Diversity of greenspace design and management impacts pollinator communities in a densely urbanized landscape: the city of Paris, France

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Diversity of greenspace design and management impacts pollinator communities in a densely urbanized landscape: the city of Paris, France

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Abstract
The response of insect pollinator communities to increasing urbanization is shaped by landscape and local factors. But what about habitats that are already highly artificial? We investigated the drivers of pollinator diversity in a dense urban matrix, the city of Paris. We monitored insect pollinator communities monthly (March-October) for two consecutive years in 12 green spaces that differed in their management practices, focusing on four insect orders (Hymenoptera, Diptera, Lepidoptera, Coleoptera). Pollinator abundance and species richness were both positively tied to green space size and flowering plant species richness, but negatively linked to surrounding impervious surfaces. In addition, environmental features at both the local and landscape scales influenced the composition and functional diversity of wild bee communities. Indeed, small and large bees responded differently, with the occurrence of large-bodied species being impaired by the proportion of impervious surfaces but strongly enhanced by plant species richness. Also, sites with a majority of spontaneous plant species had more functionally diverse bee communities, with oligolectic species more likely to be found.

These results, consistent with the literature, can guide the design and management practices of urban green spaces to promote pollinator diversity and pollination function, even in dense urban environments.

Keywords Bees · Community ecology · Functional traits · Impervious surfaces · Ornamental plants · Spontaneous plants

Introduction

Urbanization is among the strongest changes in land use, and thus one of the main drivers of global change. Multiple factors have been documented as driving insect diversity loss in cities (Fenoglio et al. 2021). Among insects, pollinators receive considerable attention because of their recognized contribution to ecosystem services. In particular, cities have been shown to support a wide variety of bee species in temperate climates (Baldock et al. 2015; Theodorou et al. 2020). Nevertheless, numerous studies have demonstrated that both local and landscape factors influence pollinator communities in an urban context (Majewska and Altizer 2020; Ayers and Rehan 2021).

Landscape-scale drivers of pollinator abundance and diversity are often studied along rural to urban gradients; they mostly encompass the proportion of impervious surfaces, landscape heterogeneity, and the presence of large green spaces in the surroundings. Several studies have highlighted the negative effect of impervious cover at the landscape scale on wild bee abundance and species richness (Geslin et al. 2016; Burdine and McCluney 2019; Egerer et al. 2020). This negative effect seems consistent across bee guilds with various functional traits (Birdshire et al. 2020), though in some cases impervious landscapes seem to favor *Bombus* and *Apis* abundance (Bennett and Lovell 2019). High levels of urbanization may also come with higher proportions of non-native bee species (Gruver and Caradonna

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2021). Since moderate levels of urbanization can benefit some wild bees, greater bee diversity may occur for intermediate levels of impervious surfaces (Fortel et al. 2014). Besides, there is evidence that the presence of large green spaces in urban surrounding landscapes promotes bee richness and small bee abundance (Turo et al. 2021). Also, in addition to the adverse effects of impervious surfaces, bee abundance has been shown to decline with urban warming (Hamblin et al. 2018).

Local drivers of urban pollinator communities include green space size, urban design, and quantity and quality of floral resources. Such local characteristics vary according to the type of green space (community gardens, parks, cemeteries, private gardens, etc.), leading to distinct pollinator communities (Baldock et al. 2019). Community gardens host the greatest abundance of pollinators (Baldock et al. 2019; Lanner et al. 2020; Daniels et al. 2020), due to high flower availability, making them effective tools for sustaining pollinator communities in the city. Indeed, high floral richness consistently comes with high bee abundance and/or species richness (Quistberg et al. 2016; Ballare et al. 2019; Burdine and McCluney 2019; Birdshire et al. 2020; Gruver and Caradonna 2021). Not only does the number of plant species matter, but also their origin, as there is evidence that the presence of native species supports wild bee diversity (Egerer et al. 2020); although spontaneous non-native plant species may provide important resources and attract numerous pollinators (Turo et al. 2021). In addition, the spatial arrangement of floral resources within green spaces may influence bee species richness and diversity (Plascencia and Philpott 2017). The size of the local habitat provided by green spaces is also critical. Indeed, garden size often drives bee abundance and species richness (Quistberg et al. 2016; Egerer et al. 2020), though not always (Makinson et al. 2017). Besides, at the local scale, the presence of hardscape (built impervious structures) (Bennett and Lovell 2019) and mulch (Cohen et al. 2021) within green spaces is detrimental to pollination services, while bare ground surfaces enhance bee diversity by supporting ground-nesting bees (Ballare et al. 2019).

However, not all pollinators equally respond to urbanization, with hoverfly and butterfly communities experiencing more consistent losses than bee communities. Persson et al. (2020) thus reported an effect of landscape-scale vegetation cover, human density, and urban form on species richness that applied differently to wild bees and hoverflies. Urban hoverflies assemblages constituted a subset of rural assemblages, suggesting that urbanization drives a pure loss of hoverflies species, as also documented by Bates et al. (2011). As for butterflies, Kuussaari et al. (2021) brought evidence that their abundance and species richness declined with human population density and impervious built-up areas. Concerning local factors, butterfly and hoverfly communities appear to be sensitive to vegetation cover, and flower abundance (Matteson and Langellotto 2010; Majewska et al. 2018; Dylewski et al. 2019). In particular butterfly richness depends on greenspace management practices, as less intensively managed spaces have more species and fewer species losses (Aguilera et al. 2019). Overall, Coleoptera and Lepidoptera may be more affected by urbanization than other insect groups (Fenoglio et al. 2020). These differences among insects with various functional traits highlight the need to consider the full range of pollinators.

The city of Paris (France) is one of the densest cities in the world with more than 2 million inhabitants for 105 km². The impacts of urbanization on wild bee communities have already been studied in the administrative region of Paris by Geslin et al. (2016); along a rural-to-urban gradient, the proportion of impervious surfaces (500 m radius) was negatively associated with wild bee abundance and richness. But at the urban end of this gradient, are the bee communities homogeneous? Is there variation in the abundance and composition of these communities within a dense urban landscape, depending on urban context and greenspace management? Local factors are often reported to be the best predictors of bee abundance and richness in urban gardens (Quistberg et al. 2016; Lanner et al. 2020; Gerner and Sargent 2022). These local factors, such as flower availability, may be stronger drivers of pollinator communities than landscape-scale artificialization. Is this also the case in the city of Paris?

In this paper we examine how pollinator communities vary across green spaces in the dense urban matrix of downtown Paris, depending on environmental factors. We, therefore, differentiate sites according to: 1/ landscape-scale (200 to 1000 m) features such as the proportion of impervious surfaces, the number of entomophilous trees, and local temperature; 2/ local features of green spaces and their management: green space size, flowering plant species richness, flower density, the share of spontaneous plant species ("weeds") and their contribution to flower density. We are interested in unraveling the links between pollinator diversity and the above-mentioned characteristics of the Parisian green spaces. To this end, we monitored five diurnal pollinator groups, belonging to four insect orders: bees (Anthophila clade, Hymenoptera), hoverflies and bee flies (Syrphidae and Bombylidae families, Diptera), butterflies (Lepidoptera), and beetles (Coleoptera). This gave us a broader view of the urban drivers of pollinator communities than focusing solely on bees. We expect landscape and local features to be associated with variation in pollinator abundance and species richness, either positively (for floral resources) or negatively (for impervious surfaces and temperature). We also hypothesize that environmental features may influence

pollinator community composition, and in particular the frequency of some bee species traits. As an indicator of overall urban density, landscape-scale impervious surfaces may be more detrimental to large, ground-nesting, oligolectic and/or solitary species, that are often impaired by urbanization (Buchholz and Egerer 2020). On the contrary, these species may be more represented in green spaces that include spontaneous plants, reflecting environmentally friendly management. In addition, green space size and local temperatures may have different effects depending on bee body size, as this trait is associated with foraging distance and thermal tolerance (Ayers and Rehan 2021). Last, indicators of flower resource density and diversity may be linked to bee foraging behavior, thus interacting with traits such as body size, sociality, and pollen acquisition strategy.

Methods

Site selection

All survey sites were located in Paris (France), within 12 selected green spaces distributed throughout the city (Fig. 1) (average distance to the closest survey site: 1,902 m ± 170 m SE). These green spaces were of varying sizes (see Table 1) to estimate the effect of habitat patch size on pollinator diversity. Since some of these green spaces were adjacent to private gardens and other planted areas, their size measurement included contiguous vegetation patches. Conversely, all vegetated areas of a green space that were separated from the main space by roadways or other impervious surfaces wider than 5 m were excluded from the surface measurement. Each green space featured one survey site where we conducted inventories of flowering plants and insect pollinators.

Although all were pesticide-free, the 12 green spaces studied were not subjected to the same management practices and were classified along a gradient of management intensity of their vegetation. At the one end of this gradient, some green spaces were intensively managed, with mowed lawns and flowerbeds that were often renewed and watered, trees and shrubs pruned regularly, and few spontaneous plants allowed to grow (LB.: Jardin Catherine Labouré; VL.: Jardin Villemin). At the other end of this gradient, green spaces were lightly managed, allowing only spontaneous vegetation to develop, with one or two annual cuts (PE.: Jardin Pierre-Emmanuel; AP.: Jardin Abbé-Pierre); two were even closed to the public (MT.: Réservoir Montsouris; SV.: Jardin Saint-Vincent). The remaining six green spaces combined both styles of management practices (BR.: Parc de Bercy; BS.: Parc Georges Brassens; CT.: Parc André Citroen; MC.: Parc Monceau; JP.: Jardin des plantes; BL.: Parc de Belleville).

Landscape features

Even though the entire study design was set in a dense urban landscape, there were slight variations in the amount of

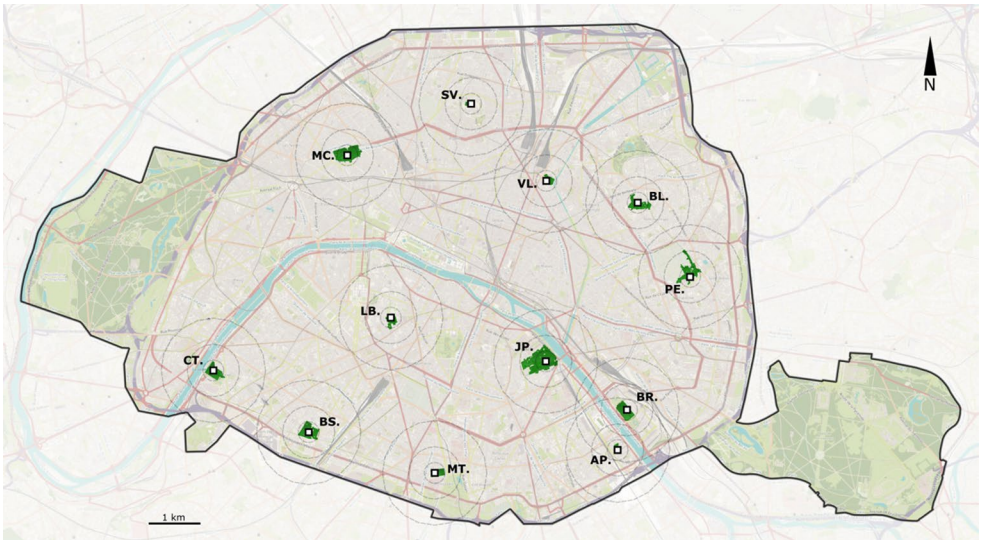


Fig. 1 Distribution map of survey sites. We highlighted the administrative boundaries of Paris, including the two main vegetated areas on the outskirts of the city: the Boulogne wood (west) and the Vincennes wood (east). Green spaces that include a survey site are colored in dark green (AP.: Jardin Abbé-Pierre; BL.: Parc de Belleville; BR.: Parc de Bercy; BS.: Parc Georges Brassens; CT.: Parc André Citroen; JP.: Jardin des plantes; LB.: Jardin Catherine Labouré; MC.: Parc Monceau; MT.: Réservoir Montsouris; PE.: Jardin Pierre-Emmanuel; SV.: Jardin Saint-Vincent; VL.: Jardin Villemin). Within each of these green spaces, white squares indicate the location of the survey site where the inventories of insect pollinators and flowering plants were carried out. Dashed circles represent the 200 m, 500 m, and 1000 m radii around each site (map base: © OpenStreetMap contributors)

Table 1 Landscape and local environmental characteristics of the survey sites. % Impervious: percentage of impervious surfaces within 200, 500, and 1000 m-radii around each survey site; Plant richness: total number of flowering plant species recorded in each survey site over the two years of the survey (% spont.: percentage of recorded plant species that are spontaneous); Rel. T°: mean temperature within a 200 m-radius in UHI conditions (August 16, 2016), relative to the mean Parisian temperature; Floral density: mean number of floral units per m² over the 2 years (% spont.: percentage of floral units provided by spontaneous species); Trees: number of entomophilous trees within a 200 m-radius around each survey site. Details on each site throughout the year are available in Online Resource 3

Site	Green space size *(m²)*	% impervious *(200–500–1000 m)*	Plant richness *(species nb. and % spont.)*	Rel. T° *(°C)*	Floral density *(/m² and % spont.)*	Trees *(200 m)*
AP.	7,245	83–95–81	30 (73% spont.)	-0.08	13.6 (73% spont.)	237
BL.	44,665	58–87–77	73 (30% spont.)	0.07	80.5 (18% spont.)	484
BR.	58,786	35–93–82	56 (41% spont.)	-0.27	73.8 (6% spont.)	483
BS.	58,540	44–90–77	72 (29% spont.)	-0.62	66.4 (7% spont.)	357
CT.	50,126	49–92–77	58 (52% spont.)	-0.55	131.4 (10% spont.)	528
JP.	161,540	26–83–79	54 (56% spont.)	-0.67	38.3 (24% spont.)	544
LB.	21,715	60–96–80	54 (19% spont.)	-0.69	63.1 (2% spont.)	222
MC.	97,361	37–93–87	65 (43% spont.)	-0.03	57.3 (37% spont.)	306
MT.	29,828	63–68–70	21 (100% spont.)	-0.89	16.2 (100% spont.)	103
PE.	61,547	55–62–72	39 (74% spont.)	0.07	29.4 (80% spont.)	456
SV.	7,809	70–83–84	29 (86% spont.)	-0.13	15.0 (76% spont.)	307
VL.	17,212	75–85–89	55 (16% spont.)	0.29	88.9 (14% spont.)	204

impervious surfaces surrounding each survey site (APUR 2015). All surfaces that were not covered in vegetation were considered impervious and quantified within 200 m, 500 m, and 1000 m of survey sites using QGIS software (QGIS Development Team 2016) (Table 1).

The studied green spaces also varied according to their local climatic conditions, resulting from differences in topography and urban planning. We evaluated the local intensity of the Urban Heat Island (hereafter UHI) effect by studying the temperature at each green space in hot summer night conditions (Aerial thermography on the 16 August 2016 – APUR, 2016). We calculated the mean temperature within 200 m of each survey site, and compared it to the city-wide average (the two Parisian woods removed) (Table 1). Such a radius was chosen because it corresponds to the maximum foraging distances of smaller pollinators, and it encompassed most of the surface of each green space, even the largest ones.

Insect collection

The study was conducted over two consecutive years (2019 and 2020) from early spring to early fall. Each survey site was visited once a month (between the 1st and 15th of the month), in alternating order, beginning in March and ending in October. April 2020 was skipped because of a lockdown due to the COVID crisis. All sites were sampled when weather conditions were favorable for insect pollinator activity (i.e., no rain, low wind speed, temperature above 10 °C), with two sites per day in alternating order. There were at least 3 weeks between visits to a single site. Sampling was conducted between 8:00 am and 3:00 pm (local solar time).

Insect pollinators were surveyed using two complementary collection methods: pan traps and active sampling along transects. Each month, two sets of pan traps (yellow, white, and blue) were set in each green space in open grasslands, at least 50 m apart from each other. They were left in position for 2 h while active sampling was performed. Upon retrieving the traps, insects were collected and preserved in ethanol (70%) before being processed in the laboratory. Active sampling was conducted along 50 m transects with insect nets and clear plastic boxes to catch pollinators on sight. Sampling was stratified, meaning that 50 m transects were subdivided into smaller segments representing three vegetation strata: grasslands, shrubs, and flowerbeds. The sizes of these segments were calculated in each green space to be representative of the local respective proportions of these strata. We walked along the transects monitoring the flowers and capturing all visible flower visitors, our reach extending 1 m on either side of the transect line and up to a height of 2 m, including flowers hanging from trees and bushes. Each transect was walked twice during each visit, with a 10 min interval between the two runs to allow for the return of disturbed insects. Captured insects were euthanized with ethyl acetate vapors.

Some unambiguously identifiable insects were either identified on the field or discarded after collection. However, most insects were pinned, dried, and labeled for identification by specialists. The majority (99.9%) of bees, hoverflies, butterflies, bee flies, and beetles were identified to the species level. The specimens are kept in collection at the iEES Paris laboratory.

Information on wild bee species nesting habits, diet, and sociality was obtained from several published trait databases (see the list of species and their traits in Online Resource 1). In addition, for each bee species, inter-tegular distance (ITD) was measured on up to three specimens for each sex, when sufficient individuals were available. Bee species were then classified as "small" (mean ITD < 2 mm) or "large" (mean ITD > 2 mm) based on the measurements of female bees (or male bees when no females were found). We focused on worker body size for eusocial species, which were all "large" anyway.

Plant inventory

Flowering plants were inventoried in each green space at each monthly visit to describe the resources available to pollinators and to characterize management practices. We identified flowering plants to the species level in five 1 m x 1 m quadrats, set up regularly along the 50 m insect sampling transect. In addition, we recorded plant species that were visited by foraging pollinators during the active sampling sessions. These data allowed us to compile lists of plant species representative of each green space surveyed, every month between March and October and over the two consecutive years of the study (see Online Resource 2).

Plants were categorized as either "spontaneous" or "ornamental". Here this distinction is based on the growing conditions of each plant at the precise location where it was observed. "Ornamental" plants were actively planted or sown by a gardener, whereas "spontaneous" plants ("weeds") grew freely from wild seeds or by vegetative reproduction. We calculated the proportion of inventoried plant species classified as "spontaneous" in each site (Table 1). The native status of each plant species in the Ile-de-France region was also considered (Jauzein and Nawrot 2011). However, we preferred to focus on the spontaneous flora rather than the native flora, as it better reflects greenspace management. In any case, the proportions of native plant species and spontaneous plant species were strongly correlated ($r_{Pearson}$=0.95, $p < 0.00001$).

Additionally, we counted the number of floral units in each 1 m x 1 m quadrat every month. A floral unit, as defined by Baldock et al. (2015), is an inflorescence or part of an inflorescence clearly separated from the others, that would require small pollinators to take flight to visit successively. Asteraceae capitula, but also some cymes, corymbs, umbels, and spikes bearing very small flowers, were thus classified as single floral units. For each site, we defined the floral density as the mean number of floral units per 1 m²-quadrat per two-month period (March-April / May-June / July-August / September-October), as flower availability fluctuates throughout seasons because of natural variations and management practices in the ornamental flower beds. We also calculated the proportion of these floral units provided by spontaneous plant species (Table 1, Online Resource 3).

As insect-pollinated tree species are widely planted in urban streets and parks and can provide important floral resources for pollinators (Somme et al. 2016), we counted the number of entomophilous trees within 200 m of all study sites using the open database of the Paris administration (Ville de Paris - DEVE 2021) complemented by our own inventories (Table 1).

Statistical analyses

All data analyses were performed on R software version 4.0.5 (R core team 2021). First, the absence of spatial autocorrelation was checked for pollinator species abundance and richness using Moran's test ("ape" package, function Moran.I) (Paradis and Schliep 2019) – no significant spatial autocorrelation was found for either of these variables (respectively $p = 0.24$ and $p = 0.98$).

We calculated the Chao estimator of the species richness (Chao 1984) based on abundance data, and generated rarefaction curves for all pollinators across all green spaces, then more specifically for bees ("fossil" package, function chao1; and "vegan" package, function specaccum) (Vavrek 2011; Oksanen et al. 2019).

We then used linear mixed models ("lme4" package, function lmer) (Bates et al. 2015) to study variations of pollinator abundance and species richness across green spaces according to environmental variables. We used a gaussian error distribution as it best respected model assumptions, as verified with "DHARMa" package (Hartig 2021). The best fit was obtained via stepwise variable selection with "LmerTest" package (Kuznetsova et al. 2017). We checked for multicollinearity since several of the landscape and local variables were correlated ("performance" package) (Lüdecke et al. 2021). Response variables were successively pollinator abundance and pollinator species richness per green space ($n = 12$), per year (2019/2020), and per two-month period (March-April / May-June / July-august / September-October; March-April 2019 was lacking due to the COVID crisis). Both response variables were log-transformed ($\ln(1 + x)$). Fixed effects were the proportions of impervious surfaces around each survey site (200 m, 500 m, and 1000 m radii), the green space size (square-root transformed), the relative UHI intensity (200 m radius), the number of entomophilous trees (200 m radius), and the recorded descriptors of local plant communities for a given two-month time period. These descriptors encompassed flowering plant species richness, the proportion of spontaneous plant species, the floral density (mean number of floral units per m²), and the share of floral density provided

by spontaneous plant species. In addition, we considered the survey site and the period nested in the year as random effects. We excluded managed honey bees from this analysis as their presence in urban habitats largely depends on local hive densities (Ropars et al. 2019).

We performed distance-based redundancy analysis (db-RDA) to determine which environmental variables are associated with dissimilarities across insect pollinator communities (based on Bray-Curtis distance which accounts for species distribution and abundances, capscale function of "vegan" package). Environmental variables were the same as those involved in abundance and species richness models, though here flowering plant community descriptors were calculated over the whole year (March to October). We performed stepwise selection (function ordistep, "vegan") to keep only the environmental variables that were the best predictors of pollinator community composition. The significance of constraints was assessed through ANOVA-like permutation tests with the anova.cca function ("vegan", 999 permutations). For this analysis, we excluded managed honey bees, as well as rare pollinator species, defined as those that represented less than 1/1000 of all catches (here corresponding to less than 5 catches) or species that occurred in one site only during the two years: this left 73 remaining species.

For each wild bee species found in our study, we analyzed the probability of occurrence per site and per year as a function of environmental variables, interacting with bee species traits. To this end, we used a generalized linear mixed model (GLMM) with a binomial error distribution (package "glmmTMB") (Brooks et al. 2017), treating the presence/absence of each species in each site. Again, environmental variables were the same as those involved in abundance and species richness models, calculated over the whole sampling season. Their effects on bee species occurrence were treated in interaction with bee species traits, encompassing body size (either "small": ITD < 2 mm; or "large": ITD > 2 mm), nesting habits (either "Above-ground" or "Below-ground"), pollen diet (either "Polylectic", "Oligolectic", or "Cleptoparasitic"), and sociality (either "Social" for eusocial and primitively eusocial species, or "Solitary"). Model selection was achieved through backward stepwise method to obtain the best fit on an AICc basis. Additional variables were the year (2019/2020) as a fixed effect, and the survey site (n = 12) and bee species (n = 57) as random effects. Again, for this analysis, we excluded rare species, defined as species that represented less than 1/1000 of total bee catches (here corresponding to less than 4 bee catches). This also excluded bee species that occurred in one site only during the two years.

For each model, we kept only one scale for the proportion of impervious surfaces, the one that provided the best fit to the data.

Results

Pollinator abundance and species richness

We inventoried 4880 insect pollinators, among which 3142 wild bees (belonging to 118 distinct native species, Online Resource 1), 410 Diptera (37 species of hoverflies and 3 species of bee flies), 140 Lepidoptera (belonging to 14 species), and 20 Coleoptera (belonging to 4 species). Managed honey bees represented 23.9% of identified pollinators (1168 individuals). We thus identified a total of 177 pollinator species across sites within the city of Paris, which represented 82.3% of the Chao estimator for all diurnal pollinators ($Chao_1 = 215.08$). Specifically, for bees, which are the dominant pollinator group in our sampling, we inventoried 119 species, accounting for 89.8% of the chao estimator ($Chao_1 = 132.6$) (including honey bees) (Online Resource 4). This indicates that our sampling method provides a rather exhaustive overview of the diversity of diurnal insect pollinators in Parisian green spaces.

Both pollinator abundance and species richness were positively associated with the number of plant species and green space size (Table 2; Fig. 2). However, pollinator abundance and species richness declined with the proportion of impervious surfaces in a 1000 m-radius (Table 2; Fig. 3).

Table 2 Best-fitting linear mixed models of pollinator abundance and species richness across green spaces. χ^2 and associated p-values give the results of Type-III Wald analysis of deviance. The two-month period nested in the year was an additional random effect in both models. Green space size is square-root transformed

Response	Predictor	Coeff. (± SE)	χ^2	p	AICc	r^2
All pollinator abundance *Ln(1 + x)*	% impervious (1000 m)	-0.12 ± 0.06	4.37	0.037	147.60	0.56
	Plant richness	0.32 ± 0.07	23.11	< 0.001		
	Green space size	0.16 ± 0.06	7.96	0.005		
All pollinator Richness *Ln(1 + x)*	% impervious (1000 m)	-0.10 ± 0.03	9.61	0.002	67.96	0.64
	Plant richness	0.19 ± 0.04	22.38	< 0.001		
	Green space size	0.17 ± 0.03	23.15	< 0.001		

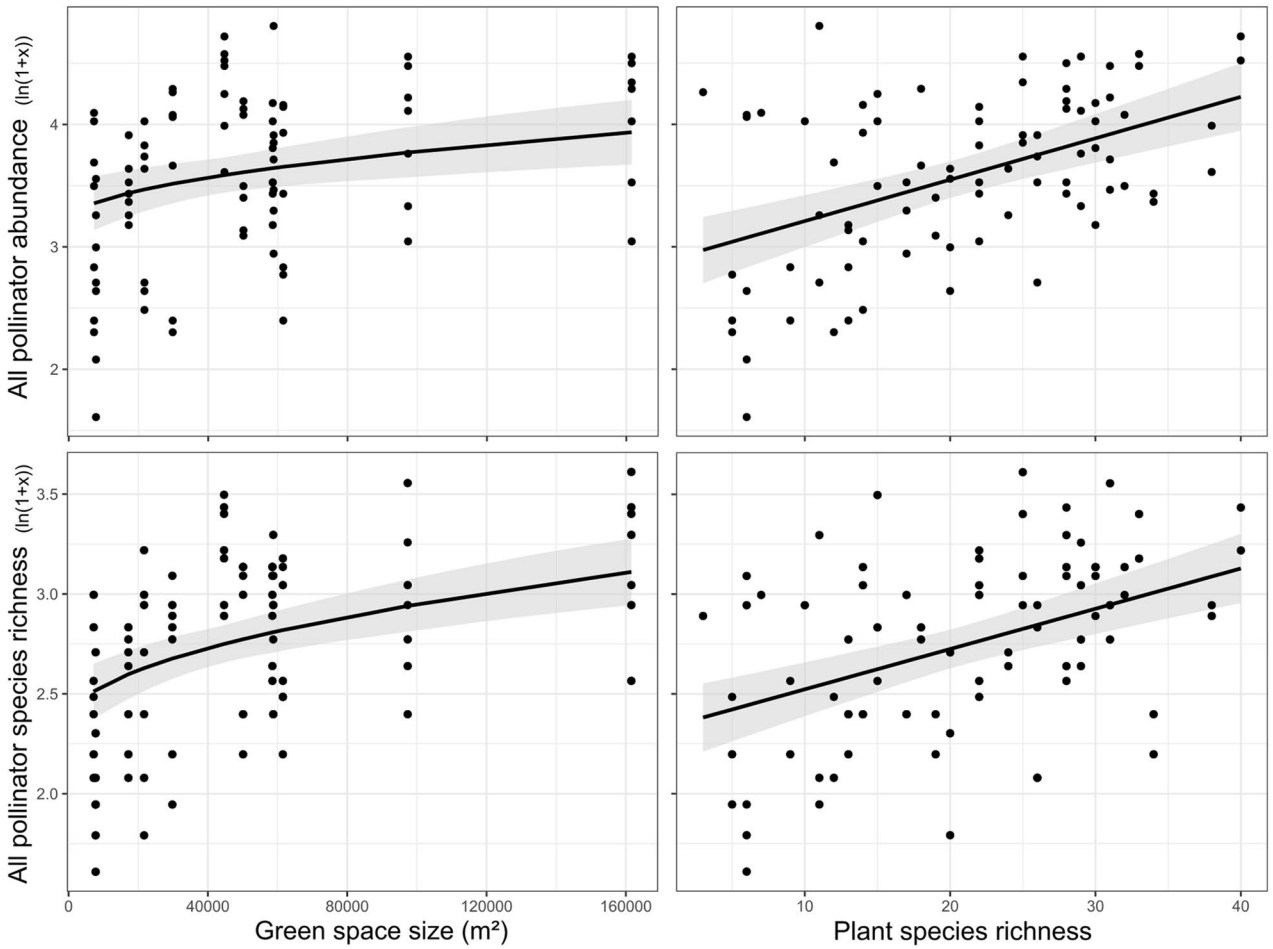
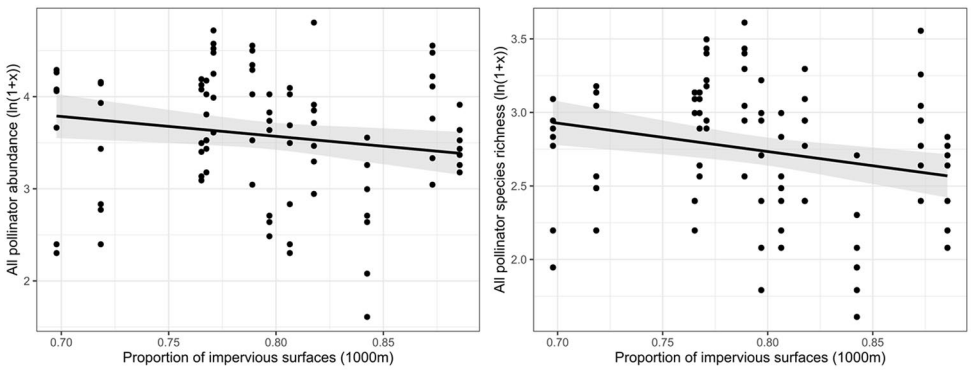


Fig. 2 Abundance and species richness of all pollinators in response to local drivers: green space size and the number of flowering plant species. Dots represent measures per site, two-month period, and year. Lines and intervals represent the predictions and SE from the linear mixed models

Fig. 3 Abundance and species richness of all pollinators in response to a landscape driver: the proportion of impervious surfaces in a 1000 m-radius around the survey sites. Dots represent measures per site, two-month period, and year. Lines and intervals represent the predictions and SE from the linear mixed models



Pollinator community composition

The db-RDA shows that shifts in pollinator community composition across green spaces, accounting for species abundances, were associated with only one of the measured habitat variables: the percentage of spontaneous plant species (999 permutations, pseudo-$F_{(1df)} = 1.80$, $p = 0.017$) (Fig. 4). However, this variable only explained up to 15.2% of total inertia, leaving most variation unexplained. Some bee species appear to contribute more than others to the dissimilarity between communities across green spaces: *Bombus pascuorum* (associated with a low percentage of spontaneous plants), and several species from the

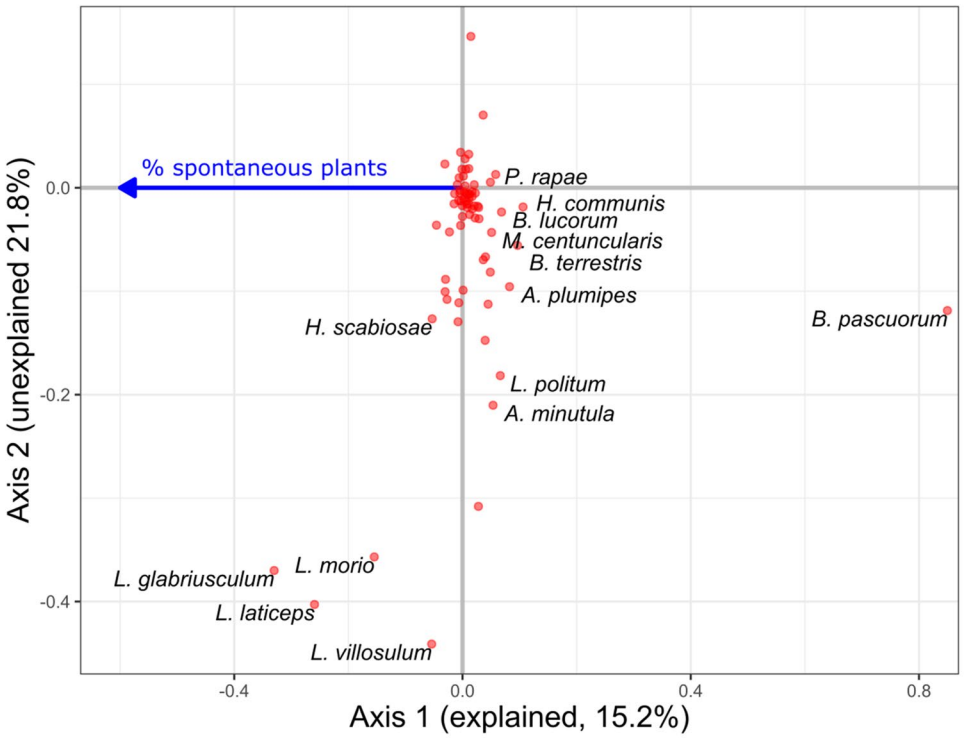


Fig. 4 db-RDA ordination of pollinator species, constrained by the percentage of spontaneous plant species within survey sites (blue arrow aligned with Axis 1). Red dots represent pollinator species; labeled species drive the most variation in community composition in response to spontaneous plants (coordinates on Axis 1 > 0.05 in absolute value). Only 15.2% of inertia is explained by habitat variables, thus most species are clustered near the center of the plot. Axis 2 illustrates further variation in community composition (21.8% of total inertia), unexplained by the habitat variables we measured

Table 3 Best-fitting generalized linear mixed model of bee species probability of occurrence, per site and per species depending on traits (binomial distribution; AICc = 1555.6, $R^2_{cond.}$ = 0.46). χ^2 and associated p-values give the results of Type-III Wald analysis of deviance. Green space size is square-root transformed. NS: non-significant. Spont. plants: spontaneous plant species. The percentage of impervious surfaces is calculated in a 500 m-radius around sites. Pollen diet: P., Polylectic; C., Cleptoparasitic; O., Oligolectic. Additional random effects included the Site and Bee species

Predictors of species occurrence			χ^2	p	Direction and Coefficient
Not interacting with traits:					
		Green space size	5.75	0.016	0.35 ± 0.15
		Year	3.33	0.068	NS
Interacting with traits:					
Body size	x	Intercept	1.42	0.233	NS
		% impervious	4.98	0.026	Large (-0.25 ± 0.19) < Small (0.10 ± 0.18)
		Plant richness	6.98	0.008	Large (0.57 ± 0.28) > Small (0.14 ± 0.28)
Pollen diet	x	Intercept	13.66	0.001	P. (0.78 ± 0.49) ≈ C. (-0.27 ± 0.77) > O. (-1.30 ± 0.80)
		% of spont. plants	6.66	0.035	P. (0.11 ± 0.28) ≈ C. (0.43 ± 0.50) < O. (2.6 ± 1.04)
		Plant richness	4.96	0.084	NS
Sociality	x	Intercept	6.93	0.008	Eusocial (0.78 ± 0.49) > Solitary (-0.26 ± 0.33)
		% impervious	2.81	0.094	NS
Nesting	x	Intercept	0.20	0.654	NS

Lasioglossum genus (*L. glabriusculum*, *L. laticeps*, and *L. morio*, associated with higher percentages of spontaneous plants).

Wild bee species probability of occurrence

Overall, oligolectic and solitary bee species had a lesser probability of occurrence than polylectic and social species respectively (Table 3). Moreover, environmental variables had significant effects on the probability of occurrence of wild bee species in each green space (Table 3). First, species occurrence rose with green space size, independent of the traits of bee species (Fig. 5a.). Also, we detected a negative effect of the proportion of impervious surfaces in the landscape (500 m radius) on species occurrence, although it was only detectable on large bee species and not on small ones (Fig. 5b.). In addition, plant species richness was positively associated with bee species occurrence, and this effect was

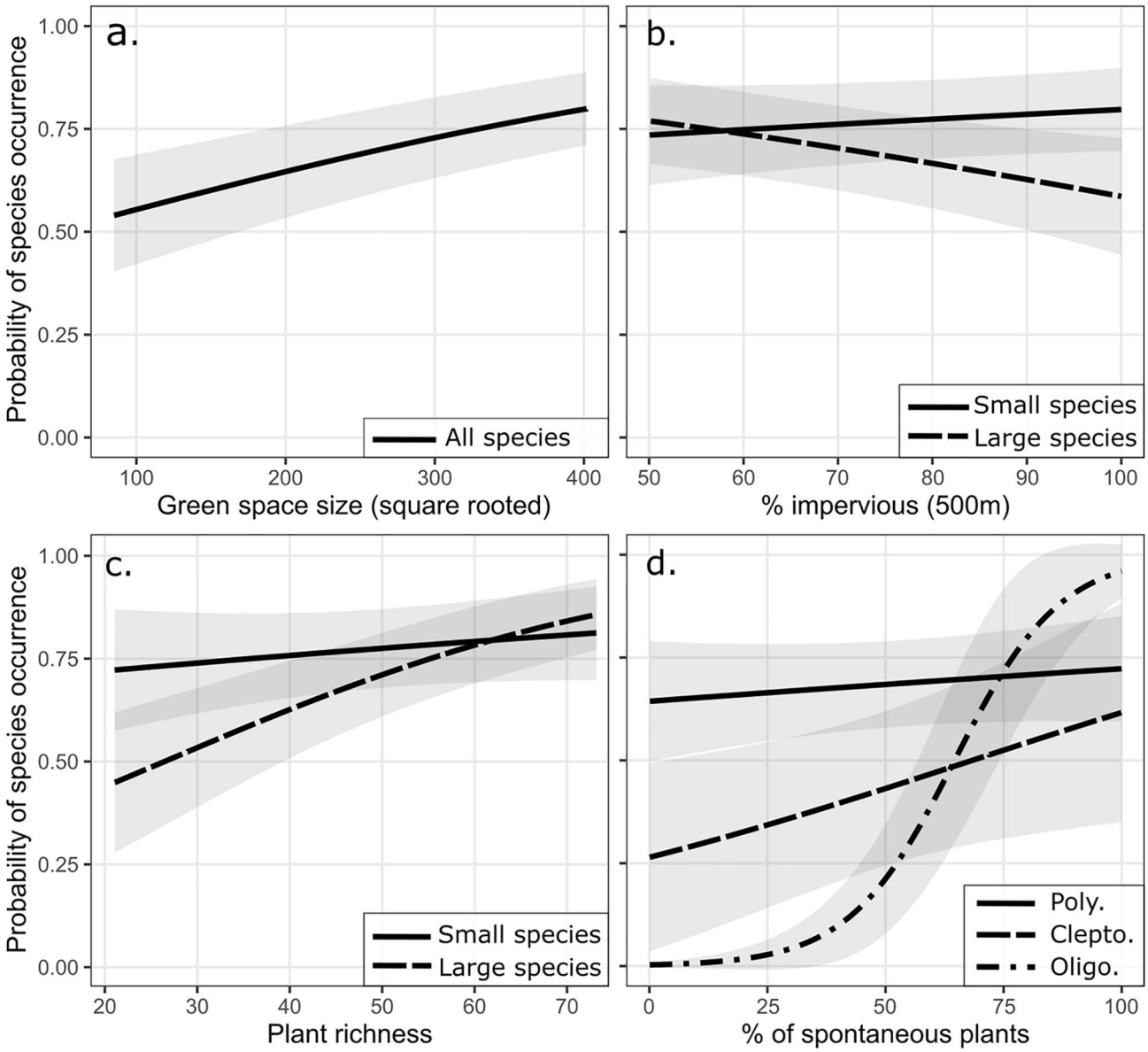


Fig. 5 Probability of occurrence of wild bee species in response to environmental variables: (a) the green space size (square-root transformed); (b) the percentage of impervious surfaces in a 500 m radius; (c) plant species richness; (d) the percentage of spontaneous plant species. Lines and intervals represent the predictions (± SE) from the GLMM presented in Table 3. For b. and c., species are categorized according to their size ("Small": ITD < 2 mm; or "Large": ITD ≥ 2 mm). For d., species are categorized according to their pollen diet ("Poly.": polylectic; "Clepto.": cleptoparasitic; "Oligo.": oligolectic)

more pronounced for large bee species (Fig. 5c.). Finally, plant management appears to be important, as there was a positive relationship between the occurrence of oligolectic bee species and the proportion of spontaneous plant species (Fig. 5d.); this relationship was not significant for polylectic and cleptoparasitic bees.

Discussion

Overall, we found both local (green space size, plant richness, and spontaneous plants) and landscape (impervious surfaces) environmental factors to impact pollinator communities in Paris, with local factors being stronger drivers of abundance and species richness.

There is growing evidence that large green spaces in urban landscapes can sustain abundant and diverse pollinator

communities (see Wenzel et al. 2020, for a review). Here, in the dense cityscape of Paris, we investigated the effects of the size of green spaces on the pollinator communities they support. As we expected, the area of contiguous greenspace was tied to pollinator abundance and species richness. Large green spaces hosted more pollinator species, with in particular more wild bee species likely to be found, regardless of their traits. Conversely, pollinator abundance and species richness declined with the proportion of impervious surfaces at the landscape scale (1000 m-radius), which is an indicator of urban built density.

Greenspace management was also critical, as evidenced by the relationship between pollinator diversity and local floral resources. As expected, plant species richness was strongly linked to overall pollinator abundance and species richness. However, we did not find a significant effect of flower density on pollinator diversity, contrary to Braatz et al. (2021), suggesting that the number of plant species is a better indicator of local floral resource availability. Nor did we detect any effect of the number of entomophilous trees at the landscape level. Since we sampled pollinators from 0 to 2 m in height, the insects we surveyed may not be customary tree visitors, and thus may not be reliant on the presence of trees. There was also no impact of relative temperatures across green spaces on pollinator communities. Thermal conditions may not vary enough within the dense Parisian landscape to contribute to differences between these communities. In our case, the temperature gradient varied between − 0.89 and + 0.29 °C around the city-wide mean temperature. In contrast, along an urban-rural gradient encompassing a 2.5 °C temperature gradient, Hamblin et al. (2018) recorded a significant negative impact of temperature on wild bee abundance.

Bees (Anthophila) represented the most abundant and most speciose pollinator group in our survey. Previous research has already been conducted in downtown Paris and resulted in a list of 93 bee species (Geslin et al. 2015; Ropars et al. 2018; Zaninotto et al. 2021). Here, with the inclusion of new green spaces and a broader inventory period, we have increased this number to 133; which fits well with the Chao estimator we calculated in this study ($Chao_1 = 132.6$). Consistent with some literature (Buchholz and Egerer 2020), we found that eusocial bee species were more prominent than solitary ones in this dense urban landscape; and polylectic bee species were more prominent than oligolectic ones. However, we did not find that polylectic species prevailed over cleptoparasites (brood parasites), unlike what has been reported in other studies (Banaszak-Cibicka and Dylewski 2021). Similarly, we found no influence of nesting habits, despite evidence that below-ground nesting bees are more sensitive to urbanization and impervious surfaces than above-ground nesting bees (Fortel et al. 2014; Geslin et al. 2016; Zaninotto et al. 2021). Such differences in nesting habits may not be relevant within a very dense urban landscape, like downtown Paris.

In addition, we found a positive effect of spontaneous flora on the occurrence of oligolectic bee species, which was expected. Indeed, to fulfill their life cycle, oligolectic bees depend on resources provided by their specific floral hosts, which are often native and spontaneous plant species (Minckley and Roulston 2002). Therefore, weed management in green spaces plays an important role in the functional diversity of bees. Urban green spaces where spontaneous plants prevail are unmanaged wastelands, known to be highly attractive to pollinators (Twerd and Banaszak-Cibicka 2019). At the other end of the management intensity gradient, we find the classical French gardens with various ornamental plants. In Paris, intensively managed gardens displayed high plant species richness and therefore supported abundant pollinator communities. But these communities might be lacking in functional diversity, as seen with the dominance of polylectic bee species. More generally, the share of spontaneous flora was the only environmental variable that contributed significantly to pollinator community dissimilarity across green spaces. The most common of these spontaneous plants were native weeds from the families Asteraceae (e.g. *Bellis perennis*, *Picris hieracioides*, *Taraxacum officinale*), Ranunculaceae (e.g. *Ranunculus repens*), Apiaceae (e.g. *Daucus carota*), and Fabaceae (e.g. *Trifolium repens*) (Online Resource 2). These results are consistent with evidence that spontaneous, and especially native, floral resources are crucial to sustaining diverse pollinator communities in urban landscapes (Lowenstein et al. 2019; Turo and Gardiner 2021). Here, green spaces with few spontaneous plants hosted communities dominated by the bumblebee *Bombus pascuorum*; while those rich in spontaneous plants were characterized by the presence of *Lasioglossum* bees. In the Paris region, Geslin et al. (2016) had previously shown that the population of some *Lasioglossum* species population decreased along an urbanization gradient. Thus, although *L. glabriusculum*, *L. laticeps*, and *L. morio* are polylectic and primitively eusocial species, they may be quite sensitive to urban constraints, and their range may be limited to weedy and lightly managed green spaces. In contrast, *B. pascuorum* is a highly generalist species that seems to thrive in urban green spaces and forage on ornamental garden flowers (Garbuzov and Ratnieks 2014; Theodorou et al. 2020).

Large bee species appeared to be more sensitive to the extent of impervious surfaces (500 m radius) than small ones. These large bees need more floral resources and have higher mobility which allows them to forage across green patches (Buchholz and Egerer 2020). Thus, they might be more constrained than small bees by landscape-scale urban

fragmentation beyond the edges of the surveyed green space. As shown by O'Connell et al. (2021), high levels of urban cover in the landscape reduce the mobility of bumblebees, in turn driving greater within-garden foraging patterns. Moreover, large bee occurrence was strongly related to overall plant species richness. Because of their large size, they may be able to draw resources from a broader diversity of flowers. Indeed, a larger size may be associated with a long tongue that allows deeper uptake of floral resources (Stang et al. 2009). Larger bees also have greater resource requirements, as they must maintain their massive bodies and provide for their likewise large offspring (Oliveira et al. 2016). For example, in an urban landscape, Hamblin et al. (2018) observed that floral density positively affected the abundance and species richness of large bees only. In general, large bees may be more dependent on the availability of abundant and diverse floral resources than smaller species.

Conclusion

Overall, our results indicate that, in a densely urbanized habitat, green space size is critical to maintaining pollinator diversity. Since it may be impractical to increase the extent of greenspace in a city center, efforts should be made to enhance the connectivity between vegetated areas (Goddard et al. 2010).

Local factors have been reported to be strong drivers of wild bee and butterfly species richness (Matteson and Langellotto 2010; Quistberg et al. 2016), suggesting that increasing flower availability is one of the best way to promote pollinator diversity within green spaces. Our data confirm that the overall abundance and species richness of insect pollinators rely on the diversity of local plant resources. We recommend that gardeners plant a wide variety of entomogamous plant species, paying particular attention to seasonal flowering successions. Indeed, as our approach spanned over most of the year (March to October), ensuring a sufficient floral display throughout seasons seems critical. Besides, our results suggest that native, spontaneous flora may be more valuable to sustain pollinator diversity. Such flora may be more suitable for specialist pollinators, including oligolectic bee species, thus contributing to functional pollinator diversity. Overall, we recommend reducing the frequency of mowing and maintaining or establishing wild patches of spontaneous plants to support insect pollinators in green spaces. At the city scale, the presence of lightly managed ruderal spaces would thereby not only host a diversity of pollinators but enhance all aspects of urban biodiversity.

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Data Availability All data is available on the open repository Zenodo, within the iEES-Paris community: 10.5281/zenodo.7772147

Declarations

Conflicts of interest/competing interests The authors declare no conflict of interest.

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Consent Not applicable.

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