorded a total of 3667 plant-pollinator interactions. A large majority of the insects were identified at the species level (95.9%) and the remaining at the genus level. They were distributed among five orders: Hymenoptera, Diptera, Lepidoptera, Coleoptera and Hemiptera. Hymenoptera were dominated by wild bees, of which we recorded 90 species (accounting for 52.3% of interactions), and honey bees (30.2% of interactions); although we also collected non-bee Hymenoptera (16 taxa, 1.2% of interactions). The second most abundant order was Diptera, (55 taxa, 12.3% of interactions), including 30 species of hoverflies. Next came Lepidoptera, (13 species, 3.7% of interactions); Coleoptera (4 species, 0.4% of interactions); and Hemiptera (only one collected individual).

Meanwhile, we recorded a total of 346 plant species and varieties (Table S2, Online Resource). Of these, 158 species were categorized as native (79.8% were visited by insects), and 188 as exotic (75.0% were visited). Exotic plants comprised seven invasive species, five of which were visited by pollinators during our surveys (*Buddleja davidii*, *Erigeron canadensis*, *Galega officinalis*, *Impatiens balfourii*, and *Senecio*

inaequidens) and two that were not (*Berberis aquifolium* and *Erigeron annuus*). From among the 180 insect taxa identified, 40.6% visited only native plant species, 12.2% visited only exotic species, and 47.2% visited both native and exotic species.

4.2. Flower resources availability and attractiveness at the community level

We used flower density and floral species richness as indicators of flower resource availability at the community level, and studied them over time and by origin (Fig. 2). As revealed by the significant interaction “Day² x Origin”, exotic and native plants followed different unimodal seasonal patterns (Table 1), with a two-months delay in maximal values. Indeed, the peak of flower density came in May for native flora and in July for exotic flora (Fig. 2a), whereas the peak of floral species richness came in July for native flora and in September for exotic flora (Fig. 2b). Overall, the exotic flora displayed more floral units and plant species from mid-summer to fall. Thus, we observe two phases: the first in spring with equivalent resources of both types, and the second from July onwards when resources provided by exotic plants became dominant (red boxes in Fig. 1).

Table 1

GLMM of the seasonal variations in flower resources (flower density and floral species richness), and their attractiveness to pollinators (number of interactions; number of pollinator species) at the community level, for native and exotic plants. χ^2 and associated p-values give the results of Type-III Wald analysis of deviance; df: degrees of freedom of the χ^2 test.

Response variable	Predictors	χ^2	p	AICc
Flower density (Negative binomial)	Day ²	32.9 (2df)	< 0.0001	3919.7
	Origin	9.5 (1df)	0.0020	
	Day ² x Origin	30.0 (2df)	< 0.0001	
	Year	18.1 (1df)	< 0.0001	
Floral species richness (Negative binomial)	Day ²	69.4 (2df)	< 0.0001	1785.2
	Origin	39.2 (1df)	< 0.0001	
	Day ² x Origin	31.6 (2df)	< 0.0001	
Number of interactions (Quasi-Poisson)	Flower density (log)	99.0 (1df)	< 0.0001	1969.4
	Floral species richness	124.9 (1df)	< 0.0001	
	Day ²	63.7 (2df)	< 0.0001	
	Origin	44.6 (1df)	< 0.0001	
Pollinator richness (Quasi-Poisson)	Flower density (log)	40.0 (1df)	< 0.0001	1463.4
	Floral species richness	137.9 (1df)	< 0.0001	
	Day ²	59.3 (2df)	< 0.0001	
	Origin	46.8 (1df)	< 0.0001	

At the community level, the number of interactions and pollinator species richness per month were strongly and positively related to flower resources (both flower density and floral species richness, Table 1; and Fig. S1, Online Resource). Notably, for a given level of flower resources, the native flora was always more attractive to pollinators than the exotic flora. Also, pollinator interactions exhibited unimodal seasonal patterns independent of variation in flower availability. Both types of flora attracted more pollinator individuals and species during summer, with a peak in early July (Fig. 2c-d.). Controlling for flower resources, there was no mismatch between attractiveness patterns of native and exotic plant species, as the interaction term “Day² x Origin” was not significant. Because of the seasonal increase in interaction abundance and pollinator species richness, but also the rise in plant diversity, we observed a summer increase network size (Fig. 1).

4.3. Network properties at the plant species level

At the plant species level, we also observed significant differences based on plant origin (Table 2). Native plant species individually received more visits than exotic ones, here reaching a peak in late May (Fig. 3a). Besides, the number of interacting pollinator species (degree) was higher for native plants than for exotic plants, especially in early season (Fig. 3b). The number of interactions per plant species and the degree were also positively influenced by flower density (Fig. S1, Online Resource).

Table 2

GLMM of the seasonal variations in plant-pollinator interactions structure at the plant species level (number of interactions, degree, contribution to nestedness, and specialization index d'), for native and exotic plants. χ^2 and associated p-values give the results of Type-III Wald analysis of deviance; df: degrees of freedom of the χ^2 test.

Response variable	Predictors	Chi ²	p	AICc
Number of interactions (Poisson)	Flower density per species (log)	321.2 (1df)	< 0.0001	6521.2
	Day ²	113.5 (2df)	< 0.0001	
	Origin	6.2 (1df)	0.013	
	Year	6.3 (1df)	0.012	
Pollinator richness (degree) (Poisson)	Flower density per species (log)	63.5 (1df)	< 0.0001	4742.8
	Day ²	74.1 (2df)	< 0.0001	
	Origin	4.9 (1df)	0.026	
	Day ² x Origin	8.1 (2df)	0.017	
Contribution to nestedness (Gaussian)	Flower density per species (log)	4.5 (1df)	0.033	2218.1
	Day ²	22.8 (2df)	< 0.0001	
	Origin	4.7 (1df)	0.030	
	Year	9.3 (1df)	0.0023	
Specialization (d') (Beta-regression)	Day	8.7 (1df)	0.0033	-1677.4
	Origin	12.6 (1df)	0.00039	
	Day x Origin	8.0 (1df)	0.0046	
	Year	5.6 (1df)	0.018	

Plant contribution to monthly network nestedness, at the species level, followed a similar seasonal pattern with a maximum occurring in summer (late July, Fig. 3c). Although exotic and native plant species followed the same temporal pattern (the interaction effect “Day² x Origin” was not significant), exotic plants overall contributed more to the nestedness than native ones (Table 2). Meanwhile, network-level nestedness (NODF) followed a unimodal seasonal pattern with a peak in July, coinciding with maximum size and diversity of the networks (Fig. S2a & Table S3, Online Resource).

In addition, we calculated the specialization index (d') for each plant species. For native plants, d' remained stable over time around a value of 0.63. Meanwhile, for exotic plants, d' decreased over time from 0.68 in March to 0.40 in October (Fig. 3d). Thus, exotic plant species were more generalist than native species in late season, whereas there was no difference between them in early season. Overall network-level specialization ($H2'$), encompassing both native and exotic flora, similarly decreased over time (Fig. S2b & Table S3, Online Resource).

Discussion

Despite being overall more abundant than natives in urban greenspaces, especially in late season, exotic plants were less attractive after controlling for flower abundance and diversity. Also, these plants occupied different positions in urban pollination networks, as exotics showed greater generalism levels and contributed more to nestedness than native plants, partly driving the seasonal dynamics of network structure.

5.1. Exotic plants are not as attractive as natives, but more available in late season

Our results bring further support to the importance of native plants for urban pollinators, as found previously in city private gardens (Salisbury et al. 2015; Lowenstein et al. 2019). In the context of a densely-populated city, native plants attracted more pollinator individuals and species than exotic plants, both at plant community level and species level. This became clear when correcting for flower availability, meaning that natives are more attractive than exotics when equally available. Given such preferences, promoting native flora in greenspaces seems beneficial for pollinator abundance and diversity.

We found that flower density and diversity contribute strongly to pollinator richness and abundance, as is typically observed at the community level (Ayers & Rehan, 2021, for a review). Here, however, native and exotic flower resources are not equally available, with distinct seasonal dynamics. In particular, late in the season, exotic flowers are more abundant and diverse than native ones. This finding has also been recently reported in private residential gardens (Staab et al. 2020), suggesting that the relative importance of native and exotic plants for pollinators can only be fully understood with a seasonal perspective. Late season abundance of exotic plants can be explained by better resistance to summer heat and drought, as well as better maintenance by gardeners; while many native plants decline in bloom by the end of the season. As a result, exotic plants may be more visited than natives from late-summer on, as previously reported (Salisbury et al. 2015; Staab et al. 2020). This suggests that exotics may indeed supplement the resources provided by native plants late in the season, while being less attractive on their own.

Though the native flora attracted overall more pollinators than the exotic flora, seasonal patterns of plant attractiveness were similar. Pollinators were more abundant and diverse during summer, with a maximum in early July for native and exotic floras alike. This may reflect a general increase in pollinator abundance in the environment at this time of the year (Zaninotto et al. 2020). In contrast, there was a difference in

seasonal dynamics at the plant species level, with native plant species attracting more pollinator species than exotic ones during spring. This is consistent with the observations of Cecala and Wilson Rankin (2022), with higher bee diversity in native-rich nurseries than in conventional nurseries, albeit exclusively in spring. Previous studies have shown that early-flying bees are more dependent on natural habitats within urban areas (Harrison et al. 2018; Banaszak-Cibicka et al. 2018), possibly relying more on native plants. This would explain why visitors of exotic flowers are much less diverse in early season.

5.2. Exotic and native plants affect network structure differently

Our results show that exotic species tend to have a central position in urban pollination networks, and that this position varies throughout seasons. Indeed, as we hypothesized, native plant species were involved in more specialized interactions than exotic species. This effect was most pronounced late in the season, as exotics displayed decreasing values of the specialization index (d') over time. Thus, from August onwards, exotic plants attracted visitors in a generalist way, without distinguishing among the available pollinators. This is consistent with evidence that exotic plants attract less specialized bee species than native plants (Cecala and Wilson Rankin 2021). The observed seasonal trend could be due to higher proportions of generalist pollinators in late season, which are themselves associated with the prevalence of exotic plants. In any case, exotic plants appear to drive a general decrease in specialization at network scale ($H2'$ index). The urban environment is known to apply filtering on bee traits, among which generalism. As a result, generalist bees are more prominent in cities (Casanelles-Abella et al. 2021), as also demonstrated in Paris (Geslin et al. 2016). Our results suggest that this phenomenon may partly rely on the abundance of exotic plants, which favor generalist pollinators.

As we also hypothesized, exotic plants contributed more to network nestedness than native ones. Exotic plants occupy a central position in the networks, consistent with what has been observed with invasive species (Bartomeus et al. 2008; Larson et al. 2016; Russo et al. 2019). Although a nested structure implies potential competition between generalist and specialist pollinators, it is generally thought to provide a buffer against specialist extinction (Tylianakis et al. 2010). Hence, by increasing nestedness, exotic plants may contribute to network stability, although our knowledge is still insufficient to accurately predict population levels and ecosystem functions from network properties only (Valdovinos 2019). In addition, we noted seasonal dynamics of contribution to nestedness, which were similar for exotics and natives. Interaction networks became bigger in the summer, with a more nested structure. This again underlines the need to consider month-to-month variations in networks structure (CaraDonna and Waser 2020). However, like most studies, we constructed our interaction networks based on pollinator foraging behavior. Yet, some interactions bear low value to plant species fitness. When considering the efficiency of pollination interactions, networks can be considerably smaller, with less connected, generalized and nested structures (de Santiago-Hernández et al. 2019). The centrality of exotic garden plants in urban pollination networks may likewise not be supported by actual pollen transfers. In fact, the presence of these plants often does not depend on reproductive success, as they are regularly replaced by gardeners.

5.3. Guidelines to greenspace managers

In urban greenspaces, pollinator-friendly varieties are frequently planted without regard to species origins. While this is a way to increase flower availability, this practice can lead to the introduction of invasive plants (Johnson et al. 2017), illustrating potential unintended consequences of garden plants. Meanwhile, similar issues apply to managed pollinator fauna. Indeed, here, nearly one-third of the interactions involved managed honey bees. They visited 71 native and 82 exotic plant varieties (representing respectively 56.3% and 58.2% of visited varieties). As can be seen in Fig. 1, they are core contributors to Parisian pollination networks. As such, they may enhance network stability, much like exotic plants. However, in Paris, high density of honey bee hives has been shown to drive a decrease in wild pollinator visitation activity (Ropars et al. 2019). Honeybees could also facilitate the integration of exotic plants into pollination networks, as they visit them abundantly (Urbanowicz et al. 2020; Parra-Tabla and Arceo-Gómez 2021). In return, the dominance of exotic plants in urban greenspaces may benefit honey bees but hinder more specialized bees (Threlfall et al. 2015).

In British cities, Baldock et al. (2019) took note of native and exotic plant species that attracted more pollinators than expected based on their flower densities. Here we recovered most of the plants they recorded as attractive, and again found that they were visited abundantly. Our most visited plants, however, were not on their list, and comprised both native and exotic species: e.g. *Helminthotheca echioides* and *Trifolium repens* (native species), *Verbena bonariensis* and *Phacelia tanacetifolia* (exotic species). We recommend planting such pollinator-friendly plant species, with consideration for seasonal successions. As confirmed by our results, flower density and diversity are key to attracting and sustaining pollinators, though it is better to favor plant species that are complementary in both phenology and insect visitor assemblage composition. Without being an absolute criterion, the geographical origin of plant species must be taken into consideration when designing greenspaces (Buckley and Catford 2016). On the one hand, exotic garden plant species may support more nested networks and provide additional resources for generalist pollinators. On the other hand, native plants attract more pollinators for a given level of flower density, and support more diverse pollinator communities. As they are involved in more specialized interactions, they also contribute to functional diversity. While it may be difficult to maintain high floral density with only native plants, we strongly recommend that these plants be given preference in the design and management of greenspaces.

Declarations

Declaration of authorship: VZ and ID conceived the ideas and methodology; VZ collected the data; VZ analyzed the data and wrote the manuscript in consultation with ID and ET. All authors gave final approval for publication.

ACKNOWLEDGEMENTS

We thank the MNHN (P. Barré), Eau de Paris (L. Robilliard) and all greenspace management services of the City of Paris for providing access to the sites. We thank the specialists who identified the insects: D.

Genoud, R. Rudelle, and E. Dufrêne. We also thank N. Quaghebeur, A. Fauviau, Y. Kraepiel and E. Motard for their contributions to data collection.

Funding: This work was partially funded by the City of Paris (CIFRE n°2018/0699), by the Institut de la Transition Environnementale – Sorbonne University (“Yapudsaison” 2019 and 2020), and by the Société Centrale d’Apiculture (« Pollinisateurs sauvages et communautés végétales urbaines », 2019).

Conflicts of interest: The authors declare no conflict of interest.

Ethics approval: Not applicable

Consent to participate: Not applicable

Consent for publication: Not applicable

Availability of data and material: Data will be available in the publicly accessible repository Zenodo, within the “iEES-Paris OpenData” community.

Code availability: Not applicable

Authors’ contributions: *VZ and ID conceived the ideas and methodology; VZ collected the data; VZ analyzed the data and wrote the manuscript in consultation with ID and ET. All authors gave final approval for publication.*

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Figures

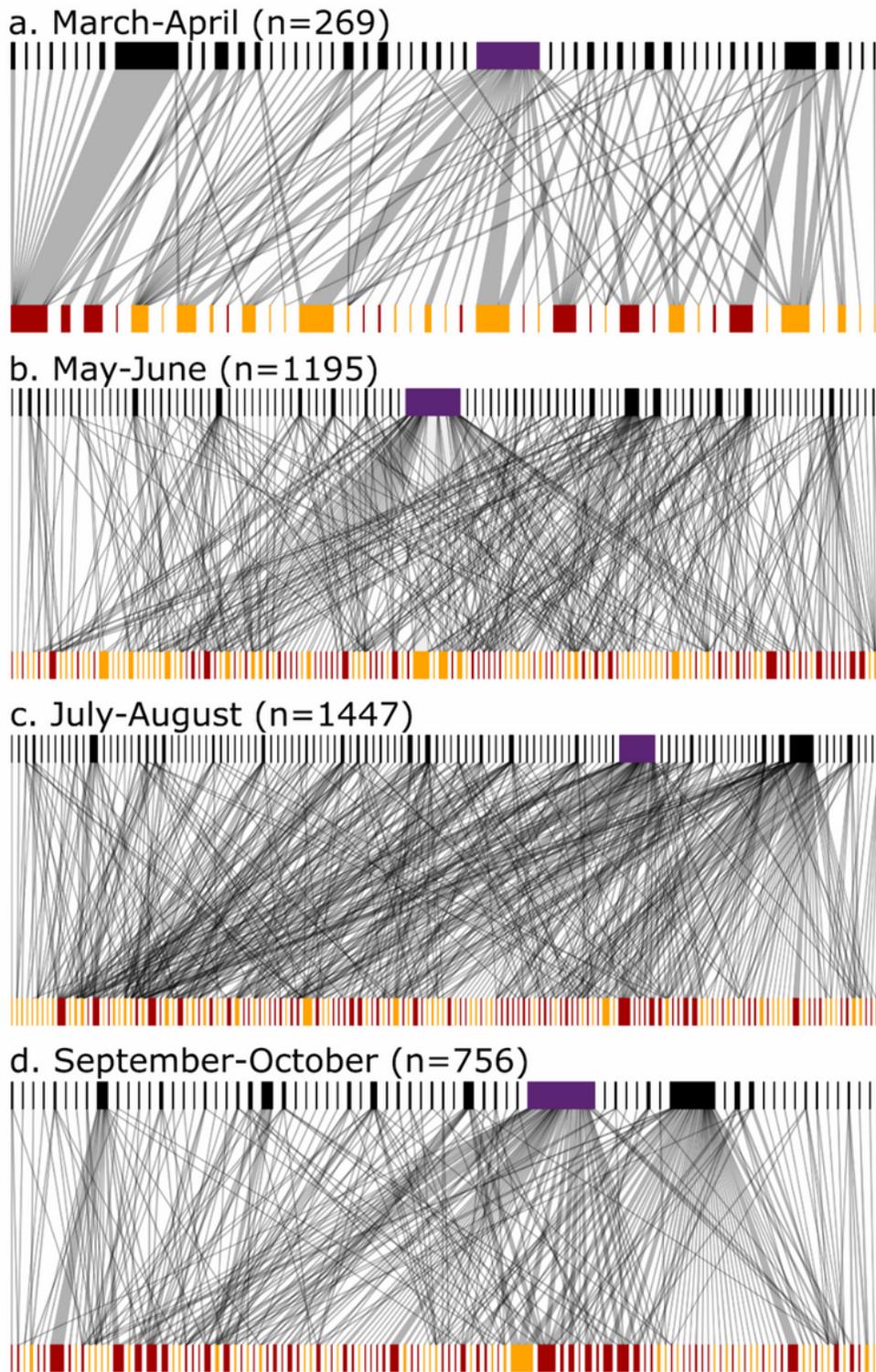


Figure 1

Representation of the bipartite plant-pollinator networks over seasons. Data are pooled across all sites and per two-months period. Upper boxes represent pollinators, width is proportional to the number of interactions performed by each species (n: total number of interactions per period) (purple box: *A. mellifera*, black boxes: other species). Lower boxes represent plant varieties according to their origin

(orange: native, red: exotic), width is proportional to each plant species flower density (log-transformed) during each period. Grey links represent interactions.

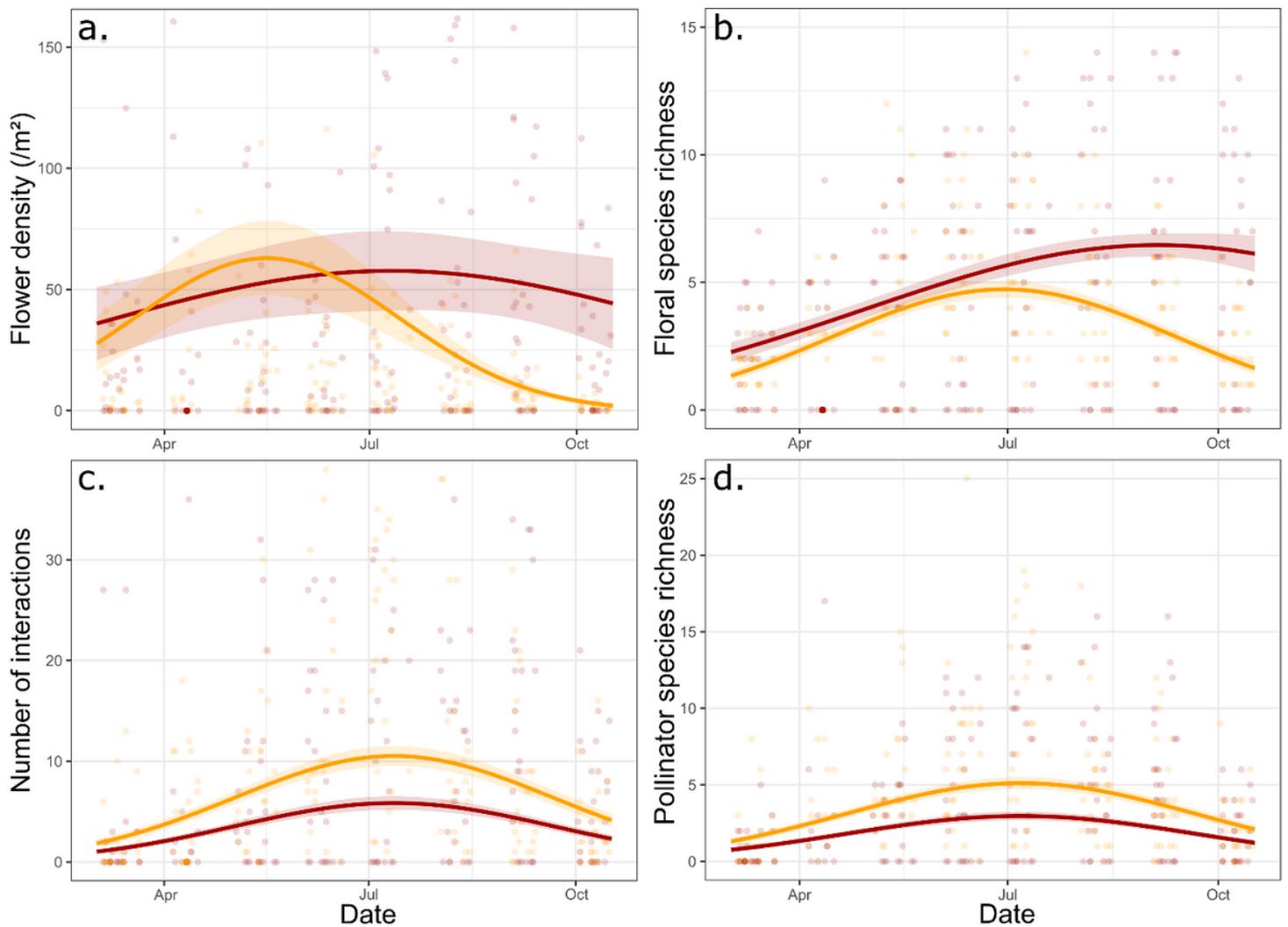


Figure 2

Seasonal variations in flower resources (a. flower density per m² and b. floral species richness per site), and their attractiveness to pollinators (c. number of interactions and d. number of pollinator species) at the community level, for native and exotic plants (native: orange, exotic: red). Lines indicate predictions from the GLMM presented in Table 1 (±SE), points represent observed values. The number of interactions and pollinator species richness (c. and d.) are modelled accounting for the variations of flower resources (a. and b.).

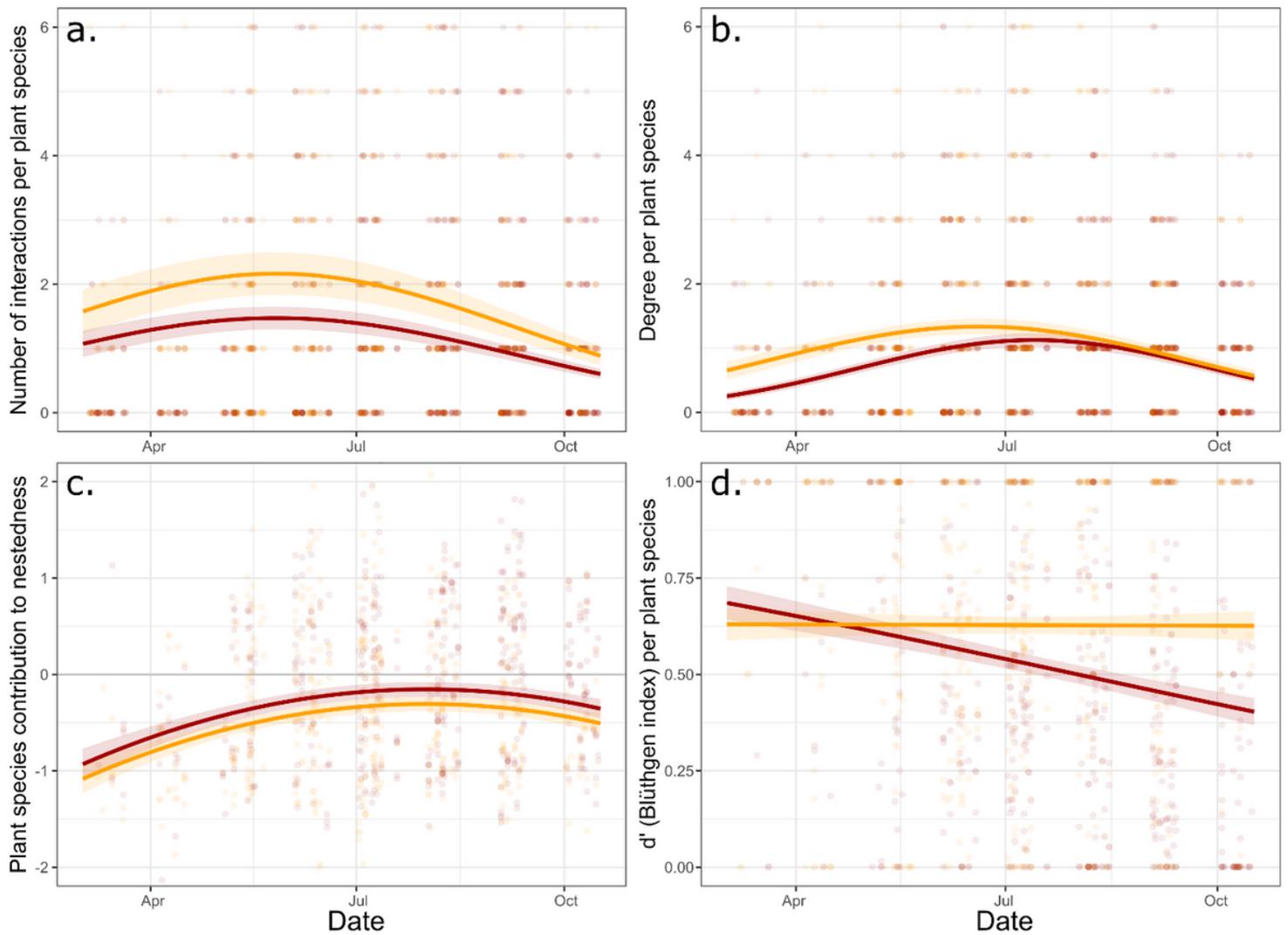


Figure 3

Seasonal variations in plant-pollinator interactions at the plant species level, for native and exotic plants (native: orange, exotic: red): a. Number of interactions per plant species, b. number of interacting pollinator species per plant species (degree), c. contribution to monthly network nestedness per plant species, d. specialization index d' per plant species. Lines indicate predictions from the GLMM presented in Table 2 (\pm SE), points represent observed values. Indices are modelled also accounting for the variations of flower density per plant species.

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