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Vincent Zaninotto

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Vincent Zaninotto. Écologie et fonctionnement des communautés plantes-pollinisateurs en milieu urbain dense : l'exemple de la ville de Paris à travers les saisons. Biodiversité et Ecologie. Sorbonne Université, 2022. Français. NNT : 2022SORUS202 . tel-04143747

HAL Id: tel-04143747

<https://theses.hal.science/tel-04143747v1>

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Sorbonne Université

École doctorale 227 : Sciences de la Nature et de l'Homme,

Évolution et Écologie

iEES-Paris / DCFE / Équipe EERI

Écologie et fonctionnement des communautés plantes- pollinisateurs en milieu urbain dense

L'exemple de la ville de Paris à travers les saisons

Par Vincent Zaninotto

Thèse de doctorat d'Écologie Évolutive

Dirigée par Isabelle Dajoz

Présentée et soutenue publiquement le 27 juin 2022

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« Les quelques centaines de milliers d'êtres humains qui s'étaient rassemblés sur cet espace étroit avaient beau mutiler la terre sur laquelle ils s'entassaient ; ils avaient beau écraser ce sol sous des blocs de pierre afin que rien n'y pût germer, arracher toute herbe qui commençait à poindre, enfumer l'air de pétrole et de charbon, tailler les arbres, chasser bêtes et oiseaux, le printemps était toujours le printemps, même dans la ville. Le soleil était chaud. »

Léon Tolstoï, *Résurrection*, 1899 (trad. Edouard Beaux)

Remerciements

Aux membres du jury, qui ont accepté d'évaluer mes travaux avec enthousiasme,

À Isabelle, toujours radieuse et optimiste, si généreuse en encouragements, dont la bonne humeur m'a soutenu tout au long de ces années,

À Philippe ainsi qu'à toute l'équipe de la Division Biodiversité de la Ville de Paris, qui ont su me pardonner ma distance lors des périodes de terrain, de crise sanitaire et de rédaction,

À la Ville de Paris, ses élus et ses services, Sorbonne Université, ainsi qu'à l'ANRT, qui m'ont permis de mener à bien mon projet dans le cadre du dispositif CIFRE,

À mes collègues de l'institut, collaborateurs, coéquipiers, agents de restauration, et jeunes chercheurs, qui oeuvrent sans cesse à la convivialité à iEES-Paris, même lorsque les pandémies mondiales s'en mêlent,

À tous ceux qui m'ont prêté main forte sur le terrain, collègues de iEES-Paris, de la station écologique de Fontainebleau et du CEREEP de Foljuif, du MNHN et de la CIUP, ainsi que les nombreux stagiaires, qui ont tous su faire preuve de persévérance face aux éléments parfois capricieux,

Aux équipes de jardiniers du SEJ (Ville de Paris, DEVE), ainsi qu'aux agents de la serre de Jussieu, pour le partage de leurs connaissances botaniques, leur assistance et leur profonde bienveillance,

À ma famille et mes proches, qui m'ont toujours soutenu et fait confiance,

Aux Parisiens, visiteurs des espaces verts, curieux et badauds, ainsi qu'à leur oncle apiculteur,

Merci

Table des matières

INTRODUCTION GÉNÉRALE.....	6
1. Insectes pollinisateurs et fonction de pollinisation	6
2. Urbanisation et diversité des pollinisateurs	10
3. Une homogénéisation fonctionnelle et temporelle	16
4. Quelles solutions pour favoriser la diversité des pollinisateurs urbains ?	23
5. Problématiques.....	28
CHAPITRE 1	30
CHAPITRE 2	53
CHAPITRE 3	79
CHAPITRE 4	98
CHAPITRE 5	119
DISCUSSION GÉNÉRALE	141
1. Un milieu urbain relativement favorable	142
2. Milieu urbain et filtre fonctionnel.....	144
3. Milieu urbain et homogénéisation temporelle	147
4. Recommandations d'aménagement et de gestion	153
PERSPECTIVES.....	157
CONFÉRENCES ET COLLOQUES.....	158
ENSEIGNEMENTS.....	158
BIBLIOGRAPHIE	159
ANNEXES	183
TABLE DES FIGURES.....	196
TABLE DES TABLEAUX.....	197
TABLE DES ANNEXES.....	197

INTRODUCTION GÉNÉRALE

1. INSECTES POLLINISATEURS ET FONCTION DE POLLINISATION

1.1. Enjeux de la fonction de pollinisation

La pollinisation joue un rôle de support essentiel aux écosystèmes naturels et aux sociétés humaines (Potts et al., 2010). En effet, Ollerton et al. (2011) ont estimé à 87,5% la proportion de plantes à fleurs dont la reproduction est dépendante de la pollinisation animale, essentiellement assurée par les insectes en milieu tempéré. Parmi ces espèces végétales, de nombreuses plantes sont cultivées pour la production alimentaire ; si bien que selon les estimations, jusqu'à 35% du volume de production agricole mondiale dépend directement des pollinisateurs (Klein et al., 2007) (**Figure 0. 1**). Ainsi, Gallai et al. (2009) ont pu calculer, à l'aide d'un modèle bioéconomique, la valeur économique globale annuelle du service écosystémique de pollinisation animale. En 2005, elle atteignait 153 milliards de dollars. La préservation de la fonction de pollinisation, par son rôle clé dans le maintien de la biodiversité et dans la production alimentaire, est donc un enjeu majeur du développement durable. Par conséquent, il est fondamental d'analyser la réponse et les capacités de résilience de cette fonction écologique face aux changements globaux.

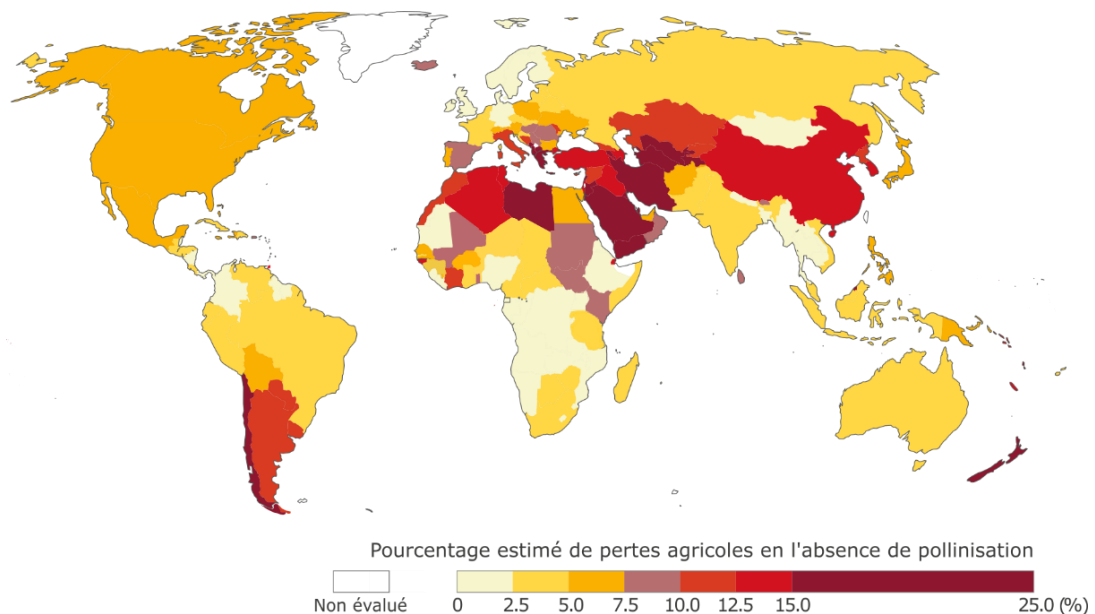


Figure 0. 1 . Carte mondiale des dépendances de l'agriculture à la pollinisation d'origine animale en 2012, en pourcentage du volume de production perdu en l'absence de pollinisation. Si les cultivateurs de céréales sont moins touchés, les grands producteurs de fruits, et dans une moindre mesure d'oléagineux, sont très sensibles (à partir de données de la FAO, Aizen et al., 2016).

1.2. Zoogamie et diversité des pollinisateurs

La pollinisation zoogame repose sur des transferts involontaires de pollen entre plantes conspécifiques, opérés par des animaux. Ces animaux visitent les fleurs pour y récolter des ressources trophiques (nectar, pollen), tout en assurant reproduction et brassage génétique pour les plantes. Il s'agit donc d'une relation de mutualisme, générant des bénéfices réciproques (Waser, 2006). Cette relation est le fondement d'une coévolution entre plantes et pollinisateurs, se traduisant par une grande diversification de traits morphologiques, physiologiques et comportementaux, et à l'origine de la diversité des espèces de pollinisateurs et de plantes à fleurs que l'on peut observer aujourd'hui (Bascompte, 2019; Guimarães et al., 2011). Mammifères, lacertiliens, oiseaux, mais surtout insectes, les pollinisateurs se retrouvent dans de nombreuses classes d'animaux (Ollerton, 2017) (**Tableau 0. 1**). Cependant, en France métropolitaine, la quasi-totalité des pollinisateurs sont des insectes ; on parle alors d'entomogamie.

Au sein des insectes, les lépidoptères, les coléoptères, les diptères et les hyménoptères sont les ordres parmi lesquels on trouve le plus d'insectes floricoles, dont certains ne consomment que des ressources florales (Waser, 2006). C'est le cas des abeilles (Hyménoptères, clade Anthophila). Chez ces insectes, les stades adultes se nourrissent de nectar, et les femelles accumulent des réserves de pollen pour alimenter les larves (Michener, 2007). Ainsi entièrement inféodées aux ressources florales, les abeilles constituent des pollinisateurs de grande importance. Parmi les abeilles, l'espèce la plus connue est l'abeille à miel européenne (*Apis mellifera*), largement domestiquée, et qui forme des colonies eusociales regroupant plusieurs dizaines de milliers d'ouvrières (Michener, 2007). Cette espèce est d'autant plus reconnue que son élevage constitue un secteur économique à part entière, générant miel et produits de la ruche, ainsi que des services de pollinisation pour l'agriculture. L'abeille domestique joue également le rôle d'espèce « porte-drapeau » du militantisme environnementaliste : c'est une espèce emblématique mise en avant pour promouvoir la protection des écosystèmes (Iwasaki & Hogendoorn, 2021).

Mais il existe en réalité un très grand nombre d'abeilles sauvages, que l'on retrouve dans la plupart des biotopes (Michener, 2007). Au niveau global, plus de 17 000 espèces ont été recensées (Michener, 2007), dont près de 2000 en Europe (Nieto et al., 2014). En France, on compte près d'un millier d'espèces d'abeilles sauvages (961 d'après Ropars et al., 2020), une large majorité étant méconnue du grand public. Aucune de ces abeilles sauvages ne présente de structure sociale aussi développée qu'*Apis mellifera*, qualifiée d'« hautement eusociale ». En effet, parmi les espèces d'abeilles sauvages indigènes en France, la plupart sont solitaires. On rencontre toutefois quelques espèces sauvages eusociales, dont les colonies ne comptent pas plus de quelques centaines d'ouvrières (bourdons et certaines Halictidae), ainsi que d'autres formes de socialité moins complexes (Michener, 2007). Enfin, les autres ordres d'insectes ne sont pas à négliger car ils participent considérablement à la fonction de pollinisation : c'est le cas des lépidoptères, surtout nocturnes (Hahn & Brühl, 2016), qui constituent l'ordre d'insectes pollinisateurs le plus riche en termes d'espèces ; mais aussi des diptères, notamment les syrphes (Doyle et al., 2020; Orford et al., 2015) ; et des coléoptères (Sayers et al., 2019). Cette diversité des communautés de pollinisateurs est cruciale, car elle détermine l'efficacité de la fonction de pollinisation (Loy & Brosi, 2022).

Tableau 0. 1. Nombre estimé d'espèces de pollinisateurs dans le monde, par taxon (données issues de Olesen & Valido, 2003; Ollerton, 2017; Regan et al., 2015; Wardhaugh, 2015).

Taxon	Nombre d'espèces de pollinisateurs
Insecta (insectes)	347 487
Lépidoptères (papillons de jour et de nuit)	141 600
Coléoptères (dont scarabées, cétoines etc.)	77 300
Hyménoptères (dont guêpes, abeilles, fourmis)	70 000
Diptères (dont syrphes, bombyles et mouches)	55 000
Thysanoptères (thrips)	1 500
Hémiptères (punaises)	1 000
Autres insectes	1 087
Collemboles	400
Aves (oiseaux)	1 089
Mammalia (mammifères)	344
Lacertilia (lézards)	37

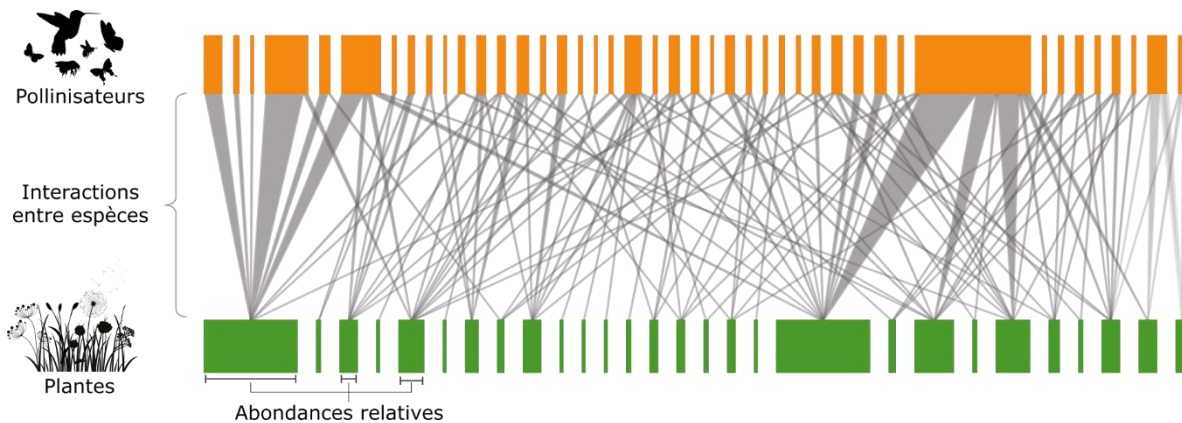
1.3. Réseaux d'interactions plantes-pollinisateurs

C'est à travers l'approche des réseaux mutualistes que s'est récemment développée l'étude des interactions entre les communautés de plantes et de pollinisateurs (Bascompte, 2019). Les réseaux, parfois complexes, formés par ces interactions sont dits « bipartites », car ils associent deux ensembles distincts d'organismes : les plantes, et les pollinisateurs (**Figure 0. 2**). Au sein de ces réseaux, les espèces de pollinisateurs se distinguent par leurs préférences et leur capacité à collecter du pollen sur différents types de fleurs. On peut parler de lectisme : une espèce polylectique récolte du pollen sur un grand nombre d'espèces de plantes, alors qu'une espèce oligolectique a des préférences marquées pour certaines plantes bien précises. Plus rarement, un pollinisateur ne dépend que d'une seule espèce de plante, il s'agit alors de monolectisme (Willmer & Stone, 2004). Ainsi, on trouve des espèces généralistes, qui interagissent avec des partenaires nombreux et variés ; tandis que d'autres espèces sont plutôt spécialistes, n'interagissant qu'avec un petit nombre de partenaires bien définis (Minckley & Roulston, 2002). Ce continuum entre généralistes et spécialistes s'observe aussi chez les plantes, selon les interactions auxquelles elles prennent part. Les préférences des pollinisateurs au sein des réseaux d'interactions dépendent de leurs traits fonctionnels (Coux et al., 2016), et ce sont les communautés de pollinisateurs les plus diversifiées fonctionnellement qui maintiennent la plus grande diversité végétale (Fontaine et al., 2006).

Selon les propriétés et la structure des réseaux d'interactions plantes-pollinisateurs, l'on peut estimer leur stabilité dans le temps et leur robustesse face aux perturbations et aux extinctions. Les réseaux de pollinisation se distinguent souvent par des structures particulièrement emboîtée (« nested ») (Bascompte et al., 2003; Thébault & Fontaine, 2010). C'est-à-dire que les interactions réalisées par les spécialistes sont des sous-échantillons de l'ensemble des interactions réalisées par les généralistes. Il existe donc des redondances fonctionnelles entre les interactions des spécialistes et des généralistes. Ainsi, malgré la disparition d'un pollinisateur spécialiste, l'ensemble des plantes qu'il visitait peuvent toujours être pollinisées par les pollinisateurs généralistes subsistants. De plus, les réseaux sont asymétriques ; ce qui signifie que lorsqu'une espèce dépend fortement de l'un de ses partenaires, cette dépendance n'est souvent pas réciproque (Bascompte et al., 2006). On considère que cette

structure emboîtée et asymétrique assure une plus grande stabilité des réseaux face aux perturbations et à l'extinction des espèces (Tylianakis et al., 2010).

Figure 0. 2. Schéma d'un réseau d'interaction plantes-pollinisateurs. Les interactions de la première plante à gauche illustrent l'emboîtement et l'asymétrie du réseau : plusieurs pollinisateurs spécialistes interagissent uniquement avec une même plante, généraliste, qui a de multiples partenaires (issu de Aizen et al., 2016).



2. URBANISATION ET DIVERSITÉ DES POLLINISATEURS

2.1. Les insectes pollinisateurs face aux changements globaux

Depuis plusieurs décennies, les communautés d'insectes font face à un déclin considérable. Ceci se manifeste par une perte de diversité à l'échelle mondiale, puisqu'on estime que 40 % des espèces d'insectes sont menacées d'extinction dans les années à venir (Sánchez-Bayo & Wyckhuys, 2019). Cette proportion est deux fois plus élevée que pour les vertébrés, bien que ceux-ci suscitent un effort de conservation plus important. Les niches écologiques laissées vacantes par les espèces disparues sont alors occupées par des espèces ubiquistes et généralistes. De plus, on constate des pertes d'abondance, avec un déclin de 2,5% de la biomasse des insectes par an au niveau global (Sánchez-Bayo & Wyckhuys, 2019). Ce déclin, qui touche particulièrement les insectes aquatiques, n'épargne pas les populations terrestres, notamment chez les hyménoptères, lépidoptères, et coléoptères. Ce phénomène affecte même les milieux naturels, comme l'illustre la perte de 75% de la biomasse d'insectes dans les aires protégées allemandes au cours des dernières décennies (Hallmann et al., 2017). Cette crise mondiale de la diversité des insectes constitue une menace pour les insectes pollinisateurs, dont les abeilles, et pour la fonction de pollinisation (Potts et al., 2010; Zattara & Aizen, 2021).

Les principaux facteurs à l'origine de cette crise sont les pertes d'habitat, les pollutions chimiques, la dispersion de pathogènes et d'espèces introduites, ainsi que le réchauffement climatique (IPBES, 2016; Potts et al., 2010; Sánchez-Bayo & Wyckhuys, 2019). Les changements d'usages des terres, qui occasionnent des pertes d'habitats, sont souvent considérés comme le facteur principal de déclin à l'échelle globale. Ils résultent de la conversion de paysages naturels en paysages artificialisés, à travers les processus d'urbanisation et de déforestation, mais surtout lors de la création de terres agricoles. Ce faisant, les habitats des espèces sauvages sont directement détruits, ou bien fortement fragmentés. À cela s'ajoutent les pressions exercées par les polluants chimiques, principalement les pesticides de synthèse. Leur déploiement est tributaire des pratiques agricoles, et donc en interaction avec les conversions des terres. Les insecticides, parfois en synergie, soumettent les insectes à des effets toxiques létaux et sublétaux, tandis que les herbicides réduisent les ressources disponibles. Par ailleurs, les activités humaines sont à l'origine d'introductions massives d'espèces envahissantes et de pathogènes qui menacent les communautés d'insectes. Ceci se manifeste notamment par les nombreux agresseurs biologiques (*Varroa destructor*, *Vespa velutina*, *Aethina tumida*, *Nosema* sp. etc.) qui s'attaquent aux élevages d'abeilles domestiques (*Apis mellifera*) en Europe, déjà affaiblis par les pesticides. Enfin, le réchauffement climatique devrait contraindre les espèces sauvages à modifier leurs répartitions géographiques pour se conformer à leurs niches thermiques. Toutefois, un tel déplacement pourrait s'avérer impossible pour les espèces déjà installées aux plus hautes latitudes et altitudes.

2.2. L'urbanisation : un changement extrême d'habitat

Les écosystèmes terrestres font face à une urbanisation croissante qui menace les habitats naturels et la biodiversité. Ainsi, de 2000 à 2030, la surface urbaine globale aura vraisemblablement triplé (Seto et al., 2012). Dès aujourd'hui, la moitié de la population mondiale réside en ville, et l'Europe est une des régions du globe les plus urbanisées (ONU, 2018). L'urbanisation se traduit par des modifications extrêmes du milieu : imperméabilisation des sols et changement des régimes hydriques, modifications des climats locaux et des cycles biogéochimiques, perturbations directes par les activités et équipements humains, pollutions multiples, introductions d'espèces exotiques etc. Ces conditions sont à même de modifier

profondément les dynamiques éco-évolutives des organismes qui persistent en milieu urbain (Alberti, 2015). Aussi l'urbanisation représente-t-elle une composante majeure des changements globaux, qui pèse sur l'avenir des écosystèmes naturels, et place l'écologie urbaine au cœur des enjeux globaux de durabilité (Grimm et al., 2008). Cette discipline figure donc parmi les domaines scientifiques émergents les plus actifs en écologie.

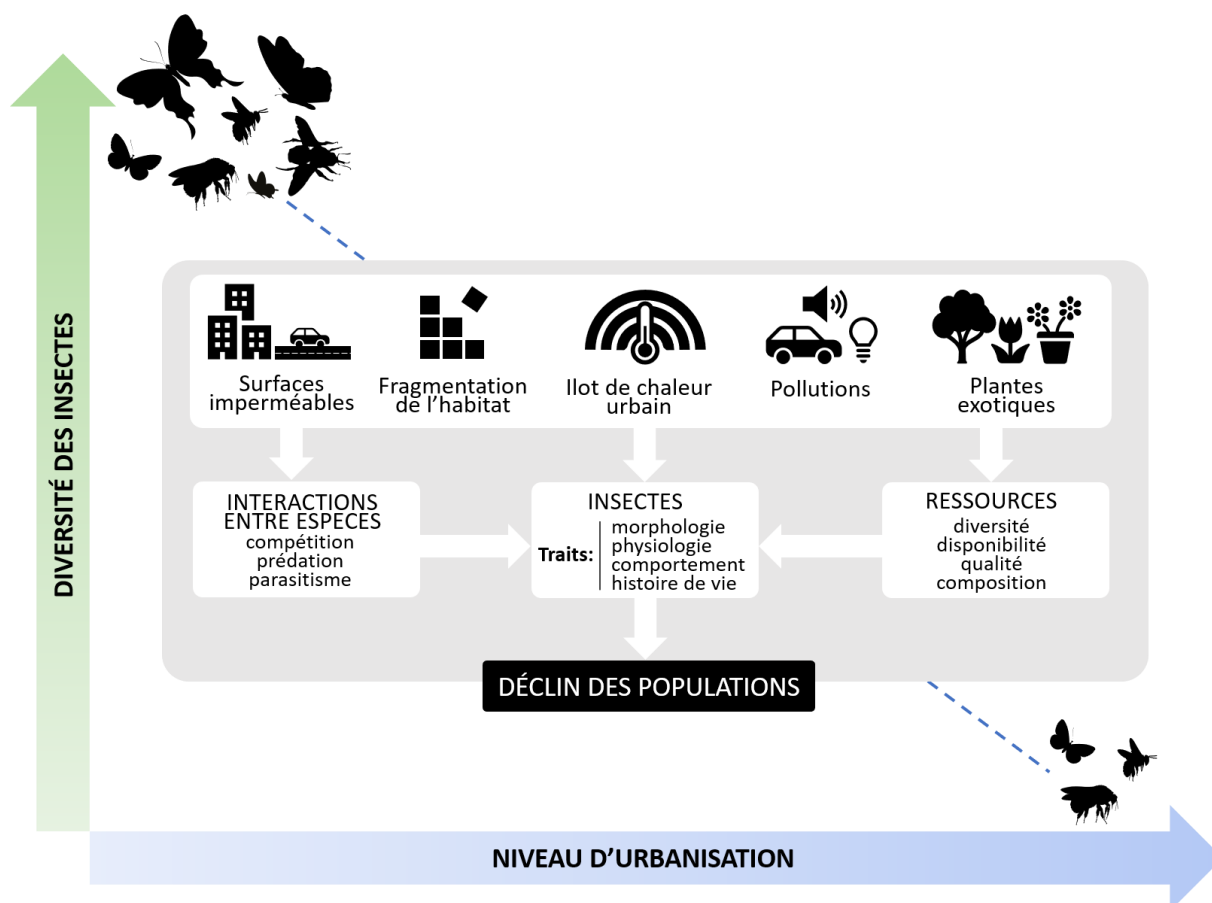


Figure 0. 3. Schéma des facteurs et des processus à l'origine d'une réduction de la diversité des insectes pollinisateurs selon le niveau d'urbanisation. Les différents facteurs environnementaux illustrés sont susceptibles d'affecter directement les insectes, en fonction de leurs traits ; ou bien de les affecter indirectement via l'altération des ressources et des interactions biologiques (inspiré de Fenoglio et al., 2021).

L'urbanisation génère des conséquences néfastes sur l'abondance et la diversité des arthropodes, avec de fortes variations selon les groupes taxonomiques. Les insectes floricoles ne sont pas épargnés : les contraintes urbaines se révèlent souvent délétères pour leurs communautés (Deguines et al., 2012; Harrison & Winfree, 2015), et en particulier concernant les coléoptères et lépidoptères (Fenoglio et al., 2020). Ainsi, l'urbanisation structure les

assemblages de pollinisateurs, et limite leurs densités de population (A. J. Bates et al., 2011; Fortel et al., 2014), de façon directe ou indirecte (**Figure 0. 3**). Par exemple, Geslin et al. (2013) ont montré que l'activité de butinage sur des répliques d'une même communauté de plantes était moins importante en milieu urbanisé qu'en milieu semi-naturel. La subsistance des insectes pollinisateurs en ville est également compromise par l'appauvrissement des communautés végétales. Conséquence de l'imperméabilisation massive des sols et de l'élimination de la végétation spontanée, cet appauvrissement réduit l'offre en ressources végétales nécessaires à l'alimentation et à la nidification des insectes pollinisateurs (nectar, pollen, fibres, feuilles, résines) ; et fait disparaître les partenaires préférentiels des pollinisateurs spécialistes. D'autre part, l'imperméabilisation des sols réduit la disponibilité de sites de nidification pour les espèces terricoles, comme le sont pourtant de nombreuses abeilles sauvages (Geslin et al., 2016; Potts et al., 2010). En outre, les insectes pollinisateurs urbains font face à diverses pollutions chimiques (Baldock, 2020), mais aussi sonores ou lumineuses (Harrison & Winfree, 2015). Les conditions climatiques urbaines, avec des températures généralement plus chaudes qu'en milieu rural, peuvent aussi nuire aux communautés de pollinisateurs. Ainsi, à Raleigh (Caroline du Nord, USA), un écart d'un degré de température moyenne est associé à une perte de 40 % de l'abondance d'abeilles (Hamblin et al., 2018).

2.3. Des communautés urbaines adaptées

Les villes ne sont pourtant pas des milieux dénués de biodiversité, notamment en ce qui concerne la faune pollinisatrice. Souvent entourées de milieux agricoles intensifs, les villes peuvent offrir aux pollinisateurs une plus grande diversité de ressources alimentaires et de sites de nidification (Baldock et al., 2015; Hall et al., 2017). Ainsi, des communautés relativement riches de pollinisateurs sauvages ont été répertoriées dans des grandes villes comme Lyon (Fortel et al., 2014), Paris (Geslin et al., 2015), New-York (Matteson et al., 2008) et Chicago (Lowenstein et al., 2014). Les milieux urbains et périurbains auraient le potentiel pour constituer de véritables « refuges » pour la faune pollinisatrice, en opposition aux zones agricoles intensives (Hall et al., 2017) (**Figure 0. 4**). Il ne faut pas pour autant négliger les contraintes avec lesquelles doivent composer les insectes pollinisateurs sauvages qui persistent en milieu urbain. Ces contraintes environnementales peuvent avoir des effets différents selon

les traits des espèces (**Figure 0. 3**). Typiquement, certaines espèces s'accommodent mieux que d'autres aux facteurs de stress urbains.

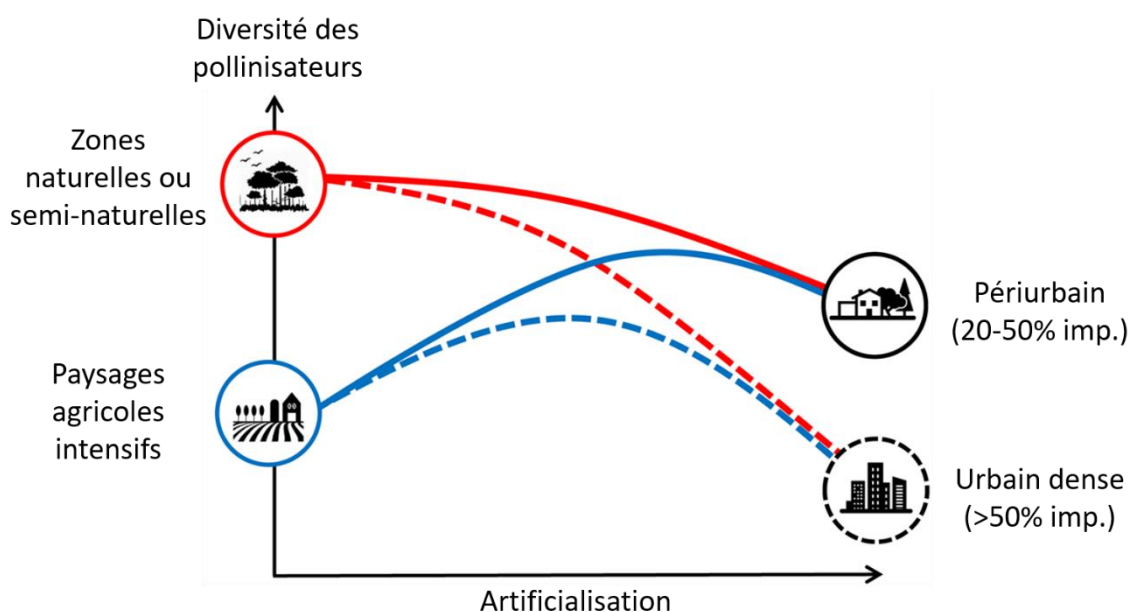


Figure 0. 4. Comparaison théorique de la diversité des pollinisateurs en milieu naturel, agricole, périurbain, et urbain dense. À noter que selon la densité du bâti (ici, pourcentage de surfaces imperméabilisées), cette diversité peut être supérieure à celles des paysages agricoles, mais reste inférieure à celle des zones naturelles (issu de Wenzel et al., 2020).

Dans un paysage urbain dense, les habitats favorables se limitent essentiellement aux espaces verts. Selon leur aménagement et leurs pratiques de gestion, ceux-ci n'offrent pas tous les mêmes conditions d'accueil pour les espèces sauvages. Par conséquent, l'abondance et la diversité des insectes pollinisateurs sont très variables en fonction des catégories d'espaces verts. Il apparaît souvent que les espaces les plus précieux pour les pollinisateurs sont ceux qui disposent d'une grande diversité florale, tels que les jardins privés et les jardins partagés (Baldock et al., 2019) ; dont certains peuvent être qualifiés de « hotspots » de diversité. Ceci illustre le rôle fondamental des pratiques de gestion des espaces verts urbains dans leur capacité à accueillir des communautés de pollinisateurs diversifiées. Avec leur absence totale de gestion, les friches urbaines, plus sauvages, semblent aussi être des habitats adéquats, en substitution des espaces naturels (Twerd & Banaszak-Cibicka, 2019). Cependant, dans les paysages urbains denses, les jardins privés et partagés sont rares, tandis que les friches sont souvent temporaires.

2.4. Un milieu fragmenté

Par ailleurs, les espaces verts urbains sont souvent isolés les uns des autres au sein d'un paysage artificialisé. Cette fragmentation les rend analogues à des îlots répartis dans une matrice inhospitalière (Wang et al., 2022) (**Figure 0. 5**). Elle s'oppose aux migrations, aux transferts génétiques, et à la survie des populations. Bien que dotés de la capacité de vol, les insectes pollinisateurs sont des organismes de petite taille, limités dans leurs capacités de dispersion et leurs distances de prospection alimentaire (Geslin et al., 2016). La fragmentation de l'habitat est donc susceptible d'altérer leur comportement de butinage, et donc d'influencer la structure des interactions plantes-pollinisateurs (Harrison & Winfree, 2015). De manière générale, les distances maximales de prospection sont étroitement liées à la taille des individus (Greenleaf et al., 2007). Ainsi, des insectes plus volumineux sont capables de parcourir de plus grandes distances d'un espace vert à un autre pour rechercher de la nourriture. En revanche, les insectes plus petits ont des besoins en ressources plus modestes, qu'ils peuvent satisfaire en demeurant au sein d'un même espace vert (Harrison & Winfree, 2015). Par ailleurs, les espèces eusociales semblent être avantagées face à la fragmentation, telle l'abeille domestique qui butine dans un rayon pouvant dépasser 5 km lorsque les ressources sont éparées (Beekman & Ratnieks, 2000). Aussi les conséquences de la fragmentation des habitats sont-elles très variables d'un pollinisateur à l'autre.

Une solution régulièrement mise en avant pour promouvoir la biodiversité en ville est la création de vastes espaces verts. Ceux-ci sont associés à de plus grandes abondances, diversité taxonomique, et diversité fonctionnelle des pollinisateurs (Ayers & Rehan, 2021; Majewska & Altizer, 2020; Wenzel et al., 2020). Toutefois, les espaces verts de tailles réduites ont aussi leur utilité, car ils peuvent former des réseaux interconnectés qui améliorent la perméabilité de la matrice urbaine (Shwartz et al., 2013). C'est également le cas de certaines « infrastructures vertes », telles que les toitures et parois végétalisées. Quand ces infrastructures offrent une flore et des habitats diversifiés, elles peuvent soutenir des communautés d'insectes variés, bien qu'elles ne se substituent pas aux habitats au niveau du sol (Braaker et al., 2017; Filazzola et al., 2019). Dans une perspective de renaturation, ces nouveaux espaces verts permettent de

multiplier les habitats favorables et de renforcer les corridors écologiques au sein d'une matrice urbaine dense, où la pression foncière est grande (Fenoglio et al., 2021; Wang et al., 2022).



Figure 0. 5. Schéma des conséquences progressives de la fragmentation de l'habitat sur les pollinisateurs dans un contexte d'urbanisation. Les rectangles verts représentent l'habitat favorable, réduit à des îlots de plus en plus réduits et isolés dans une matrice artificialisée (mini-cartes ; rouge : urbain dense, gris : urbain, jaune : agricole, verts : milieux naturels) (issu de Kovács-Hostyánszki et al., 2016).

3. UNE HOMOGENÉISATION FONCTIONNELLE ET TEMPORELLE

3.1. Filtrage et homogénéisation fonctionnels en milieu urbain

En faisant obstacle à l'installation de certaines espèces, les contraintes environnementales du milieu urbain appliquent un filtrage fonctionnel aux communautés biologiques (Alberti, 2015). Les assemblages urbains de pollinisateurs ne sont souvent que des sous-ensembles des assemblages des milieux naturels régionaux, caractérisés par leur tolérance aux conditions urbaines (Fournier et al., 2020). Ce sont des traits précis qui sont sélectionnés en ville, au détriment d'autres (**Figure 0. 3**, **Figure 0. 6**). Ainsi, de façon classique, on constate que les

communautés d'abeilles urbaines comprennent moins d'espèces terricoles, d'espèces spécialistes, d'espèces solitaires, et d'espèces à émergence précoce, que les communautés rurales (Buchholz & Egerer, 2020; Wenzel et al., 2020). Au contraire, le milieu urbain semble favoriser les abeilles généralistes, eusociales, ou bien rubicoles (qui nichent dans des tiges creuses) (Figure 0. 6).

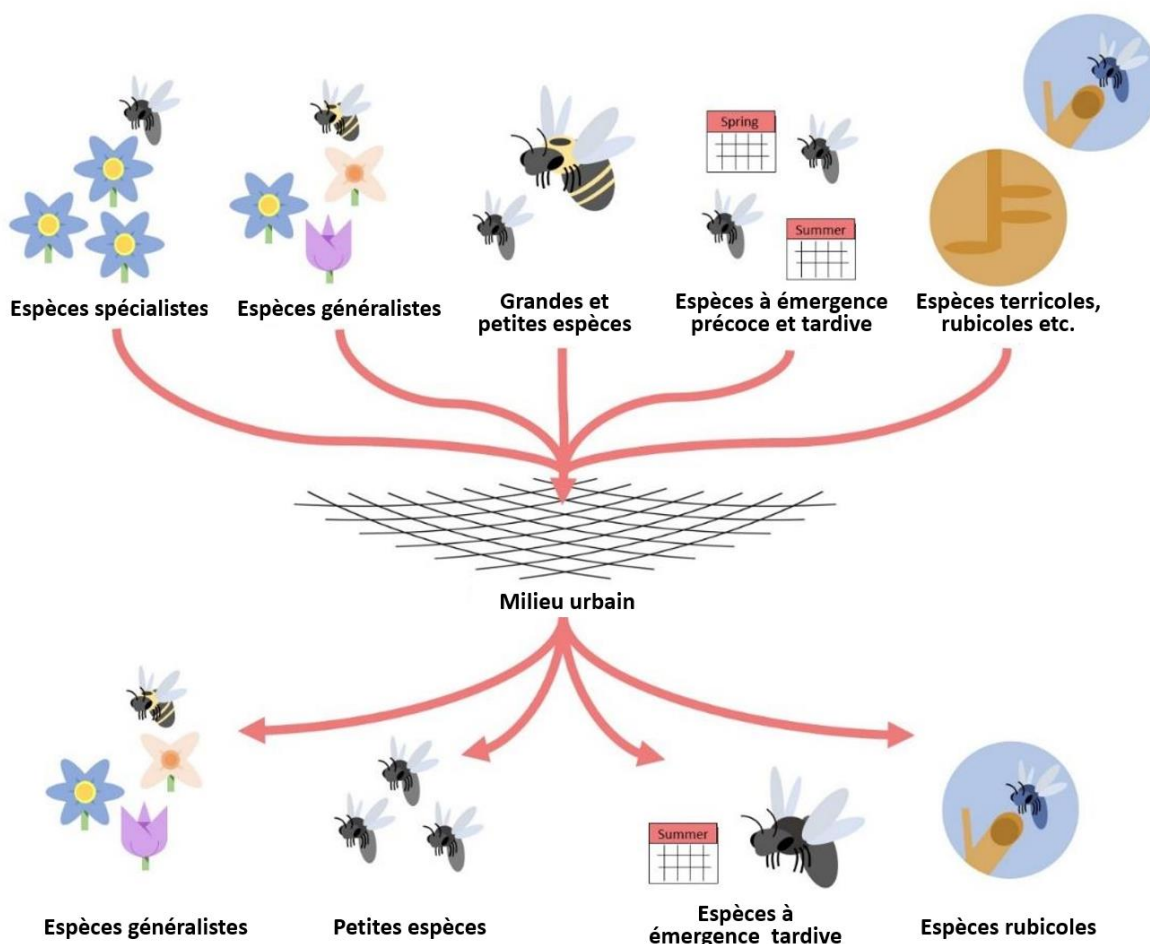


Figure 0. 6. Schéma simplifié du phénomène de filtrage fonctionnel des communautés d'abeilles sauvages en milieu urbain. Celui-ci est assimilé à crible ne laissant filtrer que les espèces dotées de certains traits : généralisme, petite taille, émergence tardive et nidification rubicole. Dans la littérature, ces traits sont souvent rapportés comme dominants en ville (issu de Ayers & Rehan, 2021).

Puisque les paysages urbains résultent souvent des mêmes processus, ils se ressemblent davantage entre eux qu'avec les zones rurales qui les entourent. Aussi, les phénomènes de filtrages fonctionnels sont-ils les mêmes dans tous les contextes urbains. Par conséquent, les communautés urbaines se retrouvent souvent constituées d'espèces similaires, à travers des zones géographiques très étendues : on assiste à une homogénéisation biotique (Alberti, 2015).

À terme, tous les écosystèmes urbains risquent alors de devenir identiques, occasionnant une perte de diversité à grande échelle. C'est ce qui a été montré à l'échelle de la France par Deguines et al. (2016), avec un basculement des communautés d'insectes floricoles en faveur des espèces généralistes, au sein des milieux urbanisés de tout le territoire métropolitain.

3.2. Changements climatiques et phénologie de la pollinisation

La relation de mutualisme qui lie les plantes entomogames et les insectes pollinisateurs impose une synchronisation entre la floraison des premières et l'activité des seconds. Ceci requiert une coordination des traits phénologiques des différents partenaires mutualistes, sans laquelle la fonction n'est plus assurée (Rafferty et al., 2015). En milieu tempéré, les phénologies des organismes sont contraintes par les saisons et les variations environnementales qui leur sont associées. Selon les espèces, la phénologie se synchronise avec les saisons sur la base de signaux physiques : la photopériode, le couvert neigeux, mais surtout les températures (Forrest & James, 2011). Or, les changements climatiques perturbent les signaux thermiques qui pilotent d'une part la phénologie des plantes, et d'autre part celle des pollinisateurs (Duchenne et al., 2020; Walther et al., 2002). Ceci pourrait provoquer une désynchronisation entre la floraison et l'activité pollinisatrice, fragilisant ainsi la relation mutualiste entre les plantes et les insectes.

Des travaux de modélisation (Memmott et al., 2007; Schleuning et al., 2016) ont ainsi donné lieu à des prédictions très alarmistes, projetant des désynchronisations majeures entre plantes et pollinisateurs (**Figure 0. 7**). De telles désynchronisations seraient particulièrement délétères pour les interactions spécialistes et pourraient conduire à des extinctions d'espèces. Ces prédictions sont corroborées par les suivis empiriques longs des réseaux d'interactions plantes-pollinisateurs (Burkle et al., 2013), qui témoignent de fortes dégradations de leur structure, en partie imputables à des décalages phénologiques entre plantes et pollinisateurs.

Néanmoins, il n'existe que peu d'études empiriques concernant l'impact des variations phénologiques des plantes et des pollinisateurs face au réchauffement climatique (Forrest, 2015). Les réponses de la fonction de pollinisation apparaissent très variables. Ainsi, tantôt une progression parallèle des phénologies des partenaires mutualistes permet d'épargner la fonction de pollinisation (Bartomeus et al., 2011; Cariveau & Winfree, 2015; Forrest & James, 2011; Rafferty et al., 2015); tantôt le décalage de phénologie des plantes, en les soumettant à des

communauté de pollinisateurs moins diversifiées et donc moins efficaces, occasionne un effet délétère sur leur succès reproducteur (Rafferty & Ives, 2011). Ceci suggère un rôle capital de la diversité de la faune pollinisatrice dans la résilience de la fonction de pollinisation aux changements climatiques (Bartomeus et al., 2013).

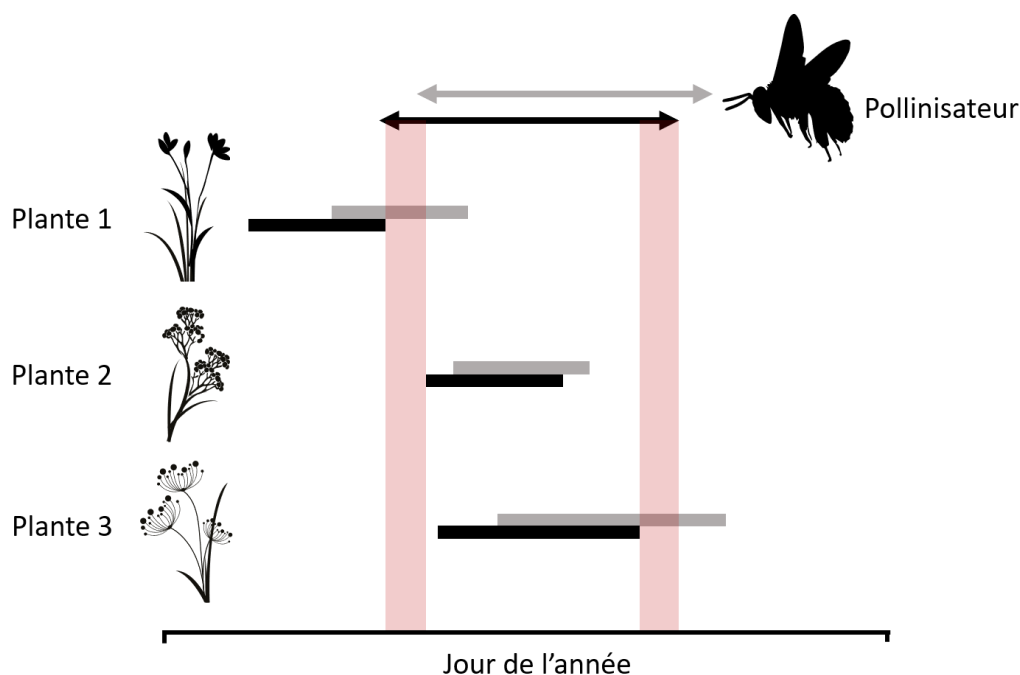


Figure 0. 7. Schéma de désynchronisation entre la phénologie d'un pollinisateur et de ses ressources florales successives en raison du réchauffement climatique. Chaque organisme voit sa phénologie modifiée en réponse au réchauffement (gris : état initial, noir : phénologie avancée en réponse au réchauffement), y compris le pollinisateur (flèches). En raison d'une adaptation hétérogène des phénologies des organismes, des périodes de disette apparaissent pour le pollinisateur (rouge) (inspiré de Memmott et al., 2007).

3.3. Modifications phénologiques en milieu urbain : une homogénéisation temporelle

L'îlot de chaleur urbain (ICU), documenté dans de nombreuses métropoles, se traduit par une modification locale du climat, à l'origine d'augmentations de températures moyennes allant classiquement de $+0,5^{\circ}\text{C}$ à $+3^{\circ}\text{C}$ (Kuttler, 2004) (**Figure 0. 9**, pour la ville de Paris). Il est d'autant plus sensible que les aires urbaines sont grandes et les densités de population élevées (Rizwan et al., 2008). Ce phénomène est tributaire de l'émission de chaleur par les activités humaines, de l'accumulation des radiations solaires dans les constructions, mais aussi du déficit d'évapotranspiration dans ces paysages peu végétalisés (Jochner & Menzel, 2015; Rizwan et

al., 2008). Ce climat urbain plus chaud, s'il engendre des effets variables sur la phénologie des plantes, provoque le plus souvent un débourrage des bourgeons et une floraison précoces par rapport aux zones rurales (Jochner & Menzel, 2015; Neil & Wu, 2006). Ces décalages phénologiques chez les végétaux ont une amplitude de quelques jours à plusieurs semaines. Aussi l'ICU est-il suspecté de perturber les phénologies des insectes pollinisateurs (Harrison & Winfree, 2015), en plus de réduire leur abondance (Hamblin et al., 2018). D'autre part, la pollution lumineuse peut opérer des modifications phénologiques en faisant varier artificiellement la durée du jour, bien que ses effets soient moins étudiés que ceux de l'ICU (Jochner & Menzel, 2015; Merckx et al., 2021). Les insectes peuvent alors émerger de façon précoce, en réponse à des photopériodes trompeuses. Dans le contexte urbain, il existe donc une crainte que ces changements phénologiques des plantes et des pollinisateurs puissent générer des décalages qui affecteraient la fonction de pollinisation.

En outre, en milieu urbain, les pratiques de gestion à des fins ornementales des espaces verts et jardins privés assurent la présence quasi-permanente de plantes horticoles, souvent exotiques. Certaines d'entre elles constituent des sources alimentaires pour les insectes pollinisateurs (Erickson et al., 2020; Lowenstein et al., 2019; Staab et al., 2020; Stelzer et al., 2010), ce qui se répercute sur la composition de leur communauté (Cecala & Wilson Rankin, 2021a; Pardee & Philpott, 2014), bien que la flore horticole exotique semble surtout attirer les pollinisateurs généralistes ubiquistes tels que *Apis mellifera* (Garbuzov et al., 2015; Threlfall et al., 2015). Par conséquent, en ville, les pollinisateurs sont peut-être moins contraints par la phénologie des plantes sauvages qu'en milieu rural, car ils disposent de ressources hors-saison.

Ainsi, le milieu urbain est marqué par des facteurs physiques et biologiques qui atténuent les variations saisonnières. On assiste donc à une perte d'hétérogénéité temporelle des habitats, avec une relative stabilité des conditions climatiques et des quantités de ressources au cours des saisons. Ceci a des répercussions sur les communautés de pollinisateurs, avec une altération des motifs saisonniers d'abondance et de richesse spécifique par rapport aux zones naturelles (Harrison et al., 2018; Leong et al., 2016; Luder et al., 2018; Wray & Elle, 2015). En raison de cette atténuation des contraintes saisonnières, les insectes peuvent sortir de diapause de façon précoce (Merckx et al., 2021), et même compléter des générations supplémentaires au cours

d'une année. C'est le cas avec les populations de bourdons terrestre en Angleterre, qui parviennent à établir des générations supplémentaires au cours de l'hiver grâce aux ressources apportées par des arbustes ornementaux exotiques (Stelzer et al., 2010).

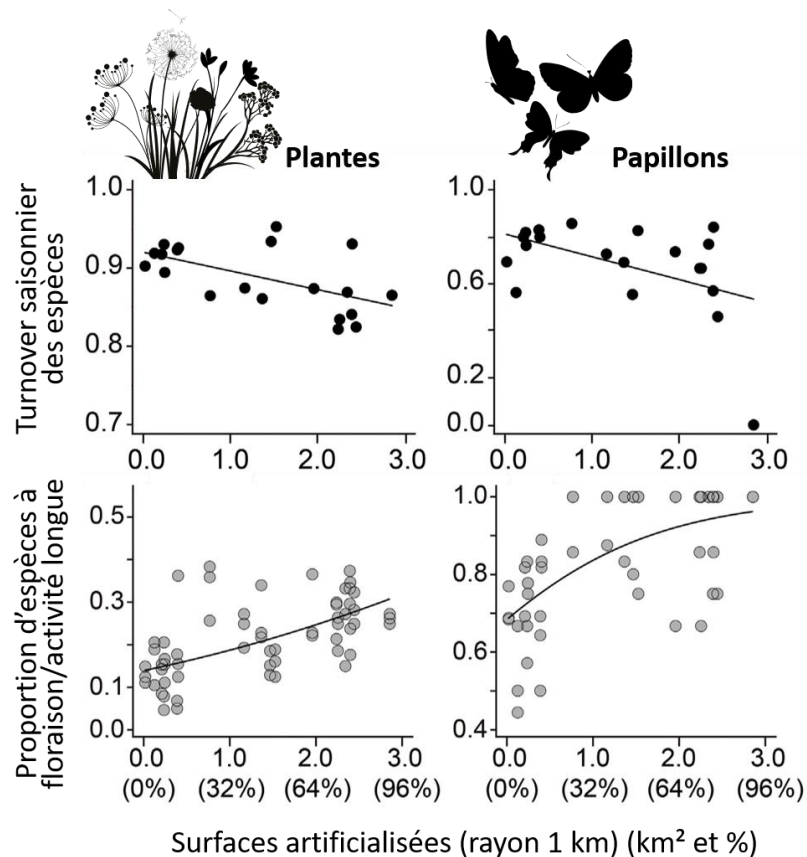


Figure 0. 8. Diminution du turnover des espèces de plantes et de papillons en milieu urbanisé, associé à la prédominance d'espèces à longue période de floraison et d'activité (figures issues de Uchida et al., 2018). Les points noirs représentent les valeurs de turnover saisonnier calculées pour chaque site, via la composante « turnover » de la dissimilarité de Jaccard. Les points gris représentent les pourcentages d'espèces par site et par échantillonnage. Les lignes représentent les coefficients significatifs ($P < 0,05$) selon le test de Wald.

À l'échelle des communautés urbaines, on assiste donc à une homogénéisation temporelle, marquée par une atténuation des variations saisonnières de la diversité et de l'abondance des insectes pollinisateurs. Cette homogénéisation temporelle s'inscrit dans le processus d'homogénéisation fonctionnelle des communautés face à l'urbanisation (Alberti, 2015). Elle se traduit notamment par un déclin du turnover des espèces de pollinisateurs au fil des saisons, et par une prédominance des espèces à longue période de floraison ou d'activité (Uchida et al., 2018) (**Figure 0. 8**) ; ce qui génère une perte de diversité à travers le temps. Face à l'homogénéisation temporelle de l'habitat, on observe donc une perturbation de la succession

saisonnaire des espèces. Ainsi, leurs niches phénologiques, distinctes en milieu naturel, pourraient tendre à se superposer.

3.4. La ville un laboratoire phénologique ?

Les changements globaux se caractérisent par des atteintes aux grands processus biophysiques qui stabilisent les écosystèmes au niveau planétaire : artificialisation des sols, réchauffement climatique, pollutions, cycles géochimiques perturbés, érosion de la biodiversité etc. (Rockström et al., 2009; Steffen et al., 2015). Or, en ville, l'on retrouve au niveau local presque toutes les pressions environnementales caractéristiques de ces changements globaux, de manière exacerbée (Alberti, 2015; Fenoglio et al., 2021). C'est pourquoi certains auteurs voient dans la ville un « laboratoire » des changements globaux : ce serait un aperçu des conditions terrestres futures à l'issue des crises environnementales actuelles. Ainsi Harrison & Winfree (2015) décrivent le milieu urbain comme un système modèle pour mesurer les conséquences des changements globaux sur les interactions plantes-pollinisateurs. Elles y ont répertorié les composantes majeures de ces changements, déjà identifiées comme délétères sur les mutualismes plantes-pollinisateurs (Tylianakis et al., 2008), mais ici poussées à l'extrême : perte et fragmentation des habitats, introduction d'espèces exotiques et cultivées, pollutions diverses et modification du climat.

Dans ce contexte, les milieux urbains constituent un laboratoire naturel idéal pour analyser la réponse de la fonction de pollinisation aux variations de phénologie des plantes et des pollinisateurs. En effet, l'îlot de chaleur urbain génère des augmentations locales des températures, d'une magnitude comparable à celle des projections du réchauffement climatique global (de +1,4°C à +4,4°C à l'horizon 2100, moyennes selon les scénarios, IPCC, 2021). On peut donc penser que les conséquences de l'ICU sur la phénologie des interactions plantes-pollinisateurs soient analogues à celles du réchauffement climatique, bien que cette hypothèse n'ait pas encore été l'objet d'analyses expérimentales (Harrison & Winfree, 2015). Ainsi, l'îlot de chaleur urbain pourrait préfigurer, au niveau local, les impacts du réchauffement climatique global (Grimm et al., 2008; Jochner & Menzel, 2015).

Si cette observation s'applique aux régions tempérées, les variations phénologiques dues à l'urbanisation dans les climats tropicaux et arides sont moins étudiées, avec des résultats plus

variables (Jochner & Menzel, 2015). De plus, les effets de l'îlot de chaleur urbain ne constituent pas une pression constante et uniforme. Ils sont exacerbés lors des nuits calmes et peu venteuses, où la chaleur est restituée par les infrastructures urbaines et peine à s'évacuer par convection. Les différences de températures seraient à leur maximum pendant les nuits d'hiver (Jochner & Menzel, 2015), bien que les conséquences sur les populations humaines soient plus délétères pendant les épisodes caniculaires estivaux (Lemonsu et al., 2015). Le réchauffement varie selon les quartiers, se révélant plus intensif au centre-ville. Très localement, il est atténué selon l'ombrage, la nature des surfaces, la présence d'eau et de végétation (Rizwan et al., 2008) (**Figure 0. 9**). L'îlot de chaleur urbain ne constitue donc pas un modèle parfait des conditions futures face au réchauffement global. Il reste néanmoins un outil intéressant pour l'étude *in situ* des effets des conditions climatiques sur les communautés d'insectes pollinisateurs.

4. QUELLES SOLUTIONS POUR FAVORISER LA DIVERSITÉ DES POLLINISATEURS URBAINS ?

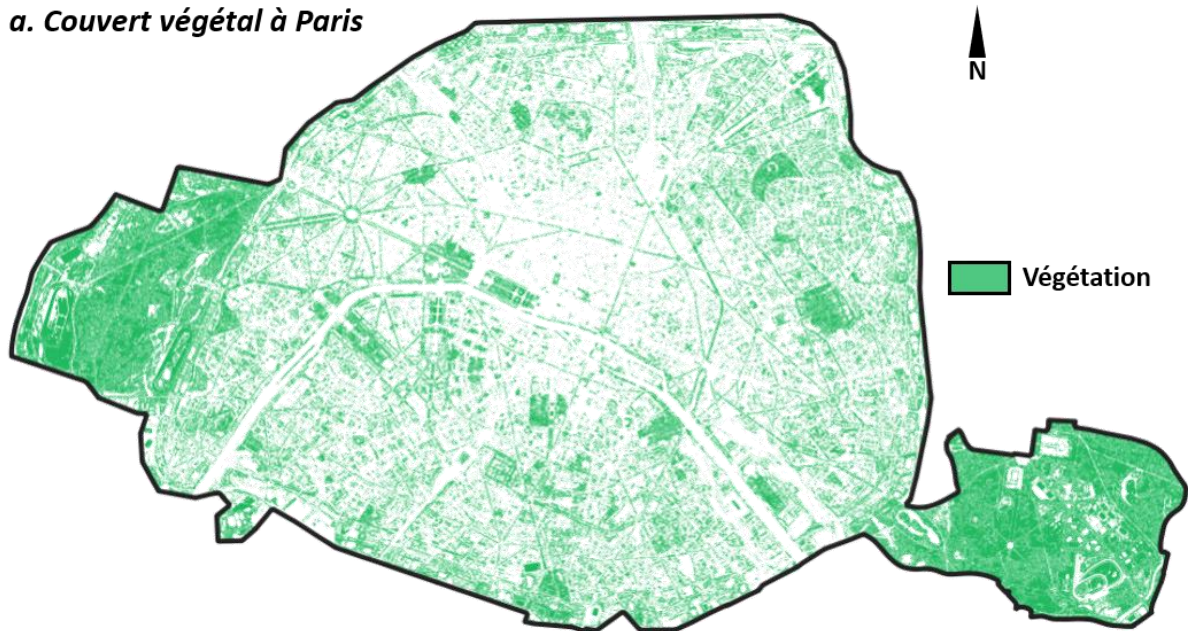
4.1. Comment la gestion des espaces verts peut influencer la biodiversité urbaine

La diversité des communautés de pollinisateurs est directement influencée par les pratiques de gestion des espaces verts, et en premier lieu de la végétation qui y est entretenue (Baldock et al., 2019). Les espaces verts urbains arborent souvent une majorité de plantes dites « ornementales ». Ce sont des variétés sélectionnées, plantées et entretenues par des jardiniers, par opposition aux plantes « spontanées », qui se développent et fleurissent sans intervention humaine. Pourtant, l'attractivité de ces plantes ornementales pour les insectes pollinisateurs est très variable (Erickson et al., 2020; Garbuzov & Ratnieks, 2014); et beaucoup de variétés sont peu butinées (Garbuzov et al., 2015, 2017). Par ailleurs, de nombreuses plantes ornementales sont de surcroît des espèces exotiques. Or il a été montré que les plantes indigènes sont plus attractives que les plantes exotiques (Lowenstein et al., 2019; Salisbury et al., 2015), et qu'elles permettent de soutenir des communautés de pollinisateurs plus abondantes et plus diversifiées (Pardee & Philpott, 2014). Malgré tout, les variétés ornementales, y compris exotiques, pourraient représenter une ressource de substitution dans les milieux urbains, par ailleurs appauvris en flore spontanée (Erickson et al., 2020, 2021; Salisbury et al., 2015; Staab et al., 2020).

En outre, certaines pratiques de gestion peuvent contribuer à limiter les contraintes urbaines et favoriser la diversité des insectes, et en particulier des insectes pollinisateurs (Fenoglio et al., 2021; Majewska & Altizer, 2020; Shwartz et al., 2013). C'est le cas de la gestion dite « différenciée ». Cette pratique consiste à diversifier les habitats en préservant des espaces gérés de façon peu intensive : mares naturelles, prairies en fauche tardive, massifs arbustifs non taillés etc. Ces espaces, dans lesquels on privilégie l'installation de plantes indigènes, font office de refuges pour la biodiversité. En favorisant l'hétérogénéité des habitats au sein des espaces verts, les jardiniers maintiennent des communautés de plantes et de pollinisateurs plus riches (Fenoglio et al., 2021; Shwartz et al., 2013). Par ailleurs, hors de ces espaces-refuges, les pratiques de gestion peuvent permettre de maintenir la présence de plantes sauvages, notamment via une réduction des fréquences et hauteurs de tonte (Lerman et al., 2018). Il s'agit également de préserver la fertilité des sols sans intrants chimiques, à l'aide de paillage et d'amendements organiques. Ceci a pour effet de retenir l'humidité et de stimuler l'activité biologique des sols. Naturellement, l'usage de pesticides est délétère pour la diversité des insectes, mais aussi des oiseaux qui s'en nourrissent (Fenoglio et al., 2021).

La fonction de pollinisation occupe une place centrale dans les enjeux de biodiversité urbaine. De plus, l'intérêt grandissant des citoyens pour les problématiques environnementales favorise l'essor de pratiques qui dépendent du service de pollinisation, telles que la végétalisation des villes et l'agriculture urbaine (McClintock, 2010). Aussi existe-t-il une véritable volonté des citoyens pour des pratiques de gestion plus respectueuses des insectes pollinisateurs, en particulier des « abeilles ». Cependant, cette bonne volonté n'est pas toujours associée aux connaissances adéquates, notamment en ce qui concerne les assemblages floraux à privilégier (Lindemann-Matthies et al., 2021). De plus, de nombreuses initiatives sont prises par des particuliers et des gestionnaires dans l'intention de promouvoir la fonction de pollinisation en agissant directement sur les insectes : apiculture urbaine, installation d'hôtels à insectes, introduction de cocons d'Osmies dans l'environnement. Pourtant, les vertus de ces procédés sont rarement démontrées ; au contraire, ils peuvent causer des dommages aux communautés de pollinisateurs sauvages (Geslin et al., 2022).

a. Couvert végétal à Paris



b. Carte thermique de Paris

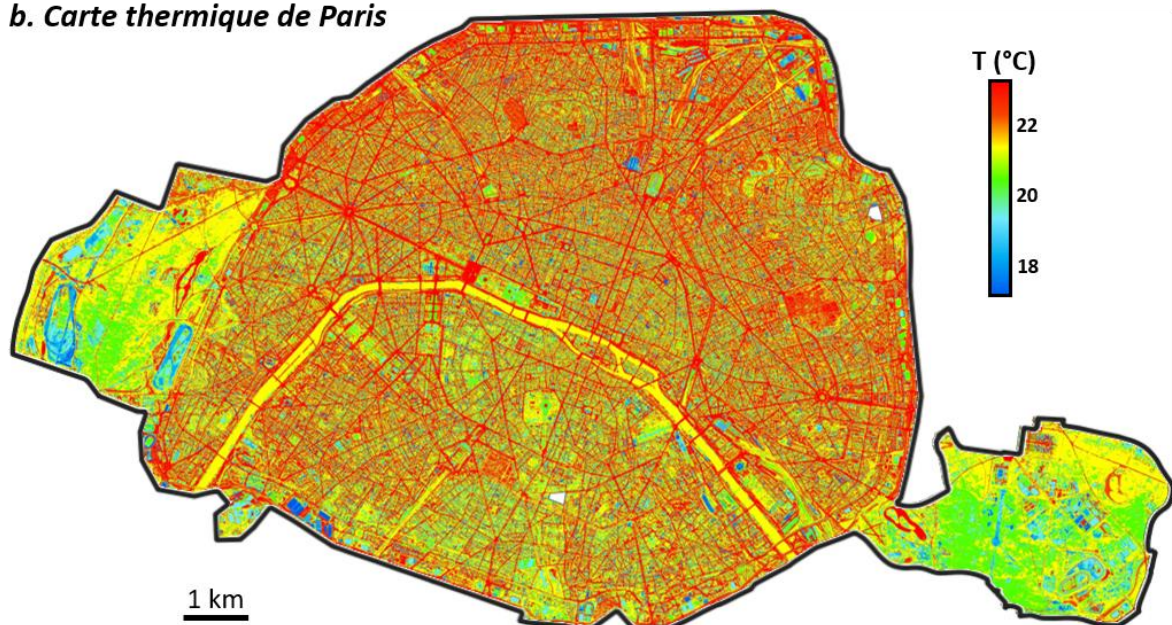


Figure 0. 9. Répartition du couvert végétal (a.) et de l'îlot de chaleur urbain à Paris (b.). La carte thermique est une thermographie instantanée acquise en conditions de canicule, en début de nuit le 16 août 2016. On note que les espaces riches en végétation sont les plus frais, à l'exception des cimetières. Les voiries sont les zones les plus chaudes (données issues de l'APUR, 2015, 2016).

4.2. Le cas de la ville de Paris

La ville de Paris s'étend sur une superficie relativement limitée (105,4 km²), au vu de sa population (2,175 millions de personnes en 2018). Ainsi, Paris figure parmi les villes les plus denses du monde (20 641,4 habitants au km²) (INSEE, 2021). Cette densité de population et de bâti rend la ville vulnérable aux vagues de chaleurs et canicules. Le phénomène d'îlot de

chaleur, en interaction avec le réchauffement climatique, y est préoccupant pour le développement urbain futur (Lemonsu et al., 2015) (**Figure 0. 9b**). Ces contraintes climatiques devraient peser sur la santé publique, les réseaux énergétiques, la disponibilité des ressources (en eau notamment) et des services (Ville de Paris, 2021). La « nature en ville » et la biodiversité apparaissent aussi menacées par ces phénomènes, mais constituent également des solutions pour en atténuer les impacts.

La ville de Paris comprend environ 530 espaces verts publics : parcs, jardins et squares municipaux (Ville de Paris - DEVE, 2021b) (**Figure 3. 1**). La plupart sont gérés par la municipalité. Les plus grands sont le parc des Buttes-Chaumont (25 ha, 19^e arr.), le Jardin du Champ de Mars (25 ha, 7^e arr.), le parc Montsouris (15 ha, 14^e arr.), le parc André Citroën (14 ha, 15^e arr.), et le Jardin des Champs-Élysées (13 ha, 8^e arr.). Cependant, la plupart des espaces verts gérés par la Ville de Paris ont des dimensions beaucoup plus réduites. Ainsi, 82% de ces espaces verts s'étendent sur des surfaces inférieures à un hectare (**Figure 0. 10**).

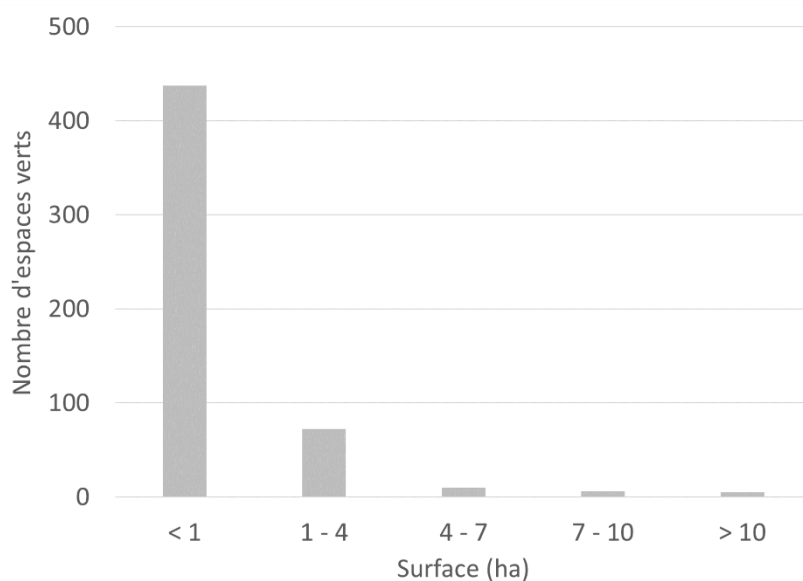


Figure 0. 10. Histogramme des dimensions des espaces verts gérés par la Ville de Paris. On note que la plupart ont des dimensions inférieures à 1 ha (données publiques, Ville de Paris - DEVE, 2021).

A noter que certains des plus grands espaces verts sont gérés par d'autres établissements publics : c'est le cas du Jardin des Plantes (Muséum National d'Histoire Naturel, 5^e arr.), du Jardin du Luxembourg (Sénat, 6^e arr.), du Jardin des Tuileries (Musée du Louvre, 1^{er} arr.), du parc de la Villette (Établissement public du parc et de la grande halle de la Villette, 19^e arr.), et

du Jardin du Palais-Royal (Centre des Monuments Nationaux, 1^{er} arr.). Par ailleurs, certains cimetières, tels que celui du Père-Lachaise (44 ha, 20^e arr.) et celui de Montmartre (11 ha, 18^e arr.) constituent de vastes espaces boisés. La capitale compte aussi de nombreux espaces verts privés, souvent de dimensions inférieures, ainsi que quelques grands parcs à accès restreint (ex : Palais de l'Élysée, 8^e arr., et Hôtel Matignon, 7^e arr.). Enfin, la ville de Paris est flanquée de deux bois, gérés par la municipalité : le bois de Vincennes à l'est et le bois de Boulogne à l'ouest (**Figure 0. 9**). Anciens terrains de chasse, ces espaces principalement boisés sont beaucoup plus vastes que les espaces verts situés *intramuros* (respectivement 995 ha et 846 ha) (Ville de Paris - DEVE, 2021b). Aussi sont-ils susceptibles d'abriter des communautés biologiques plus riches, et de jouer le rôle de réservoirs de biodiversité dans un paysage par ailleurs très artificialisé.

Au sein des espaces verts gérés par la Ville de Paris, des efforts de gestion sont entrepris pour accueillir les organismes sauvages et préserver la biodiversité. Ainsi, de nombreux parcs et jardins pratiquent une gestion différenciée en aménageant des « espaces de biodiversité », entretenus avec une perspective écologique. De plus, certains espaces verts, tels que le Jardin Naturel Pierre-Emmanuel (20^e arr.) sont entièrement dédiés aux écosystèmes naturels, reproduisant des habitats sauvages variés. De manière générale, et en accord avec la loi Labbé (entrée en vigueur en 2017 ; Loi 2014-110), la Ville de Paris n'emploie pas de produits phytosanitaires chimiques pour l'entretien des espaces verts et de la voirie. Depuis 2019, cette réglementation s'applique également aux particuliers. La Ville de Paris avait pris les devants en appliquant la démarche « zéro-phyto » depuis 2007 dans les parcs et jardins, et depuis 2015 dans les cimetières (Ville de Paris - DEVE, 2021b).

Enfin, les communautés d'insectes pollinisateurs de la Ville de Paris ont déjà fait l'objet d'un effort d'étude important. Ainsi, plusieurs inventaires, surtout d'abeilles, ont été réalisés dans la capitale. Ils ont fait l'objet de publications scientifiques (Geslin et al., 2015; Ropars et al., 2018; Shwartz et al., 2013) ou de rapports d'expertise (Ferrand et al., 2014; Stallegger, 2015). Des expériences y ont également été menées afin d'évaluer l'efficacité de la fonction de pollinisation en milieu urbain (Geslin et al., 2016; Pellissier et al., 2012).

5. PROBLÉMATIQUES

Au cours de cette thèse, nous avons étudié comment le milieu urbain dense parisien influence les interactions entre plantes et pollinisateurs, tout en imposant une homogénéisation fonctionnelle et temporelle aux communautés d'insectes floricoles. Ainsi, nous avons exploré la façon dont ce milieu filtre l'assemblage d'espèces de pollinisateurs ; sur la base de quels traits fonctionnels ; et sous l'influence de quels facteurs environnementaux. De plus, nous avons examiné les dynamiques saisonnières d'activité des pollinisateurs au niveau des communautés, et leurs conséquences en termes de structure des réseaux de pollinisation, et de succès reproducteur des plantes. Pour cela, nous avons employé plusieurs approches distinctes.

Tout d'abord, nous avons adopté une approche expérimentale semi-contrôlée afin de comparer les communautés de pollinisateurs et leur activité en milieu urbain dense et en milieu rural semi-naturel. Pour cela, nous avons examiné les insectes floricoles venus visiter des parcelles de plantes mises en place de façon standardisée dans ces deux habitats. Les questions étaient les suivantes :

Chapitre 1 : Quelles sont les différences **d'assemblage** et de diversité fonctionnelle dans les communautés de pollinisateurs en milieu urbain et en milieu rural, au fil des saisons ?

Chapitre 2 : Quelles sont les différences dans **l'activité** des pollinisateurs et l'efficacité de la pollinisation en milieu urbain et en milieu rural, au fil des saisons ?

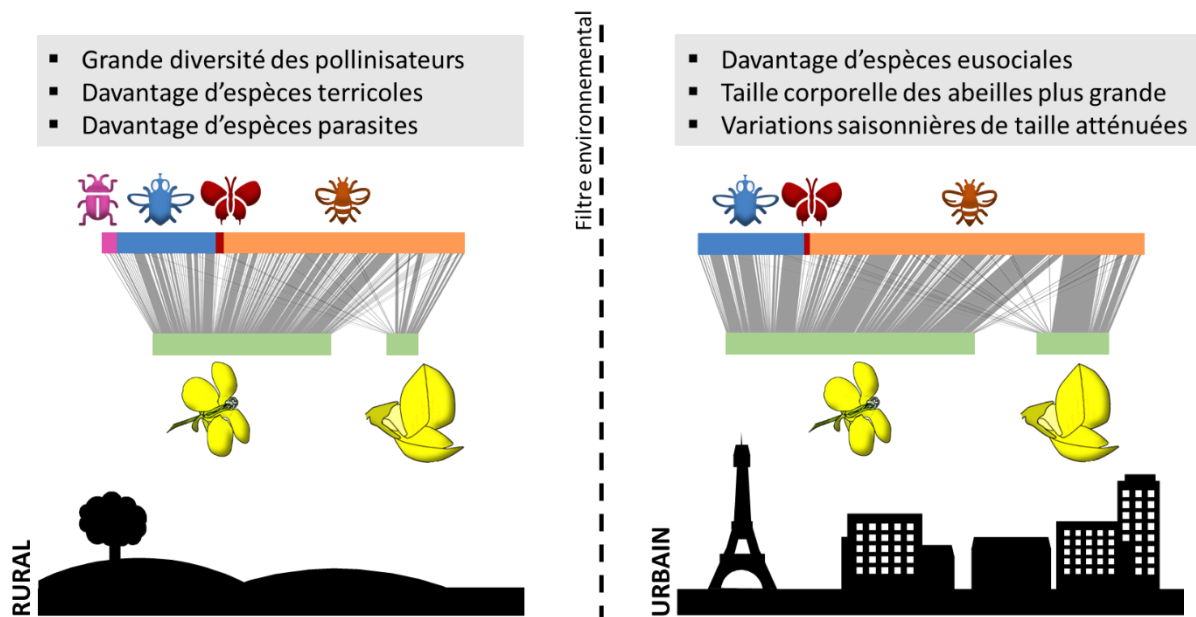
Puis, nous avons approfondi l'analyse des communautés de pollinisateurs dans le milieu urbain dense parisien. Cette fois, nous avons pris en considération les visiteurs de toutes les espèces florales disponibles, au fil des saisons. Ceci nous a permis d'avoir un aperçu exhaustif de la diversité des pollinisateurs dans ce paysage urbain, et de comprendre les facteurs environnementaux qui la façonnent. De plus, nous avons pu reconstituer des réseaux d'interactions plantes-pollinisateurs détaillés, et explorer leurs transformations saisonnières. Ces travaux ont permis de traiter les questions suivantes :

Chapitre 3 : Quelles sont les particularités de l'**assemblage** de pollinisateurs à **Paris**, et comment se positionne-t-il par rapport aux milieux naturels et aux autres grandes villes ?

Chapitre 4 : Quels facteurs **locaux** et **paysagers** façonnent les communautés de pollinisateurs à Paris ? Quelles sont les conséquences sur les diversités taxonomique et fonctionnelle ?

Chapitre 5 : Comment se structurent les **interactions** plantes-pollinisateurs dans le milieu urbain dense parisien, au fil des saisons ? Quels sont les rôles respectifs de la flore exotique de la flore indigène dans ces réseaux d'interactions ?

CHAPITRE 1 : Variations saisonnières des assemblages de pollinisateurs en milieu urbain et rural



CHAPITRE 1 : Résumé graphique

Nous comparons ici les diversités taxonomique et fonctionnelle des communautés rurales et urbaines d'insectes pollinisateurs, au niveau d'un dispositif végétal standardisé mis en place dans plusieurs sites ruraux et urbains d'Île-de-France.

- Quelles sont les différences dans l'assemblage et la diversité des espèces visitant les plantes expérimentales entre les localités rurales et urbaines ?
- En se concentrant sur les abeilles sauvages, quelles sont les dynamiques saisonnières des traits fonctionnels de ces communautés ?

L'environnement urbain filtre les traits fonctionnels des insectes pollinisateurs et modifie leurs dynamiques saisonnières. Ce sont surtout certaines espèces communes et généralistes qui semblent en bénéficier. Ceci pourrait se répercuter sur les réseaux d'interactions et sur la fonction de pollinisation.

Seasonal variations of pollinator assemblages among urban and rural habitats: a comparative approach using a standardized plant community

published in Insects, 2021

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1. ARTICLE DETAILS

Author Contributions: Conceptualization, VZ and ID; Data curation, VZ; Funding acquisition, ID; Investigation, VZ, OB, AH and CH; Methodology, VZ; Project administration, ID; Resources, AH and ID; Supervision, ID; Validation, AP and ID; Visualization, VZ and AP; Writing – original draft, VZ; Writing – review & editing, AP, AH and ID. All authors have read and agreed to the published version of the manuscript.

Funding: This project was partially funded by the CITY OF PARIS through a CIFRE PhD scholarship n°2018/0699; by the PEPS CNRS INEE Adaptation-Adaptabilité program; and by the Institut de la Transition Environnementale of SORBONNE-UNIVERSITE. This work has also benefited from technical and human resources provided by CEREPE-Écotron IleDeFrance (CNRS/ENS UMS 3194) as well as financial support from the REGIONAL COUNCIL OF ILE-DE-FRANCE under the DIM Program R2DS bearing the reference I-05-098/R. It has received support under the program "Investissements d'Avenir" launched by the French government and implemented by ANR with the reference ANR-11-INBS-0001 AnaEE France. The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results

Acknowledgments: We wish to thank the Jardin des Plantes of the MNHN (Philippe Barré), the Cité Internationale Universitaire de Paris (David Otamendi) and the Pierre et Marie Curie campus of Sorbonne-Université (Guillaume Baloup) for providing access to the sites; as well as the cultivation services of the Pierre et Marie Curie campus of Sorbonne-Université (Patrick Dumont) and of the MNHN (Alain Karg) for their help in growing plants. We thank all the specialists who identified the insects at the species level: David Genoud, Rémi Rudelle, Jean-Pierre Sarthou, and Eric Dufrêne. We also thank Elsa Blareau, Ambre Zelela-Bouvard, and Vincent Leclercq for their contribution to field work and data collection.

Complete Reference: Zaninotto, V., Perrard, A., Babiard, O., Hansart, A., Hignard, C., & Dajoz, I. (2021). Seasonal variations of pollinator assemblages among urban and rural habitats: A comparative approach using a standardized plant community. *Insects*, 12(3), 1–18. <https://doi.org/10.3390/insects12030199>

2. ABSTRACT

Even though urban green spaces may host a relatively high diversity of wild bees, urban environments impact the pollinator taxonomic and functional diversity in a way that is still misunderstood. Here we provide an assessment of the taxonomic and functional composition of pollinator assemblages and their response to urbanization in the Paris region (France). We performed a spring-to-fall survey of insect pollinators in green spaces embedded in a dense urban matrix and rural grasslands, using a plant set-up standardized across sites and throughout the seasons. We compared pollinator species composition and the occurrence of bee functional traits over the two habitats. There was no difference in species richness between habitats though urban assemblages were dominated by very abundant generalist species and displayed a lower evenness. They also included fewer brood parasitic, solitary, or ground-nesting bees. Overall, bees tended to be larger in the city than in the semi-natural grasslands, and this trait exhibited seasonal variations. The urban environment filters out some life-history traits of insect pollinators and alters their seasonal patterns, likely as a result of fragmentation and scarcity of feeding and nesting resources. This could have repercussions on pollination networks and the efficiency of the pollination function.

Keywords: pollinator communities; functional traits; urban ecology; body size; inter-tegular distance; seasonality; *Sinapis alba*; *Lotus corniculatus*

3. INTRODUCTION

Urbanization changes the environment in many ways that affect organisms (Alberti, 2015), although some species are better equipped than others (Fenoglio et al., 2020). We know that pollinators are affected (Harrison & Winfree, 2015), but it is not clear how these communities respond to urban constraints. To answer this question, we analyzed the pollinators monitored in an experimental plot of flowering plants over two years in rural and urban habitats.

Urbanization operates environmental filtering on species assemblages in general (Alberti, 2015), among which insect pollinator communities (Deguines et al., 2012). However, there is no consensus about the effect of the urban habitat on pollinators species diversity. For example, in Great Britain, both the diversity and abundance of pollinators are negatively associated with

urbanization (A. J. Bates et al., 2011), though urban habitats may support more diverse wild bee communities than agricultural landscapes (Baldock et al., 2015). Meanwhile, pollinator assemblages in downtown Paris (France) appear less diverse than those recorded in the surrounding landscapes, whether semi-natural or agricultural (Geslin et al., 2016). Indeed, densely urbanized landscapes do not seem to be suitable to host diverse communities of insect pollinators as their nesting and feeding habitats tend to become scarce and fragmented (Desaegher et al., 2018; Fortel et al., 2014).

In addition to examining species diversity, it is worth assessing how the functional diversity of pollinator assemblages responds to urbanization. Functional approaches help to understand the link between biodiversity and habitat constraints (Buchholz & Egerer, 2020). As a matter of fact, urban habitats also seem to apply filtering on functional traits of insect pollinators. There is widespread evidence that urban pollinator communities are less functionally diverse than their rural counterparts, as these communities mainly host generalist flower visitors (Antonini et al., 2013; Baldock et al., 2015; Hung et al., 2019). In France in particular, urbanization is associated with a shift in community composition suggesting a large-scale functional homogenization of flower visitor assemblages (Deguines et al., 2016). Indeed, traits such as nesting habits and lecty seem to be strongly affected by urbanization. Urban habitats would benefit cavity-nesting bees and polylectic species; while they appear unfit for ground-nesting bees and oligolectic insect pollinator species (Banaszak-Cibicka & Żmihorski, 2012; Cardoso & Gonçalves, 2018; Hinnert et al., 2012; Threlfall et al., 2015; Wray & Elle, 2015).

Among other functional traits, body size is of particular importance, since it is related to environmental characteristics that are strongly influenced by urbanization, such as floral resources quantity, habitat fragmentation, and climatic conditions. On the one hand, size is related to resource availability, as undernutrition at larval stage can result in smaller adults. Besides, small-bodied insects need less resources to survive and reproduce so they may be advantaged in resource-poor urban environments (Buchholz & Egerer, 2020; Tscharrntke et al., 2012). On the other hand, body size is associated with foraging range: large-bodied insects fly longer distances (Greenleaf et al., 2007). In the city, the fragmented habitat could advantage large-bodied bees that can easily fly from one patch to another (Warzecha et al., 2016; Wenzel

et al., 2020); however, resources are often pooled in green spaces which could render long-distance foraging unnecessary (Buchholz & Egerer, 2020). There is evidence for reduced body size of bees in urban habitats, both at the species level (Eggenberger et al., 2019) and community level (Banaszak-Cibicka et al., 2018; Banaszak-Cibicka & Żmihorski, 2012; Hinnert et al., 2012), though it is disputed (Wenzel et al., 2020). In addition, body size could also be influenced by climatic conditions, as it may be involved in thermic resistance and regulation, although there is no clear general temperature-size relationship in ectotherms (Angilletta et al., 2004; Angilletta & Dunham, 2003; Shelomi, 2012). Hence, Gerard et al. (2018) reported latitudinal clines in the size of wild bees following Bergman's rule (size increases with latitude) across Europe, although they found the opposite climate-size relation for some genera such as *Bombus*. Last, Osorio-Canadas et al. (2016) revealed a seasonal pattern of body size of wild bees at the community level, with small sizes becoming more prevalent during summer. To our knowledge, how bee body size varies along the season in urban habitats remains to be tested. Indeed, urban habitat characteristics such as the year-long availability of ornamental floral resources (Staab et al., 2020; Stelzer et al., 2010) and their fragmented spatial distribution should buffer variations in body size throughout the season. On the contrary, the warmer conditions due to the urban heat island (Grimm et al., 2008) could more strongly constrain the size of individuals by requiring increased thermal resistance and regulation capacities, especially during the hottest months.

Here we compare the species and functional diversities of rural and urban communities of pollinating insects, taking advantage of an experimental design where a standardized plant assemblage was set up in several rural and urban locations within the same biogeographical region (Ile-de-France region, France). We focus on the following questions: 1/ What are the differences in the species assemblage and diversity visiting the experimental plants between rural and urban pollinator communities? 2/ Focusing on wild bee communities visiting the experimental plants, how do functional traits of these urban and rural communities vary throughout the year?

We expect differences in overall species assemblage composition between the urban and rural communities visiting both plant species. For instance, we expect eusocial generalist

pollinators such as bumble bees and managed honey bees to represent a larger proportion of the urban community (Theodorou, Radzevičiūtė, et al., 2020), while syrphid flies should be more abundant and diverse in rural areas (Luder et al., 2018; Persson et al., 2020). Also on both plant species, greater species richness and diversity of pollinators are expected in the rural habitat in comparison with the urban one – here downtown Paris – one of the most densely populated cities in the world (R. H. M. Pereira et al., 2013). Concerning the functional diversity of wild bee assemblages, we also expect differences in bee levels of sociality, lecty, nesting habits and proportion of brood parasites. The urban habitat is likely to host more eusocial species but fewer ground nesting, brood parasitic and oligolectic species than the rural habitat, and these differences should be recorded throughout the season. Finally, we expect differences in bee body size between the two habitats, estimated through the inter-tegular distance (ITD). In addition, seasonal body size variations at the community level may differ between the two habitats. All of these potential differences between urban and rural pollinator communities are likely to be reflected in the assemblage of flower visitors of our plant set-ups.

4. MATERIALS AND METHODS

Sampling was conducted for two consecutive years in six (March to July 2017) and four (March to November 2018) locations in a dense urban habitat and semi-natural habitats (hereafter referred to as ‘rural’), all within the Ile-de-France region (France). Urban sites were located in downtown Paris (20,754.5 hab./km², INSEE, 2017). They were set up in green spaces with lawns and ornamental flowerbeds that were not treated with pesticides, and surrounded by a dense urban matrix (EEA, 2018). Meanwhile, rural sites were all located in the Seine-et-Marne administrative department (50-64 km from Paris) near the towns of Fontainebleau (86.5 hab./km²) and Saint-Pierre-lès-Nemours (253.6 hab./km²) (INSEE, 2016). They were set up in semi-natural grasslands, free of pesticides and surrounded by forests (EEA, 2018). The same sites were used throughout both years, with the exception of two sites that were not operational in 2018 (one in each habitat type). Details on experimental sites' surroundings can be found in **Table 2. 1** and **Figure 2. 2**.

Our pollinator surveys were carried out on replicates of a plant set-up that was standardized across sites and over the course of seasons. This enabled us to capture flower visitors throughout

time without any variation in the overall attractiveness of the plants and their floral traits, even though the collected insects represent only a subset of the whole pollinator community. In addition, this sampling method did not introduce any size bias, unlike with pan traps (Roulston et al., 2007). In each experimental site, two 1.6x1.2m plots were set up side by side in a grassland area, each containing one of the two focal plant species (the Brassicaceae *Sinapis alba* L. and the Fabaceae *Lotus corniculatus* L.). *Sinapis alba* L. is an annual forb growing along roads, in wastelands, or near crops, and is considered naturalized in the Ile-de-France region (Lombard, 2006). *Lotus corniculatus* L. is a perennial plant widespread in grasslands and disturbed habitats (Jones & Turkington, 1986), and is native to the Ile-de-France region (CBNBP, 2008; Jauzein & Nawrot, 2011). Both species bear yellow flowers with contrasting floral morphologies: *S. alba* has flat corollas with floral rewards accessible to pollinators with short mouthparts (Fontaine et al., 2006; Jones & Turkington, 1986); whereas *L. corniculatus* has deep corollas with floral rewards mainly accessible to pollinators with long mouthparts (Geslin et al., 2013). This allowed us to attract a large range of insect pollinators with diverse mouthparts morphologies and floral resources requirements (Fontaine et al., 2006). Prior to their installation in the field, plants were grown in individual pots under insect-proof greenhouse conditions (temperature: 20°C; photoperiod: 16h of day; 12cm diameter plastic pots filled with peat-enriched sowing soil: 180 g.m⁻³ N, 450 g.m⁻³ P₂O₅, 90 g.m⁻³ K₂O), and were installed in the experimental plots when flowering. In each plot, 20 pots containing one plant of the same species were buried in four rows of five, each plant being spaced from others by 25 cm in all directions. The floral cover was kept constant throughout the study period (March to November) by regular watering and by renewing the plants every twenty days, replacing them by fresh plants from the greenhouse.

Pollinator surveys in 2017 were limited to spring and early summer (March-July). In 2018, sampling was extended to summer and fall (March-November), with an interruption between mid-July and mid-August due to strong heat waves that were detrimental to the plant sets. Twice a week, and within each locality, five-minute insect pollinator sampling sessions were carried out on each of the two plant species. All sites were sampled on the same days between 11:00 a.m. and 3:00 p.m., in alternating order. A total of 33 five-minute sessions per site were

conducted in 2017, evenly distributed over 17 weeks; and 56 five-minute sessions per site in 2018, evenly distributed over 31 weeks. During these sessions, all insects coming into contact with the fertile parts of the plants were captured, using plastic boxes. The insects were then euthanized by transferring them to vials saturated with ethyl acetate vapors before being processed in the laboratory, where each specimen was labeled, pinned, and identified down to the genus, then sent to specialists for species identification. All specimens are now kept in the collection of the iEES laboratory, 4 place Jussieu 75005 Paris, France.

All data analyses were carried out using the R software (R core team, 2021). First, interaction networks (**Figure 1. 1**) and rarefaction curves (**Appendix 1. 1**) were plotted using respectively the ‘plotweb’ function of “bipartite” package (Dormann et al., 2009), and the ‘specaccum’ function of the “vegan” package (Oksanen et al., 2019). Proportions of individuals belonging to the main families of pollinators (number of individuals > 5) were compared between the two habitats using a chi-squared contingency table test (‘chisq.test’ function).

Species richness and Simpson’s diversity index of flower visitors were calculated for each plant species, locality, and year with the ‘diversity’ function of “vegan” package (Oksanen et al., 2019). Values taken by Simpson’s diversity index vary between 0 and 1, with low values recorded for communities dominated by a few, very abundant species. In contrast, functional diversity was estimated only on wild bees, using Rao’s quadratic entropy (‘dbFD’ function of “FD” package; Laliberté & Legendre, 2010) calculated over five traits: lecty, sociality level, nesting habits, brood parasitism status, and species-average inter-tegular distance (mm). Rao’s quadratic entropy provides a joint assessment of functional richness and functional dispersion, with low values indicating low functional diversity (Mouchet et al., 2010). To test whether values taken by these diversity indices per plant species, locality, and year (n=20) differed between the two habitats, we used beta-regression glmms (package ‘glmmTMB’). We defined the plant species (‘*Lotus corniculatus*’ vs. ‘*Sinapis alba*’), the habitat (‘Urban’ vs. ‘Rural’), and their interaction, as well as the year (2017 or 2018) as fixed effects, and the sampling site as a random effect. Species richness was modeled with a Poisson error distribution, whereas Simpson’s index and Rao’s quadratic entropy were modeled with a Gaussian error distribution. In order to complement our data with qualitative information on species rarity, we also

compared the number of specimens from species listed as endangered or notable in the IUCN red list (Nieto et al., 2014) and local ZNIEFF lists (Dufrière et al., 2020; Gadoum et al., 2020).

Traits data of wild bees (lecty, brood parasitism status, sociality level, and nesting habits) were recovered from Gerard et al. (Gérard et al., 2018). We used glmms to characterize the seasonal patterns in the proportions of specimens belonging to eusocial species (both primitively eusocial Halictidae species and advanced eusocial bumble bee species, Kocher & Paxton, 2014) and ground-nesting species in the two habitats, with a binomial error distribution. Explanatory variables were the plant species (*Lotus corniculatus* vs. *Sinapis alba*), the habitat ('Urban' vs. 'Rural'), the Julian day of the year (scaled), and their interactions. The sampling site and the year were included as random effects. Honey bees were excluded from these analyses.

Body size of wild bees was measured using a Zeiss stereomicroscope (Zeiss Discovery V12) with an integrated camera (AxioCam ICc5) to record pictures of each pinned specimen, using the software ZEN 2012 (blue edition). Inter-tegular distance (hereafter ITD), which is the standard measurement of body size in bees, was measured with the software ImageJ version 1.52a (Schneider et al., 2012). Analyses of ITD variations over time in the two habitats were carried out separately for bumble bees and other wild bee taxa. Indeed, bumble bees are eusocial species, with important body size differences among different categories of individuals (queens, drones, workers) (Gavini et al., 2020), and whose abundances vary along the course of the active season. In addition, they have an endogenous thermoregulation capacity, which can play a role in the temperature-height relationship (Gérard et al., 2018, 2020; Osorio-Canadas et al., 2016). On the contrary, all other wild bees sampled were either solitary species or more 'primitively' eusocial species (Kocher & Paxton, 2014) with little to no social-status-related variations in body size within the species. Log-transformed ITDs of the specimens were analyzed through glmms in a similar way that traits proportions, with a Gaussian error distribution. As a unimodal trend over time was expected for the ITD variations, we treated the Julian day as an orthogonal degree-2 polynomial.

Residuals of all glmms were inspected with the "DHARMA" package (Hartig, 2021) and no deviations from the specified error distributions were detected. The contribution of interactions

to models was tested through type-III tests with the ‘Anova’ function (“car” package, Fox & Weisberg, 2019). Model selection was performed based on the Second-order Akaike Information Criterion (AICc, “MuMIn” package, Barton, 2020) which is used instead of the AIC when the sample size is small in comparison to the number of estimated parameters. The absence of collinearity was verified via the “check_collinearity” function (“performance” package, Lüdecke et al., 2021).

5. RESULTS

5.1. Pollinator diversity

In total, 888 individuals were captured, with fewer flower visitors in the rural habitat (360 specimens belonging to 74 species, among which 86% of individuals on *S. alba* and 14% on *L. corniculatus*) than in the urban habitat (528 specimens belonging to 63 species, among which 78% of individuals on *S. alba* and 22% on *L. corniculatus*) (**Figure 1. 1**). However, flower visitor assemblages in the urban habitat were dominated by a small number of species with large populations. Thus, only six species of pollinators (in descending importance the bee species *Bombus pascuorum*, *Apis mellifera*, *Andrena pusilla*, *Lasioglossum morio*; and the syrphid fly species *Syrpitta pipiens*, *Eupeodes luniger*) contributed to more than half of the specimens collected on the two plants in the urban habitat (**Figure 1. 1, Table 1. 1**).

As expected, flower visitor assemblages differed between the two plant species and between habitats. Hence, the main families of pollinators were represented in different proportions between the two habitats. On *S. alba*, Andrenidae (urban: 23%, rural: 8%) and Apidae (urban: 19%, rural: 5%) were relatively more abundant in the urban habitat than in the rural one, while it was the opposite for Colletidae (urban: 3%, rural: 11%), Halictidae (urban: 26%, rural: 43%) and Syrphidae (urban: 26%, rural: 30%) ($\chi^2_{df4} = 82.98$, $p < 2.2e-16$) (**Figure 1. 1**). Similarly, on *L. corniculatus*, Apidae (urban: 56%, rural: 26%) were dominant in the urban habitat, whereas Halictidae (urban: 6%, rural: 18%) and Megachilidae (urban: 28%, rural: 42%) were proportionally more numerous in the rural habitat ($\chi^2_{df2} = 14.34$, $p = 0.00076$). In the urban habitat, the most abundant species visiting *S. alba* were *Apis mellifera* (with 14% of all visits) and *Andrena pusilla* (12%), while in the rural habitat *Lasioglossum politum* (9%) and *Lasioglossum aeratum* (9%) were more numerous. On *L. corniculatus*, visits were largely

dominated by *Bombus pascuorum* in both habitats, though in distinct proportions (53% in urban and 18% in rural), followed by solitary bees of the *Megachile* genus (urban: *M. willuhgiella*, 10%; rural: *M. centuncularis*, 12%) (**Table 1. 1**).

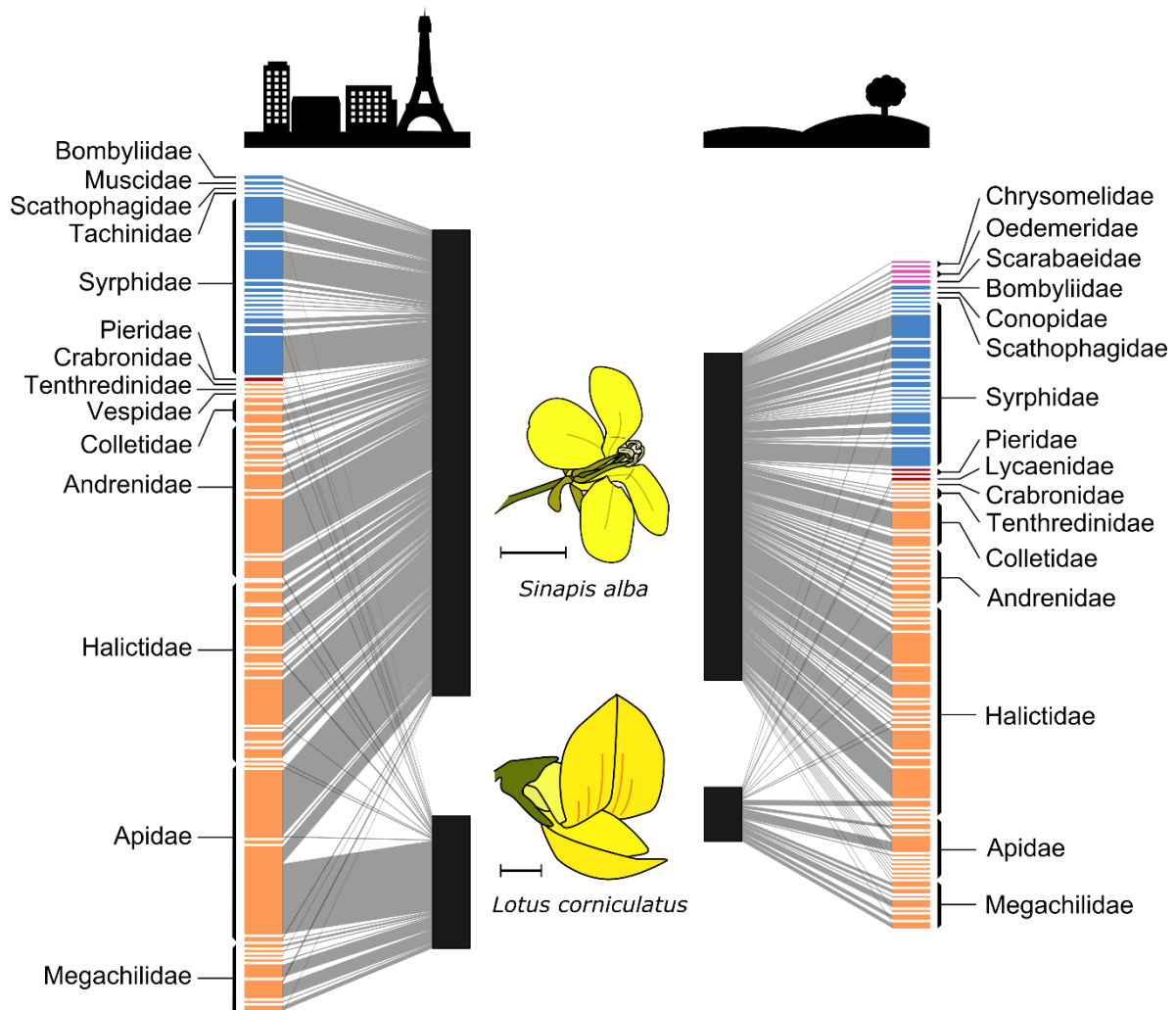


Figure 1. 1. Plant-pollinator interaction networks in both habitats (Urban: left; Rural: right), centered on our two plant species (*Sinapis alba*: top; *Lotus corniculatus*: bottom). Links represent the number of interactions between flower visitor species (colored boxes, labeled at the family level) and each plant species (black boxes). Colors represent insect orders: purple=Coleoptera; blue=Diptera; red=Lepidoptera; orange=Hymenoptera. The scale bar of the flower diagrams measures 5mm.

Species richness of insect visitors of *S. alba* over the two years was higher in the rural habitat ($N_{\text{rural}}=67$) than in the urban habitat ($N_{\text{urban}}=53$) (**Appendix 1. 1**). In contrast, the urban habitat displayed overall more species visiting *L. corniculatus* ($N_{\text{urban}}=24$) than the rural habitat ($N_{\text{rural}}=18$). For both plant species, glmms returned no significant difference in species richness between urban and rural sites (*S. alba*: mean richness per site and year \pm SE: $n_{\text{rural}}=22.3 \pm 2.0$

vs. $n_{\text{urban}}=25.5 \pm 2.2$, $t_{df15}=-1.15$, $p=0.27$; *L. corniculatus*: $n_{\text{rural}}=6.3 \pm 0.9$ vs. $n_{\text{urban}}=7.2 \pm 1.0$; $t_{df15}=-1.15$; $p=0.27$; **Appendix 1. 2**). Regarding taxonomic diversity, Simpson's diversity index λ of *S. alba* visitors did not differ significantly between the two habitats (mean Simpson index per site and year \pm SE: $\lambda_{\text{rural}}=0.91 \pm 0.03$ vs. $\lambda_{\text{urban}}=0.89 \pm 0.03$; $t_{df13}=0.40$; $p=0.69$; **Appendix 1. 2**). However, Simpson's diversity index of *L. corniculatus* visitors was significantly higher in the rural habitat ($\lambda_{\text{rural}}=0.75 \pm 0.03$ vs. $\lambda_{\text{urban}}=0.64 \pm 0.03$; $t_{df13}=2.73$; $p=0.017$, **Appendix 1. 2**), suggesting greater evenness in the abundance distribution of species visiting this plant in the rural habitat.

There were only two specimens in the rural habitat with a “NT” (near threatened) IUCN conservation status (Nieto et al., 2014): they belonged to the species *Lasioglossum laevigatum* and *Lasioglossum monstificum*, and were foraging on *S. alba*. Moreover, we found six species whose conservation status is of importance in the Ile-de-France region (five bee species and one syrphid fly species) (Dufrêne et al., 2020; Gadoum et al., 2020), meaning their presence is evidence for a noteworthy natural habitat (ZNIEFF). These species were more abundant in the rural habitat (five out of the six species mentioned above, representing 31 out of 32 specimens), and 84% of them were foraging on *S. alba*.

Table 1. 1. List of species and corresponding numbers of captured individuals in the two habitats (R.: Rural, U.: Urban).

List of species	R.	U.	List of species (continued)	R.	U.
HYMENOPTERA (BEES)			HYMENOPTERA (OTHERS)		
Andrenidae			Crabronidae		
<i>Andrena apicata</i> (Smith 1847)	1		<i>Cerceris</i> sp.		1
<i>Andrena bicolor</i> (Fabricius 1775)	2	5	<i>Pemphredon</i> sp.	1	
<i>Andrena bimaculata</i> (Kirby 1802)	2		Vespidae		
<i>Andrena cineraria</i> (Linnaeus 1758)		2	<i>Vespula germanica</i> (Fabricius 1793)		1
<i>Andrena dorsata</i> (Kirby 1802)	4	3	Tenthredinidae		
<i>Andrena flavipes</i> (Panzer 1799)	4	2	<i>Allantus</i> sp.	1	
<i>Andrena gravida</i> (Imhoff 1832)		4	<i>Athalia</i> sp.	1	
<i>Andrena haemorrhoa</i> (Fabricius 1781)		1	<i>Cladius</i> sp.		1
<i>Andrena lagopus</i> (Latreille 1809)	1	4	<i>Tenthredo</i> sp.	1	
<i>Andrena minutula</i> (Kirby 1802)	5	12	COLEOPTERA		
<i>Andrena minutuloides</i> (Perkins 1914)		3	Chrysomelidae		
<i>Andrena pusilla</i> (Pérez 1903)	4	47	<i>Cryptocephalus</i> sp.	1	
<i>Andrena</i> sp.		1	<i>Psylliodes</i> sp.	1	
<i>Andrena subopaca</i> (Nylander 1848)	2	1	Oedemeridae		
<i>Andrena tenuistriata</i> (Pérez 1895)		14	<i>Oedemera nobilis</i> (Scopoli 1763)	1	
Apidae			<i>Oedemera</i> sp.	2	
<i>Anthophora quadrimaculata</i> (Panzer 1789)		1	Scarabaeidae		
<i>Apis mellifera</i> (Linnaeus 1758)	2	59	<i>Phyllopertha horticola</i> (Linnaeus 1758)	2	

<i>Bombus lapidarius</i> (Linnaeus 1758)	4				
<i>Bombus lucorum</i> (Linnaeus 1760)	1	2			
<i>Bombus pascuorum</i> (Scopoli 1763)	14	77			
<i>Bombus terrestris</i> (Linnaeus 1758)	1	3			
<i>Nomada bifasciata</i> (Olivier 1811)	1				
<i>Nomada ferruginata</i> (Linnaeus 1767)	1				
<i>Nomada flavoguttata</i> (Kirby 1802)	1				
<i>Nomada fulvicornis</i> (Fabricius 1793)	1				
<i>Nomada panzeri</i> (Lepeletier 1841)	1				
Colletidae					
<i>Hylaeus brevicornis</i> (Nylander 1852)	6				
<i>Hylaeus communis</i> (Nylander 1852)	16	3			
<i>Hylaeus gibbus</i> (Saunders 1850)	1				
<i>Hylaeus pictipes</i> (Nylander 1852)		5			
<i>Hylaeus punctatus</i> (Brullé 1832)	9	7			
Halictidae					
<i>Halictus scabiosae</i> (Rossi 1790)	1				
<i>Halictus subauratus</i> (Rossi 1792)	5	4			
<i>Halictus submediterranea</i> (Pauly 2015)	1				
<i>Halictus tumulorum</i> (Linnaeus 1758)	5	9			
<i>Lasioglossum aeratum</i> (Kirby 1802)	28				
<i>Lasioglossum albipes</i> (Fabricius 1781)	14				
<i>Lasioglossum calceatum</i> (Scopoli 1763)	12	9			
<i>Lasioglossum glabriusculum</i> (Morawitz 1872)		1			
<i>Lasioglossum laevigatum</i> (Kirby 1802)	1				
<i>Lasioglossum laticeps</i> (Schenk 1868)	4	18			
<i>Lasioglossum leucozonium</i> (Schränk 1781)	2				
<i>Lasioglossum limbellum</i> (Morawitz 1876)		1			
<i>Lasioglossum malachurum</i> (Kirby 1802)		7			
<i>Lasioglossum marginatum</i> (Brullé 1832)	2	1			
<i>Lasioglossum minutissimum</i> (Kirby 1802)	3	5			
<i>Lasioglossum monstrificum</i> (Morawitz 1891)	1				
<i>Lasioglossum morio</i> (Fabricius 1793)	17	39			
<i>Lasioglossum nitidiusculum</i> (Kirby 1802)		1			
<i>Lasioglossum nitidulum</i> (Fabricius 1804)	3	7			
<i>Lasioglossum pallens</i> (Brullé 1832)	6				
<i>Lasioglossum pauxillum</i> (Schenck 1853)		2			
<i>Lasioglossum politum</i> (Schenck 1853)	27	7			
<i>Lasioglossum punctatissimum</i> (Schenck 1853)	5				
<i>Lasioglossum villosulum</i> (Kirby 1802)		1			
<i>Sphecodes puncticeps</i> (Thomson 1870)	1				
Megachilidae					
<i>Anthidiellum strigatum</i> (Panzer 1805)	3	2			
<i>Anthidium oblongatum</i> (Illiger 1806)		1			
<i>Anthidium punctatum</i> (Latreille 1809)	4				
<i>Chelostoma campanularum</i> (Kirby 1802)		1			
<i>Hoplitis leucomelana</i> (Kirby 1802)	1	1			
<i>Megachile centuncularis</i> (Linnaeus 1758)	6	11			
<i>Megachile willughbiella</i> (Kirby 1802)		15			
<i>Osmia bicornis</i> (Linnaeus 1758)	1	1			
<i>Osmia caerulea</i> (Linnaeus 1758)	4	4			
<i>Osmia cornuta</i> (Latreille 1805)		1			
<i>Osmia submicans</i> (Morawitz 1870)	5				
DIPTERA					
Bombyliidae					
<i>Bombylius major</i> (Linnaeus 1758)			3		2
Conopidae					
<i>Myopa</i> sp.				1	
Muscidae					
<i>Phaonia</i> sp.					2
Scathophagidae					
<i>Cordilura</i> sp.					1
<i>Scathophaga</i> sp.				1	
Syrphidae					
<i>Brachypalpus valgus</i> (Panzer 1798)				1	
<i>Cheilosia fasciata</i> (Schiner & Egger 1853)				1	
<i>Cheilosia</i> sp.				1	
<i>Episyrphus balteatus</i> (De Geer 1776)			21		22
<i>Eristalis arbustorum</i> (Linnaeus 1758)			3		1
<i>Eristalis tenax</i> (Linnaeus 1758)			10		10
<i>Eupeodes corollae</i> (Fabricius 1794)		4	6		1
<i>Eupeodes luniger</i> (Meigen 1822)					25
<i>Helophilus pendulus</i> (Linnaeus 1758)		9	1		
<i>Melanostoma mellinum</i> (Linnaeus 1758)			3		3
<i>Melanostoma scalare</i> (Fabricius 1794)					2
<i>Meliscaeva auricollis</i> (Meigen 1822)		9	4		
<i>Merodon equestris</i> (Fabricius 1794)			1		1
<i>Myathropa florea</i> (Linnaeus 1758)					1
<i>Neoascia podagrica</i> (Fabricius 1775)					1
<i>Paragus haemorrhus</i> (Meigen 1822)			1		
<i>Paragus quadrifasciatus</i> (Meigen 1822)					1
<i>Parasyrphus punctulatus</i> (Verrall 1873)			1		
<i>Platycheirus albimanus</i> (Fabricius 1781)			1		1
<i>Platycheirus scutatus</i> (Meigen 1822)		5			4
<i>Scaeva pyrastris</i> (Linnaeus 1758)			1		
<i>Sphaerophoria scripta</i> (Linnaeus 1758)		39	10		5
<i>Syrpita pipiens</i> (Linnaeus 1758)			7		34
<i>Syrphus</i> sp.			1		
<i>Syrphus nitidifrons</i> (Becker 1921)			2		
<i>Syrphus torvus</i> (Osten-Sacken 1875)		2	17		
Tachinidae					
<i>Tachina</i> sp.					1
LEPIDOPTERA					
Lycaenidae					
<i>Aricia agestis</i> (Denis & Schiffermüller 1775)				2	
Pieridae					
<i>Gonepteryx rhamni</i> (Linnaeus 1758)				1	
<i>Pieris rapae</i> (Linnaeus 1758)			1		2

5.2. Wild bees' functional traits

As for the functional diversity of wild bees, there was no significant difference between rural and urban habitats, neither on *S. alba* (mean Rao's quadratic entropy per site and year \pm SE: $Q_{\text{rural}}=0.033 \pm 0.007$ vs. $Q_{\text{urban}}=0.033 \pm 0.007$; $t_{df13}=0.06$; $p=0.95$) nor on *L. corniculatus* ($Q_{\text{rural}}=0.39 \pm 0.007$ vs. $Q_{\text{urban}}=0.22 \pm 0.007$; $t_{df13}=1.73$; $p=0.11$) (**Appendix 1. 2**).

There was no statistically detectable difference in the degree of lecty between the two habitats, with almost exclusively individuals belonging to polylectic species in both habitats. Only two species of oligolectic bees were observed, exclusively on *S. alba*: *Andrena lagopus* (four individuals in the urban habitat and one in the rural habitat), and *Chelostoma campanularum* (only one individual in the urban habitat). As for brood parasites, they were only found in the rural habitat on *S. alba* (1.9% of individuals on this plant in this habitat) and belonged to the genera *Nomada* (Apidae) and *Sphecodes* (Halictidae).

Sociality levels varied between the two habitats, and throughout the season: the proportion of eusocial species ('primitive' or 'advanced' sociality, Kocher & Paxton, 2014) increased in the urban habitat on the two plants species (**Figure 1. 2a-b; Table 1. 2**). In contrast, this proportion remained stable in the rural habitat, at a low level and not significantly different from zero for both plant species (on *S. alba*: intercept estimate = -0.61 ± 0.47 , $p=0.18$; on *L. corniculatus*: intercept estimate = -0.25 ± 0.49 , $p=0.61$).

Concerning nesting habits variations over time, the proportion of ground-nesting species decreased in both habitats on the two plants species (**Figure 1. 2c-d; Table 1. 2**). On *L. corniculatus*, this proportion remained significantly higher in the rural habitat than in the urban one throughout the season (estimated intercept difference between habitats = 1.00 ± 0.50 , $p=0.043$). In contrast, there was no difference in the proportion of ground-nesting species visiting *S. alba* between the two habitats (estimated intercept difference between habitats = 0.18 ± 0.34 , $p=0.59$).

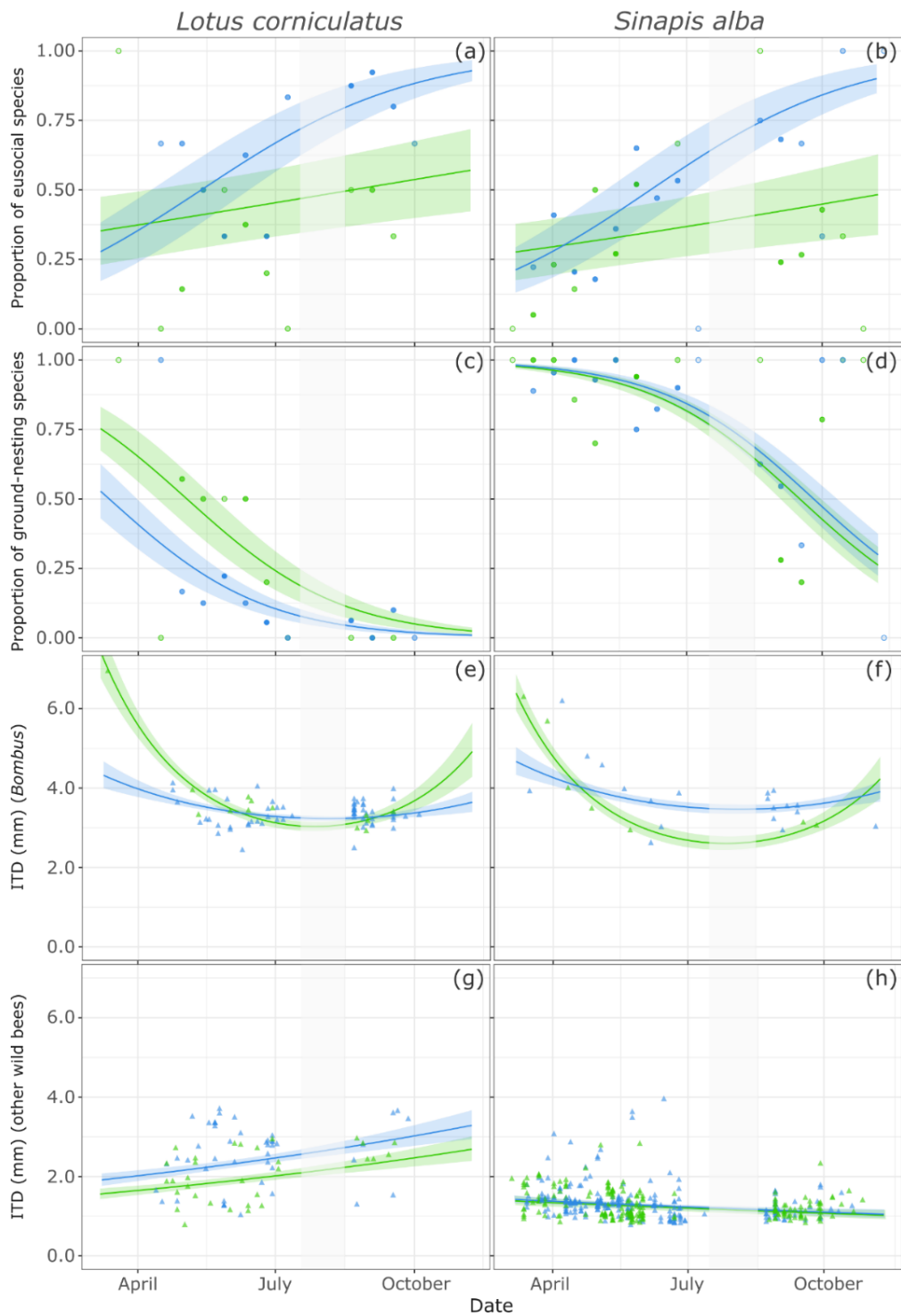


Figure 1. 2. Traits variations throughout the year in both habitats (Urban: blue; Rural: green), for insect pollinators visiting *L. corniculatus* (left panels) and *S. alba* (right panels): (a, b) Proportion of individuals belonging to eusocial species; (c, d) Proportion of individuals belonging to ground-nesting species; (e, f) Inter-tegular distance (ITD, in mm) of *Bombus* specimens; (g, h) ITD (mm) of other wild bee specimens. Curves: predictions from the models (\pm SE), dots: fortnightly mean proportion of traits (transparence level is proportional to the number of specimens collected over the period), triangles: raw ITD values. Grey-shaded part of each figure: period when sampling could not be carried out due to a severe heat wave.

Table 1. 2. Equations of the models of traits variations through time in both habitats. Equations are composed of the estimated parameters with the standard errors in brackets. NS means that the estimator is not significantly different from 0; parameters in bold indicate a significant difference between the two habitats (significance level: 5%). DAY: Julian day of the year. *L.c.*: *Lotus corniculatus*, *S.a.*: *Sinapis alba*.

Modeled trait variable	Plant	Habitat	Equation
Proportion of eusocial species (GLMM, Binomial family)	<i>L. c.</i>	Rural	-0.25 (0.49, NS) + 5.22 (3.36, NS) * DAY
		Urban	0.45 (0.47, NS) + 20.61 (3.32) * DAY
	<i>S. a.</i>	Rural	-0.61 (0.47, NS) + 5.22 (3.36, NS) * DAY
		Urban	0.09 (0.45, NS) + 20.61 (3.32) * DAY
Proportion of ground-nesting species (GLMM, Binomial family)	<i>L. c.</i>	Rural	-0.80 (0.37) + -28.02 (3.20) * DAY
		Urban	-1.80 (0.33) + -28.02 (3.20) * DAY
	<i>S. a.</i>	Rural	1.85 (0.26) + -28.02 (3.20) * DAY
		Urban	2.03 (0.25) + -28.02 (3.20) * DAY
ITD (log) genus <i>Bombus</i> (LMM, Gaussian family)	<i>L. c.</i>	Rural	1.25 (0.03) + -1.12 (0.24) * DAY + 1.31 (0.24) * DAY ²
		Urban	1.22 (0.01) + -0.46 (0.14) * DAY + 0.39 (0.15) * DAY ²
	<i>S. a.</i>	Rural	1.10 (0.05) + -1.12 (0.24) * DAY + 1.31 (0.24) * DAY ²
		Urban	1.29 (0.03) + -0.46 (0.14) * DAY + 0.39 (0.15) * DAY ²
ITD (log) Other wild bees (LMM, Gaussian family)	<i>L. c.</i>	Rural	0.65 (0.05) + 2.81 (0.89) * DAY
		Urban	0.85 (0.04) + 2.81 (0.89) * DAY
	<i>S. a.</i>	Rural	0.21 (0.02) + -1.56 (0.29) * DAY
		Urban	0.24 (0.02) + -1.56 (0.29) * DAY

On both plant species, in the rural habitat, the ITD of bumble bees followed a unimodal seasonal pattern with a decrease during summer (**Figure 1. 2e-f; Table 1. 2**). However, this seasonal trend was less pronounced in the urban habitat on both plants. Additionally, bumble bees foraging on *S. alba* in the urban habitat had overall larger ITDs than those in the rural habitat (estimated intercept difference between habitats = 0.19 ± 0.06 , $p=0.0013$). As for other wild bees (solitary or ‘primitively’ eusocial), no such unimodal seasonal pattern was detected. Indeed, the ITD of specimens visiting *L. corniculatus* steadily increased over time, and was consistently and significantly higher in the urban habitat (**Figure 1. 2g; Table 1. 2**). On the contrary, the ITD of specimens visiting *S. alba* decreased over time, with no difference between habitats (**Figure 1. 2h; Table 1. 2**).

6. DISCUSSION

As hypothesized, the pollinator assemblages visiting each plant species were different between the urban and the rural habitat. As expected, there were overall more species visiting the plant patches in the rural habitat, though species richness did not significantly differ between urban and rural sites. Also, the urban pollinator assemblage was dominated by two eusocial species: the managed honey bee (*Apis mellifera*) and one species of bumble bee (*Bombus*

pascuorum), that mainly visited *S. alba* and *L. corniculatus*, respectively. Altogether, all species encountered in the urban habitat were very common species, not benefiting from any conservation status.

In accordance with our second set of hypotheses, we recorded differences in functional diversity levels between the two habitats. Consistent with expectations, more eusocial, polylectic, or above-ground nesting species were found in the urban habitat than in the rural one. As expected, parasitic species were found solely in the rural habitat. However, these contrasts in functional diversity did not clearly translate into significant differences in the functional diversity estimator, Rao's quadratic entropy, between the two habitats. Concerning body size variations, a seasonal unimodal trend (with smaller bees during the warmest months) was recorded for bumble bees in both habitats, although less pronounced in the urban habitat, thus contradicting our hypothesis of stronger constraints on body size in the urban habitat because of the urban heat island. Last, the body size of other wild bees foraging on *L. corniculatus* was larger in the urban habitat. There was no unimodal seasonal pattern of body size, but contrasted trends were recorded between the two plant species: body size of wild bees visiting the specialist *L. corniculatus* increased with time, whereas it slightly decreased for *S. alba*.

Overall our rural habitat displayed either richer or more diverse assemblages than our very dense urban habitat, with more species representing more taxa, among which some species have special conservation status. This was expected and in agreement with other studies comparing rural and dense urban habitats (A. J. Bates et al., 2011; Deguines et al., 2012; Fortel et al., 2014; Geslin et al., 2016). In particular, the scarcity of some taxa in the urban habitat, such as the Coleoptera and Lepidoptera orders, is a reminder that although urbanization has an overall negative effect on the diversity of arthropods, not all taxa respond in the same way (Fenoglio et al., 2020).

Nevertheless, we found more numerous flower visitors in the urban habitat than in the rural one. This trend could be partially explained by the dominance of eusocial species inducing high local abundance, a result already observed in other European cities (Theodorou, Radzevičiūtė, et al., 2020). In our results, specific and functional diversity patterns of the urban habitat were

substantially affected by the over-representation of honey bees and bumble bees (mainly *B. pascuorum*). This translated into lower values of Simpson's diversity index for this habitat. In particular, the high abundance of honey bees in urban areas can be explained by the intense beekeeping activity, with hive densities in Paris (26.14 hives/ km²) far exceeding that of the Seine-et-Marne department (1.90 hives/ km²) (Ministère de l'agriculture et de l'alimentation, 2020). In fact, there is local experimental evidence that elevated hive densities are associated with lower visit frequencies of several wild pollinator categories (Ropars et al., 2019).

In the Ile-de-France biogeographic region, Halictidae and Megachilidae have previously been described as urbanophilic families; whereas Syrphidae, Apidae, Colletidae have been designated as urbanoneutral; and Andrenidae as urbanophobic (Desaegher et al., 2018). Here, we indeed detected a higher proportion of Megachilidae in the urban than in the rural habitat, but many families presented different patterns: Andrenidae and Apidae were also well represented in urban habitats, the second one due to eusocial species. In addition, Syrphidae and Colletidae individuals were proportionally more abundant in the rural habitat. Overall, this suggests that the family level may not be relevant to accurately assess the tolerance of pollinators to urbanization.

In the urban habitat, we observed proportionally more eusocial individuals and fewer ground-nesting individuals than in the rural one. This is consistent with our predictions as well as other studies. Eusocial species may be advantaged in the city as they better cope with times of scarcity (Kocher & Paxton, 2014; Samuelson et al., 2018); while ground-nesters may struggle to find suitable nesting places in impervious urban landscapes (Neame et al., 2013; F. W. Pereira et al., 2021; Threlfall et al., 2015). On the contrary, cavity-nesting bee species may benefit from a wide variety of suitable nesting opportunities in the urban habitat, thus granting them a better tolerance to urbanization (Desaegher et al., 2018; Fortel et al., 2014; Hinnert et al., 2012; Matteson et al., 2008; Pardee & Philpott, 2014). As for the temporal patterns of these traits, they differed little between the two habitats. Moreover, the proportion of individuals of eusocial species increased through the season. This could be explained by an increase in bumble bee abundance during late spring and summer, as the colonies produce more and more workers (Dicks et al., 2015; Goulson, 2010). The same could be true for primitively eusocial Halictidae

species, although worker numbers are often lower (Gibbs et al., 2012; Kocher & Paxton, 2014). On the contrary, ground-nesting bees were more numerous at the start of the season, as they were mainly represented by the genus *Andrena*, which comprises early-emerging bees (Sevenello et al., 2020).

There was no clear difference in the degree of lecty between habitats or plants, nor any detectable temporal trend. We observed a vast majority of polylectic individuals similarly in both habitats. This result cannot be generalized since it can be explained by the low diversity of the experimental plant assemblage. As it comprised only two species, it attracted only a portion of the bee community. Likewise, brood parasitic species were scarce, and all of them were found in the rural habitat, in agreement with other studies (Geslin et al., 2015; Harrison et al., 2018). This is consistent with the use of brood parasitic bees as a good indicator of the diversity of bee assemblages, as each parasitic species is dependent on finding its specific host. However, our data are too limited to suggest the absence of brood parasites in cities. Brood parasitic species have been documented in urban areas by studies with larger samples (Fortel et al., 2014; Neame et al., 2013). These results only support the hypothesis that such species are more abundant in rural habitats.

Our two plant species proved to be complementary in the study of pollinator communities, since the assemblages visiting them were quite different. This supports their use as a limited proxy for comparisons of pollinator communities across habitats. *Sinapis alba* (Brassicaceae) is a generalist species with floral resources easily accessible to a wide range of flower visitors (**Figure 1. 1**). Noteworthy, this plant attracted oligolectic bees, specialized in foraging not only on Brassicaceae (*Andrena lagopus*) but also, curiously, on Campanulaceae (*Chelostoma campanularum*). It also attracted species with special conservation status, but mostly in the rural habitat. In contrast, *Lotus corniculatus* (Fabaceae) has a narrower set of flower visitors because its floral resources are only accessible to insects with long mouthparts and a body size large enough to access the floral rewards (**Figure 1. 1**). More species were visiting this plant in the urban habitat, as long-tongued bee species might be more tolerant to urbanization (Desaegher et al., 2018; Fortel et al., 2014). Several bumble bee species are reported to flourish in the city (Samuelson et al., 2018; Theodorou, Radzevičiūtė, et al., 2020), hence more than 50% of all

individuals foraging on *L. corniculatus* belonged to a single *Bombus* species. As for the other genera visiting this plant, they exhibited greater ITD values than those of *S. alba* visitors, since long mouthparts are associated with large body size (**Figure 1. 2g-h**).

Overall, the ITDs of bumble bees visiting *S. alba* and other wild bees visiting *L. corniculatus* were larger in the urban habitat. This result refutes our hypothesis, as we expected smaller body sizes as a response to limited resources and higher temperatures in the city (Banaszak-Cibicka et al., 2018; Banaszak-Cibicka & Żmihorski, 2012; Hinnners et al., 2012). Instead, it is consistent with recent evidence of an increase in bumble bee size with urbanization at the species and community level (Theodorou et al., 2021). Would a large size be advantageous because it enables greater flying distances in a fragmented environment (Wenzel et al., 2020)? As a matter of fact, a study of wild bees in a U.S. city (Hamblin et al., 2018) showed that large bees benefit more than small bees from high floral density in an impervious and hot urban habitat. Hence large bees may be more tolerant to fragmented urban landscapes, provided that they find locally abundant resources in green spaces. Furthermore, the body size of bumble bee queens increased over the last century in Belgium, linked to the increasing fragmentation and urbanization of the habitats (Gérard et al., 2020). This occurred despite the general temperature rise, as bumble bees follow a size-temperature relationship opposite to Bergmann's rule, which is most likely the result of their partial endothermy (Gérard et al., 2018). The effect of putative diminished resources and the heat island on wild bee body size in the city appears, therefore, less pronounced than expected. It could be mitigated by opposite selective pressures related to habitat fragmentation.

In previous studies, wild bee body size seemed nonetheless affected by seasonal changes in accordance with Bergmann's rule, with a community-level size decrease during the warmer months (Osorio-Canadas et al., 2016). While we expected a seasonal decrease in wild bee body sizes and ITDs, we found this trend only for bumble bees, with a more pronounced summer decrease in rural areas. In early colonies, bumble bee worker larvae are often poorly fed and thus develop into smaller adults (Couvillon & Dornhaus, 2009; Shpigler et al., 2013). A period of floral resource shortage may also explain the summer decrease in size at the community level. Such seasonal deficits in nectar supply to bumble bees have been demonstrated in English

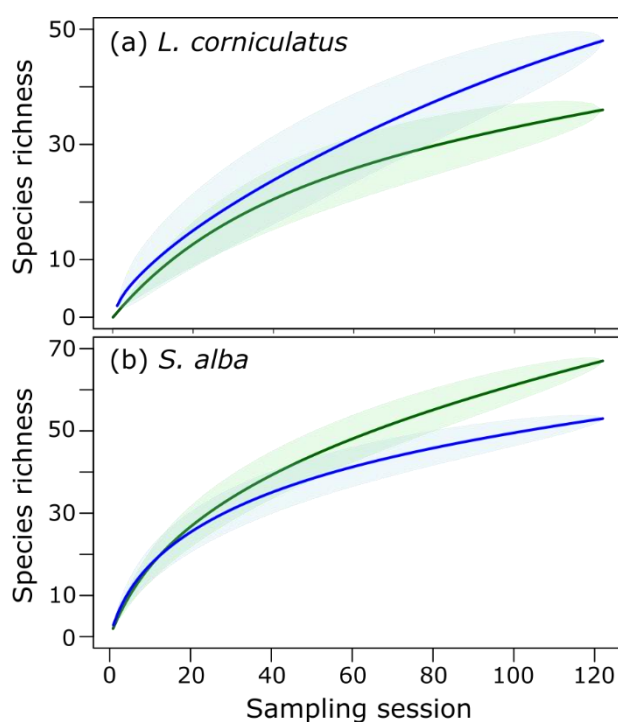
farmlands (Timberlake et al., 2019). Meanwhile, in urban habitats, seasonal resources variations might be buffered by ornamental flora (Staab et al., 2020) and watering of flower beds, hence the less pronounced seasonal decrease in body size we observed in urban sites. Besides, when measuring the ITDs of bumble bees, we did not discriminate between bumble bee castes. Therefore, in our urban habitat, these buffered seasonal size variations might also be linked to altered phenology patterns of bumble bee colonies. Indeed, the year-round activity of bumble bee queens and workers has been recorded in some urban habitats, suggesting more generations within a year (Stelzer et al., 2010). Thus, in urban sites, overlapping generations and the extended presence of larger-bodied reproductive castes – queens and males – may have attenuated the body size seasonal trend. On the contrary, in the rural habitat, large individuals belonging to reproductive castes emerge at the beginning and end of the season and may be responsible for strong seasonal variations of the ITD. Such results should be interpreted with caution, though, given the low overall number of bumble bees captured in the rural habitat.

In contrast, the ITD of other wild bees visiting *L. corniculatus* and *S. alba* changed linearly over time in both habitats, respectively increasing and decreasing. To our knowledge, these linear trends throughout seasons have not been recorded yet. In our data, we thus observed an increasing difference between the mean size of bees visiting the two plant species throughout our sampling period. One hypothesis to explain this trend would be that open flowers with easily accessible floral rewards are becoming increasingly available towards the end of summer (peak flowering of some Apiaceae and Asteraceae such as *Daucus carota*, *Helminthotheca echioides*, *Picris hieracioides*, Jauzein & Nawrot, 2011). Small bees (e.g. the genera *Hylaeus* and *Lasioglossum*), which also visit *S. alba*, could benefit from this resource and consequently be more abundant during this period. Meanwhile, apart from bumble bees (Apidae), *L. corniculatus* was mainly visited by large Megachilidae bees (e.g. the genera *Megachile*, *Anthidium*, and *Anthidiellum*) (**Figure 1. 1**), that appeared late in the season.

7. CONCLUSION

There was a strong urban signature on the taxonomic and functional diversity of pollinator assemblages visiting our experimental plant set-up. Our sampling method offers an alternative to colored pan traps, allowing us to collect accurately and exclusively flower visitors in a standardized way across habitats and seasons. Here, the manipulated flowering phenology of the plants allowed us to detect significant within-year changes in functional diversity. However, this method requires more time as well as more financial and human resources, and limits sampling to visitors of a restricted array of plant species. In the city, we found lower taxonomic diversity, lower seasonal variation in bumble bee body size, lower abundance of brood parasitic and ground-nesting bees, but overall more individuals and larger bees. This suggests that our dense urban environment can be suitable for some bees, but only a few bee species really benefit from urban functional filtering. Trends in body size in the city could be a response to habitat fragmentation combined with a weakening of seasonal constraints, though it remains to be investigated in future research. Such consideration for seasonality and connectivity between resources embedded in urban landscapes is growing in the literature (Hinners et al., 2012; Levé et al., 2019; Staab et al., 2020), as it appears to be relevant in understanding how to preserve pollinator functional diversity in the city. This could be a key factor in maintaining the pollination function despite the impacts of global changes - including climate change and increasing urbanization of habitats - on insect pollinator communities.

8. APPENDIX

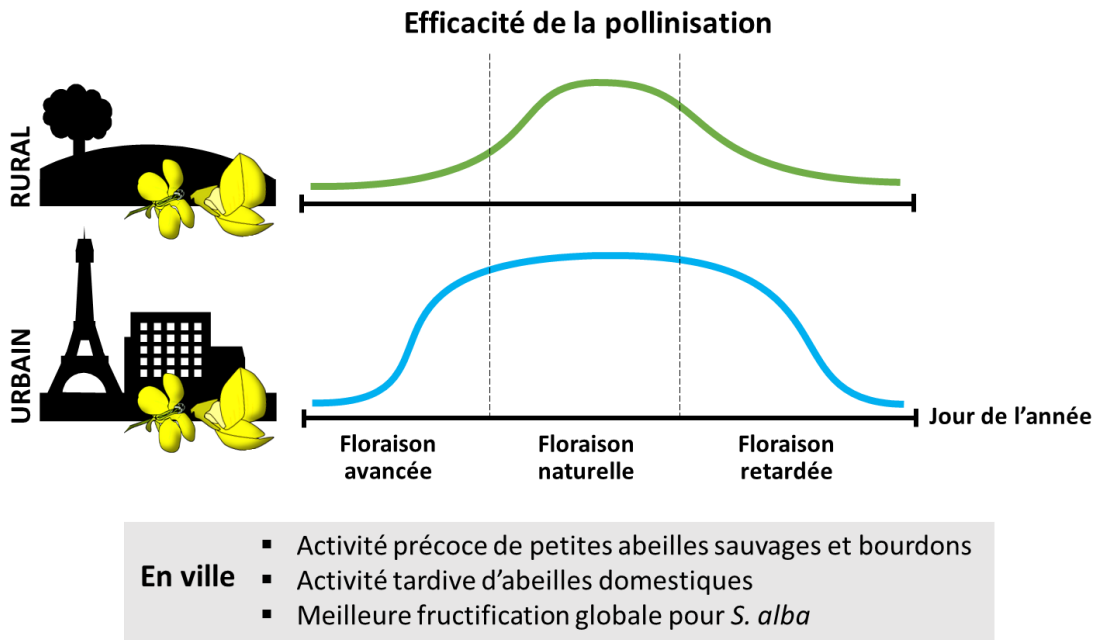


Appendix 1. 1. Rarefaction curves of insect pollinator species on both plant species, in both habitats (Urban: blue; Rural: green).

Appendix 1. 2. Mean comparison of diversity indices and Tukey post hoc test between the rural (Rur.) and urban (Urb.) habitats. *L.c.*: *Lotus corniculatus*, *S.a.*: *Sinapis alba*.

Index	Plant	Mean \pm SE (across sites and years)		Estimator of habitat type		Tukey post-hoc test	
		Rural	Urban	estimate \pm SE	p	direction	p
Species richness (GLMM, Poisson family)	<i>L. c.</i>	6.3 \pm 0.87	7.2 \pm 0.97	0.13 \pm 0.12	0.25		0.27
	<i>S. a.</i>	22 \pm 2.00	25 \pm 2.16	0.13 \pm 0.12	0.25		0.27
Simpson's index (LMM)	<i>L. c.</i>	0.75 \pm 0.029	0.64 \pm 0.029	-0.11 \pm 0.041	0.0064	Rur.> Urb.	0.017
	<i>S. a.</i>	0.91 \pm 0.029	0.89 \pm 0.029	-0.017 \pm 0.041	0.69		0.69
Rao's quadratic entropy (LMM)	<i>L. c.</i>	0.039 \pm 0.0072	0.022 \pm 0.0072	-0.018 \pm 0.010	0.084		0.11
	<i>S. a.</i>	0.033 \pm 0.0072	0.033 \pm 0.0072	-0.001 \pm 0.010	0.95		0.95

CHAPITRE 2 : Phénologie des communautés de pollinisateurs et succès de pollinisation en milieu urbain et rural



CHAPITRE 2 : Résumé graphique

Au niveau de ce même dispositif végétal standardisé dans l'espace et dans le temps, nous avons suivi l'activité de butinage de plusieurs groupes morphologiques de pollinisateurs ; ainsi que l'efficacité de la fonction de pollinisation au cours des saisons.

- Comment se décline l'activité de butinage au niveau de notre dispositif végétal en milieu urbain et en milieu rural ? Et ce, en période de floraison naturelle, en période de floraison précoce et en période de floraison tardive ?
- Quelles sont les conséquences sur le succès reproducteur des plantes et ses dynamiques saisonnières ?

Nos résultats suggèrent des adaptations phénologiques à l'habitat urbain différentes selon les groupes de pollinisateurs ; ainsi qu'un élargissement de la période d'activité des insectes pollinisateurs en ville, qui se répercute sur le succès reproducteur des plantes.

Broader phenology of pollinator activity and higher plant reproductive success in an urban habitat compared to a rural one

published in Ecology and Evolution, 2020

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1. ARTICLE DETAILS

Acknowledgements: The authors wish to thank the Jardin des Plantes of the MNHN (Philippe Barré), the Cité Internationale Universitaire de Paris (David Otamendi) and the Pierre et Marie Curie campus of Sorbonne-Université (Guillaume Baloup) for providing access to the sites; as well as the cultivation services of the Pierre et Marie Curie campus of Sorbonne-Université (Patrick Dumont) and of the MNHN (Alain Karg) for their help in growing plants. The authors also thank Ambre Zelela-Bouvard, Vincent Leclercq, and Hugo Sellan for their contribution to field work.

Funding: This project was partially funded by the City of Paris through a CIFRE PhD scholarship, by the PEPS CNRS INEE Adaptation-Adaptabilité program, and by the Institut de la Transition Environnementale of Sorbonne-Université. This work has also benefited from technical and human resources provided by CEREPEP-Ecotron IleDeFrance (CNRS/ENS UMS 3194) as well as financial support from the Regional Council of Ile-de-France under the DIM Program R2DS bearing the reference I-05-098/R. It has received support under the program "Investissements d'Avenir" launched by the French government and implemented by ANR with the reference ANR-11-INBS-0001 AnaEE France.

Authors' contributions: VZ, ID, EG, YK, and XR conceived the ideas and designed the methodology; VZ, OB, ID, EG, AH, CH, YK, EM, and XR collected the data; VZ analyzed the data; VZ and ID led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility: All data is archived in the publicly accessible repository Zenodo, within the 'iEES-Paris OpenData' community: <https://doi.org/10.5281/zenodo.3993031>

Conflict of interest: None declared.

Complete Reference: Zaninotto, V., Raynaud, X., Gendreau, E., Kraepiel, Y., Motard, E., Babiard, O., Hansart, A., Hignard, C., & Dajoz, I. (2020). Broader phenology of pollinator activity and higher plant reproductive success in an urban habitat compared to a rural one. *Ecology and Evolution*, 10(20), 11607–11621. <https://doi.org/10.1002/ece3.6794>

2. ABSTRACT

1. Urban habitat characteristics create environmental filtering of pollinator communities. They also impact pollinating insect phenology through the presence of an urban heat island and the year-round availability of floral resources provided by ornamental plants.

2. Here we monitored the phenology and composition of pollinating insect communities visiting replicates of an experimental plant assemblage comprising two species, with contrasting floral traits: *Sinapis alba* and *Lotus corniculatus*, whose flowering periods were artificially extended. Plant assemblage replicates were set up over two consecutive years in two different habitats: rural and densely urbanized, within the same biogeographical region (Ile-de-France region, France).

3. The phenology of pollination activity, recorded from the beginning (early March) to the end (early November) of the season, differed between these two habitats. Several pollinator morphogroups (small wild bees, bumble bees, honey bees) were significantly more active on our plant sets in the urban habitat compared to the rural one, especially in early spring and autumn. This resulted in different overall reproductive success of the plant assemblage between the two habitats. Over the course of the season, the reproductive success of *S. alba* was always significantly higher in the urban habitat while the reproductive success of *L. corniculatus* was significantly higher in the urban habitat only during early flowering.

4. *Synthesis.* These findings suggest different phenological adaptations to the urban habitat for different groups of pollinators. Overall, results indicate that the broadened activity period of pollinating insects recorded in the urban environment could enhance the pollination function and the reproductive success of plant communities in cities.

Keywords: plant-pollinator interactions, phenology, plant reproductive success, pollinator assemblage composition, urban-rural gradient, flowering phenology manipulation, *Sinapis alba*, *Lotus corniculatus*.

3. INTRODUCTION

Urbanization is one of the main and fastest-acting drivers of land-use changes (Grimm et al., 2008; Patacchini & Zenou, 2009), leading to strong consequences on species richness (McKinney, 2008). In dense urban habitats, pollinating insect communities are affected by habitat loss and fragmentation, contaminants, modifications of floral resources and nesting habitats, and local climate warming (Harrison & Winfree, 2015). This generates an environmental filter that can alter the composition and diversity of pollinator assemblages. While some studies have witnessed a loss of functional and taxonomic diversity in urban habitats (Deguines et al., 2016; Geslin et al., 2016), others found a positive impact on pollinator diversity, especially for wild bees (Baldock et al., 2015; Fortel et al., 2014; Theodorou et al., 2017; Wenzel et al., 2020). Indeed, several characteristics of urban habitats, such as the year-round abundance and diversity of floral resources (Baldock et al., 2019; Garbuzov & Ratnieks, 2014; Stelzer et al., 2010), and the overall warmer urban climate (Harrison & Winfree, 2015; Rizwan et al., 2008) may render them favorable for some pollinators (Hall et al., 2017), especially compared to intensive agricultural lands (Baldock et al., 2015).

Urban habitat characteristics can also impact the phenology of plant-pollinator interactions. Concerning plants, the warmer urban climate (through the presence of an urban heat island, hereafter UHI) may either advance or delay (Jochner & Menzel, 2015; Neil et al., 2010) plant flowering phenology. Moreover, the year-round presence of ornamental plants in urban green spaces may extend the availability of floral resources for pollinating insects (Tasker et al., 2020). Individual species may display various phenological responses, ultimately causing shifts in potential interaction partners and transforming the mutualistic networks (Harrison & Winfree, 2015). Concerning pollinators, the UHI should enable them to be more active throughout the season than in rural habitats. Indeed, some recent studies report a broadening of the flight period of pollinators in the city, whereas pollinator activity tends to peak earlier in spring in semi-natural habitats (Harrison et al., 2018; Leong et al., 2016; Luder et al., 2018; Wray & Elle, 2015). This extended period of activity may also be supported by the above-mentioned year-round availability of floral resources in cities. Taken together, these plant and insect phenological changes should strongly impact the pollination function in urban habitats.

However, there is concern that plants and pollinators might have different responses to warming, potentially leading to loss of phenological synchrony that would disrupt the pollination networks (Memmott et al., 2007), although this appears to be dependent on the biodiversity level (Bartomeus et al., 2013). It has been theorized that the local adaptive responses of plant-pollinator networks to the UHI effect could be considered as a small-scale model for the larger-scale consequences of global warming (Jochner & Menzel, 2015)

Here we set up all-season monitoring of the pollination activity, pollinator assemblage composition, and the resulting pollination function, in an urban-rural paired experimental design encompassing a dense urban habitat (the city of Paris, France) and rural habitats located within the same region (Ile-de-France region, France). In order to standardize our monitoring from the beginning of spring to mid-autumn, and also to simulate potential climate-change-induced modifications in the flowering phenology of plants, we used temporal transplants of an experimental plant assemblage (Morton & Rafferty, 2017), comprising two insect-pollinated plant species native to this region (**Figure 2. 1**). In other words, we brought plants to bloom in and out of their natural flowering period. These plant assemblages, whose flowering phenology was either ‘advanced’ or ‘delayed’ (in contrast to ‘natural’), thus played the role of plants with shifted phenological patterns. We aimed to investigate whether these out-of-season floral resources would find matching pollinators in the dense urban and the rural habitats investigated, and what consequences it would have on the reproductive success of the plants. Hence these controlled plant sets can be considered as “pollinometers” (Theodorou et al., 2017), as measuring their reproductive success could be a proxy to assess the efficiency of the pollination function throughout the season between urban and rural habitats within the same region.

We hypothesize that, in the city, pollinator activity would show different phenological patterns than in a rural habitat. This would lead to differences in the efficiency of the pollination function and contrasting plant reproductive success over the time between these two habitats. More precisely, we expect a broadening of the pollinator flight season in the urban habitat, thus leading to more efficient early and/or late pollination, and higher overall plant reproductive success in urban habitats compared to rural ones.

To our knowledge, this is one of the few studies (Rafferty et al., 2013) that have associated all-season monitoring of pollinator activity to the evaluation of the pollination function, through the assessment of plant reproductive success in an urban-rural paired design.



Figure 2. 1. Detail of the flowers of each focal plant species: *Sinapis alba* (Brassicaceae, left) and *Lotus corniculatus* (Fabaceae, right). © Alexis Orion (CC BY 4.0), originals can be retrieved at www.inaturalist.org/photos/56174372 and www.inaturalist.org/photos/71587817. The photos have been cropped and the scale bars added.

4. MATERIALS AND METHODS

4.1. Experimental sites

Experiments were conducted over two consecutive years in four (2018) and six (2017) locations in grasslands located in dense urban habitat and forest-dominated semi-natural habitat – hereafter referred to as ‘rural’. All sites were located in the same biogeographical region: the Ile-de France region, which encompasses a large diversity of habitats, from the city of Paris (the largest city in France) to semi-natural and rural habitats (INSEE, 2015).

In 2017, urban experimental sites were located in downtown Paris: Pierre et Marie Curie campus of Sorbonne Université (SU), Jardin des Plantes (JDP), and Cité Internationale Universitaire de Paris (CIUP); whereas rural sites were all located in the Seine-et-Marne administrative department (50-64 km from Paris): CEREEP-Ecotron Ile-de-France, with two set-ups 1km apart (CEREEP_A and CEREEP_B), and Station d’Ecologie Forestière of Fontainebleau-Avon (SEF). In 2018, the same sites were used, except for CIUP and CEREEP_A.

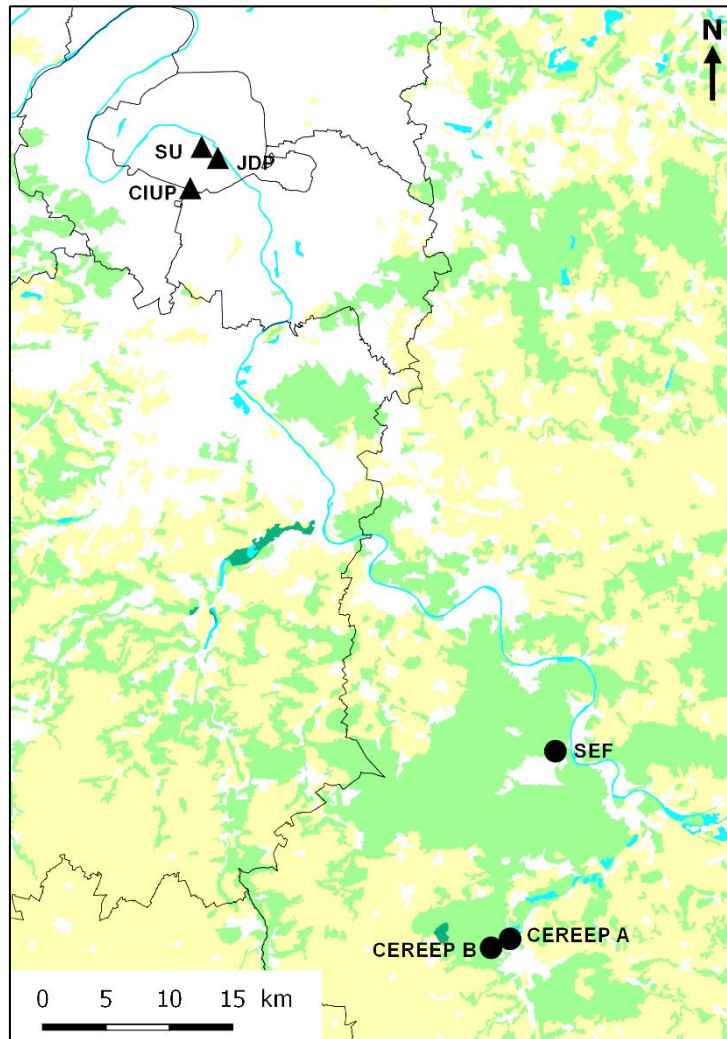


Figure 2. 2. Distribution of rural (dots), and urban (triangles) sites (SEF: Station d’Ecologie Forestière of Fontainebleau-Avon; CEREEP_A and B: CEREEP-Ecotron Ile-de-France; SU: Pierre et Marie Curie campus of Sorbonne Université; JDP: Jardin des Plantes; CIUP: Cité Internationale Universitaire of Paris). Colors represent areas dominated by agricultural landscape (yellow), by semi-natural habitats (green) or by impervious zones (white). Water-covered surfaces are represented in blue (source: EEA, 2018).

Urban sites were set in green spaces, with a combination of lawns and ornamental flower beds which do not receive any pesticide treatment. The surrounding landscapes consisted mostly of dense urban landscape and urban green spaces (**Table 2. 1, Figure 2. 2**). On the other hand, rural sites were set up in grasslands mostly surrounded by forests. These grasslands are not harvested and do not receive any chemical inputs. The SEF site is part of a forest biosphere reserve, while the two CEREEP sites are located in a large experimental ecology field station encompassing semi-natural forests and grasslands. For this reason, all these sites can be considered as “semi-natural”, despite their potential proximity to discontinuous suburban areas.

Table 2. 1. Proportions of land-use categories within a radius of 500m around the experimental sites (SEF: Station d'Ecologie Forestière of Fontainebleau-Avon; CEREEP_A and B: CEREEP-Ecotron Ile-de-France; SU: Curie campus of Sorbonne Université; JDP: Jardin des Plantes; CIUP: Cité Internationale Universitaire of Paris) (source: European Environment Agency (EEA), 2018).

	Site	Coordinates	Continuous urban	Discontinuous suburban	Linear infrastructures	Green spaces	Permanent grassland	Forests
Rural	SEF	48.4206° 2.7289°	0	43	0	0	0	57
	CEREEP _A	48.2867° 2.6781°	0	26	8	0	2	64
	CEREEP _B	48.2831° 2.6657°	0	0	0	0	49	51
Urban	CIUP	48.8189° 2.3353°	48	16	0	36	0	0
	JDP	48.8440° 2.3611°	37	3	26	34	0	0
	SU	48.8465° 2.3587°	51	0	17	32	0	0

4.2. Experimental setting

In each experimental site, two 1.6x1.2m plots were set up side by side in a grassland area, each containing one of the two focal plant species (the Brassicaceae *Sinapis alba* and the Fabaceae *Lotus corniculatus*). *Sinapis alba* L. is an annual forb that grows along roads, in wastelands, or near crops, and is considered naturalized in the Ile-de-France region (Lombard, 2006). It is an obligate outcrossing species (Cheng et al., 2012), the fruits of which are siliques containing up to 8 seeds (Jauzein & Nawrot, 2011). On the other hand, *Lotus corniculatus* L. is a perennial, nitrogen-fixing plant widespread in grasslands and disturbed habitats (Jones & Turkington, 1986). Native to the Ile-de-France region (CBNBP, 2008; Jauzein & Nawrot, 2011), this strictly entomophilous species (Pellissier et al., 2012; Stephenson, 1984) bears cylindrical pods containing up to 30 seeds. No spontaneous *L. corniculatus* or *S. alba* conspecifics were found in a 100m radius around either urban nor rural sites.

Although they both bear yellow flowers, these two plant species were chosen for their contrasting floral morphologies, in order to attract a diverse range of pollinators: *S. alba* has flat corollas with floral rewards accessible to pollinators with short mouthparts (Fontaine et al., 2006; Geslin et al., 2013; Jones & Turkington, 1986), whereas *L. corniculatus* has deep corollas with nectar and pollen resources mainly accessible for pollinators with long mouthparts (**Figure 2. 1**). Seeds of these two species (obtained from Semences du Puy, France) were germinated and grown in individual pots in a commercial potting substrate under insect-proof greenhouse conditions (temperature: 20°C; photoperiod: 16h of day; 12cm diameter plastic pots filled with

peat-enriched sowing soil: 180 g.m⁻³ N, 450 g.m⁻³ P₂O₅, 90 g.m⁻³ K₂O). Plants were installed in the experimental plots when flowering.

In each plot, 20 pots containing one plant of the same species were buried in four rows of five, each plant being spaced from others by 25 cm in all directions. We kept plants in their plastic pots to prevent competition for soil resources. A plastic tag was planted in each pot to individually number each plant, and all plants were watered regularly. The plots were regularly weeded to avoid interference from spontaneous plants.

Since the objective was to maintain a regular floral cover throughout the study period, and since the full flowering stage of both plant species did not exceed three weeks (Zaninotto, pers. obs.), the plants were renewed regularly in each plot, on the same day for all experimental sites. For both species, blooming plants were exposed to pollinators for about 20 days, before being replaced by fresh plants from the greenhouse, thus defining successive floral rounds (**Table 2. 2**). At the end of each floral round, several randomly chosen plants were brought back to an insect-proof greenhouse to estimate their reproductive success during the field exposure period (see fruit set and seed set measurement section).

This design was set up for two consecutive years, in 2017 and 2018. In 2017, the study period focused on the spring season: five 20-day floral rounds were conducted from the beginning of March to early July. In 2018, the monitoring was extended to summer and autumn, with 10 floral rounds from early March to mid-November, with an interruption between mid-July and mid-August due to the climatic conditions (severe heat waves that were harmful to the plant installations). Since the natural flowering periods of the focal plant species in the Ile-de-France region extends from May to July for *S. alba*, and from May to August for *L. corniculatus* (Jauzein & Nawrot, 2011), some of the flowering rounds were set before, and after, that period. Plants that were artificially brought to bloom during these rounds can be described as temporal transplants. Three phases were thus defined in the experiment (see **Table 2. 2**): the **advanced** (March to April for both species), the **natural** (May to July for *S. alba*, May to August for *L. corniculatus*), and the **delayed** (August to November for *S. alba*, September to November for *L. corniculatus*) flowering periods.

Table 2. 2. Summary table of flowering periods for the successive floral rounds and distribution of the floral rounds among the advanced, the natural, and the delayed flowering periods for *S. alba* and *L. corniculatus*, during both years of the experiment.

Round n°	Period	<i>S. alba</i> flowering	<i>L. corniculatus</i> flowering
1	5 Mar. - 26 Mar.		
2	27 Mar. - 17 Apr.	advanced	advanced
3	18 Apr. - 9 May		
4	10 May - 31 May		
5	1 Jun. - 25 Jun.	natural	natural
6	26 Jun. - 13 Jul.		
7	22 Aug. - 11 Sept.		
8	12 Sep. - 3 Oct.	delayed	delayed
9	4 Oct. - 25 Oct.		
10	26 Oct. - 13 Nov.		

4.3. Monitoring

During these periods, the plant-pollinator interactions on these plant plots were regularly monitored. Twice a week, all locations were monitored on the same day, in alternating order. A total of 398 five-minutes observation sessions were conducted in 2017 on each plant species, spread over 6 locations and during 4 months. A further 444 sessions were conducted in 2018 on each species, spread over 4 locations and during 7 months.

At each monitoring, the time of the day, temperature, and proportion of cloud cover were recorded. Floral display size was also qualitatively estimated at the plant level, using an index from 0 (all flowers in buds), to 3 (all visible flower buds fully opened), which provides an estimation of the quantity of floral resources in each plot. Then, for each plant species, we conducted two 5-minutes observation sessions with a 10-minutes break between sessions. During these sessions, all pollinator visits on experimental plants were recorded at the plant level. A visit was defined as an insect landing on a flower and inserting its mouthparts in the corolla, resulting in contact between the flower visitor and the fertile parts of the flower (stigma and/or anthers). Pollinators were identified on the fly as belonging to one of the following morphological groups: honey bees, bumble bees, large solitary bees (body length > 1cm), small wild bees (body length < 1 cm), syrphid flies, butterflies, and beetles.

4.4. Fruit set and seed set measurement

At the end of each 20-day floral round, and in all experimental sites, five *S. alba* and three *L. corniculatus* plants were randomly selected to estimate fruit set; while two plants of each species were selected to estimate seed set. Control plants were also grown to estimate the selfing rate and resulting fruit set and seed set of the two focal species. In 2017, one control plant per species and per round was kept in the greenhouse during its entire flowering period. In 2018, one control plant per species, per locality, and per round was set up in the field in an insect-proof mesh cage, then brought back to the greenhouse at the end of each round. This allowed to determine a selfing rate and resulting fruit set and seed set of the two species under greenhouse conditions and under natural conditions. After each round, both plants exposed to insect visitation and control plants were kept in the insect-proof greenhouse for an additional two weeks to allow for fruit development.

We used different methods of estimating fruit set for each plant species. For *S. alba*, all flower peduncles are still visible after the flowers have wilted, even in the absence of fruit. Therefore, on each insect-exposed plant and each control plant, we were able to count the number of fruits produced by 10 contiguous flowers on the stem from a random starting position. For *L. corniculatus*, fruit set was not assessed in 2017 as the fruit set estimator used at the time was not appropriate for this plant species. In 2018, it was estimated by counting all fruits produced on each plant. In order to account for size differences among plants (and thus size-related differences in floral display), plant aboveground biomass was collected individually, dried in an oven for 48h at 60°C, and weighted (scale precision: 1×10^{-4} g). For both species, seed set was estimated by counting the number of seeds contained in three fruits (when present), randomly picked on each selected insect-exposed plant and each control plant.

4.5. Data analysis

All data analysis was performed using R software (R Core Team 2021, version 3.6.1). First, visitation rates were analyzed by constructing generalized mixed effect models with the ‘glmmTMB’ function (“glmmTMB” package, Brooks et al., 2017), which deals well with zero-inflated data. The response variable was ‘Visitation rate’, defined as the number of pollinator visits per plant and per 5min-observation session, with a negative binomial distribution to

account for overdispersion. Fixed effects were the habitat ('rural' or 'urban'), the flowering period ('advanced', 'normal', and 'delayed') and their interaction, as well as the flower display size of the plant, cloud cover, the relative temperature (measured temperature relative to expected seasonal temperatures), and the year. The experimental site was included as a random effect. This model was replicated for the different morphological groups of pollinators and both plant species.

We also built generalized mixed-effect models to analyze fruit set estimators. For *S. alba*, the response variable was the proportion of flowers that gave fruits, with a binomial distribution. Fixed effects were the habitat, the flowering period ('advanced', 'normal', and 'delayed'), and their interaction, as well as the year; the experimental site was again included as a random effect. For *L. corniculatus*, the response variable was the total number of fruits on the plant, with a Poisson distribution. Fixed effects were the habitat, the flowering period, and their interaction, as well as the aboveground dry mass of the plant; with the experimental site as a random effect. The same types of models were used for both plant species to analyze seed set estimators, with the number of seeds per fruit as the response variable following a Poisson distribution.

For all models, we evaluated the contribution of each factor to the model via Type III Wald chi-square tests ('Anova' function in "car" package, Fox and Weisberg 2019), and performed model selection based on the AIC ('step' function, "backward" method). We also verified the absence of multi-collinearity between the predictors ('check_collinearity' function from "performance" package, Lüdecke et al. 2020). We compared visitation rates, fruit set, and seed set between habitats within flowering periods through post-hoc Tukey's tests with the 'emmeans' and 'contrast' functions ("emmeans" package, Lenth 2020).

In addition, non-parametric Wilcoxon tests were carried out to compare fruit set estimators of control plants kept under insect-proof conditions with plants exposed to pollinators, to estimate the rates of self-fertilization of the two plant species. Eventually, the control plants of both species did not produce enough fruits to be able to estimate their seed set.

5. RESULTS

5.1. Pollinators visit frequencies

In 2017, over the 5 conducted floral rounds, we observed 6,364 interactions between the 8 morphological groups of floral visitors and the two plant species, with 80.4% of these visits on *S. alba* and 19.6% on *L. corniculatus*. In 2018, over the 10 conducted floral rounds, 12,096 interactions were observed in total, with 59.9% of these visits on *S. alba* and 40.1% on *L. corniculatus*.

Over the two years of sampling, plant individuals of *S. alba* were most often visited by small wild bees (3,434 interactions, 42.5% of total interactions) and syrphid flies (1,029 interactions, 12.7% of total interactions) in the urban habitat, as well as in the rural habitat (1,828 interactions for small wild bees, 42.8% of total interactions; 955 interactions for syrphid flies, 22.3% of total interactions) (see **Figure 2. 3** for a graphical representation of mean visitation rates). However large solitary bees visited *S. alba* more frequently in rural sites (778 interactions, 18.2% of total interactions) compared to urban sites (295 interactions, 3.65% of total interactions); while bumble bee visits remained rare in both rural (253 interactions, 5.92% of total interactions) and urban sites (510 interactions, 6.31% of total interactions). During the delayed flowering period, domesticated honey bees generated a peak of visits in the city (2,349 interactions, 63.5% of interactions observed during this flowering period), whereas they were almost absent in rural sites (22 interactions, 1.40% of interactions during this flowering period).

On the other hand, during the 2 years of sampling, visits on *L. corniculatus* were largely dominated by bumble bees in both habitats (2,739 interactions, 67.2% of interactions in urban habitat; 945 interactions, 46.7% of interactions in rural habitat), and to a lesser extent by large solitary bees (1,005 interactions, 24.7% of interactions in urban habitat; 624 interactions, 30.8% of interactions in rural habitat) (see **Figure 2. 3**). Butterfly visits mainly occurred in the delayed flowering period in the rural habitat (159 interactions, 30.3% of interactions during this flowering period).

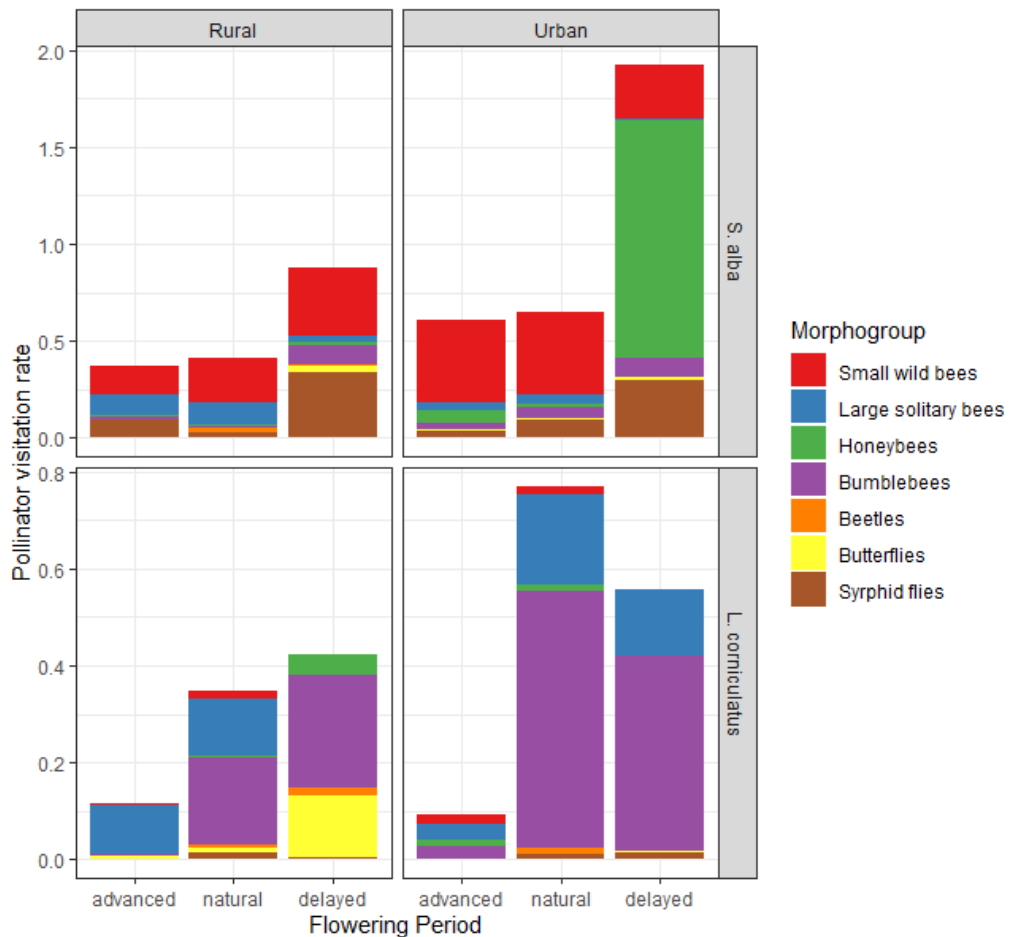


Figure 2. 3. Pollinator visitation rates (mean number of visits per 5min session) per morphogroup (stacked) and flowering period, for the two plant species: *S. alba* (upper two graphs) and *L. corniculatus* (lower two graphs).

As we could expect, our models reveal that pollinators' visitation rates to a plant are strongly associated with the floral display of that plant, but also with the relative temperature at the time of observation. On both plant species, we also observed differences between the two habitats that varied throughout the season, as evidenced by the terms “Habitat”, “Flowering Period” and their interaction (**Table 2. 3**).

Overall, pollinator visits on *S. alba* were not restricted to the natural flowering phenology of the plant in both habitats (**Figure 2. 4a**). Small wild bees and large solitary bees visited this plant species from the beginning of the advanced flowering period (**Figure 2. 4b-e**); while syrphid flies, domesticated honey bees, and bumble bees performed the most visits during the delayed blossoming period (**Figure 2. 4c-d-f**). First, overall visitation rates on *S. alba* were higher in the urban habitat during the advanced flowering period ($t_{df16830}=-2.87$, $p=0.0041$, **Figure 2. 4a**).

Table 2. 3. Summary table of the best-fitting glmm models of visitation rates on the two plant species, for main pollinators. For each term, χ^2 and p-value of the Type III Wald chisquare tests are presented, as well as the estimates of each coefficient (\pm SE) ('urb.' = urban, 'adv.' = advanced, 'del.' = delayed; rural habitat, normal flowering period and year 2017 were taken as references).

Response var.	Predictors	df	χ^2	P	Estimates
<i>Sinapis alba</i>					
All pollinators visitation rate AIC=30717	Floral display	1	2008	< 2e-16	1.19 \pm 0.03
	Relative temperature	1	191	< 2e-16	0.30 \pm 0.02
	Habitat	1	12	0.00046	NS (urb.)
	Flowering period	2	429	< 2e-16	-0.26 \pm 0.07 (adv.) 0.60 \pm 0.08 (del.)
	Habitat x Flowering period	2	28	1.0e-06	0.18 \pm 0.09 (urb. adv.) 0.56 \pm 0.11 (urb. del.)
Small wild bees visitation rate AIC=17663	Floral display	1	882	< 2e-16	1.14 \pm 0.04
	Relative temperature	1	320	< 2e-16	0.64 \pm 0.04
	Habitat	1	3.2	0.073	NS (urb.)
	Flowering period	2	30	3.7e-07	-0.73 \pm 0.11 (adv.) NS (del.)
	Habitat x Flowering period	2	58	2.7e-13	0.71 \pm 0.14 (urb. adv.) -0.45 \pm 0.16 (urb. del.)
Syrphid flies visitation rate AIC=8918	Floral display	1	321	< 2e-16	0.97 \pm 0.05
	Habitat	1	1.2	0.27	0.85 \pm 0.17 (urb.)
	Flowering period	2	375	< 2e-16	0.79 \pm 0.17 (adv.) 2.19 \pm 0.17 (del.)
	Habitat x Flowering period	2	70	6.1e-16	-1.84 \pm 0.22 (urb. adv.) -0.99 \pm 0.22 (urb. del.)
<i>Lotus corniculatus</i>					
All pollinators visitation rate AIC=15293	Floral display	1	675	< 2e-16	1.09 \pm 0.04
	Relative temperature	1	165	< 2e-16	0.50 \pm 0.04
	Year	1	117	< 2e-16	1.02 \pm 0.10 (2018)
	Habitat	1	2.8	0.092	1.01 \pm 0.34 (urb.)
	Flowering period	2	395	< 2e-16	-1.38 \pm 0.14 (adv.) -0.56 \pm 0.14 (del.)
	Habitat x Flowering period	2	40	1.7e-09	-1.21 \pm 0.19 (urb. adv.) NS (urb. del.)
Bumble bees visitation rate AIC=8882	Floral display	1	350	< 2e-16	1.24 \pm 0.07
	Relative temperature	1	47	7.9e-12	0.39 \pm 0.06
	Year	1	50	1.6e-12	1.00 \pm 0.14 (2018)
	Habitat	1	18	2.4e-05	1.32 \pm 0.30 (urb.)
	Flowering period	2	221	< 2e-16	-4.44 \pm 0.47 (adv.) NS (del.)
	Habitat x Flowering period	2	8.0	0.019	0.92 \pm 0.52 (urb. adv.) -0.52 \pm 0.27 (urb. del.)
Large solitary bees visitation rate AIC=6186	Floral display	1	195	< 2e-16	0.98 \pm 0.07
	Relative temperature	1	78	< 2e-16	0.65 \pm 0.07
	Year	1	128	< 2e-16	1.87 \pm 0.17 (2018)
	Habitat	1	0.2	0.68	NS (urb.)
	Flowering period	2	89	< 2e-16	-1.25 \pm 0.15 (adv.) -1.11 \pm 0.16 (del.)

At that time, this difference seemed to rely on higher visitation rates of small wild bees in the urban habitat ($t_{df16830}=-3.09$, $p=0.0020$, **Figure 2. 4b**), while those of syrphid flies ($t_{df16831}=6.80$, $p<0.0001$), and large solitary bees ($t_{df16832}=7.89$, $p<0.0001$), were significantly lower (**Figure 2. 4c-e**). Then, during the natural flowering period of *S. alba*, lower visitation rates of large solitary bees in the urban habitat seemed to be compensated by higher visitation rates of syrphid flies. Therefore, there was no significant difference between the overall visitation rates in the two habitats ($t_{df16830}=-1.63$, $p=0.10$). Finally, during the delayed flowering period, since there was a surge in domesticated honey bees visits in the urban habitat (**Figure 2. 3; Figure 2. 4d**) – while syrphid fly visitation rates increased substantially in both habitats (**Table 2. 3;**

Figure 2. 4c) – overall visitation rates again became significantly higher ($t_{df16830}=-5.07$, $p<0.0001$) in the urban habitat than in the rural one.

Sinapis alba

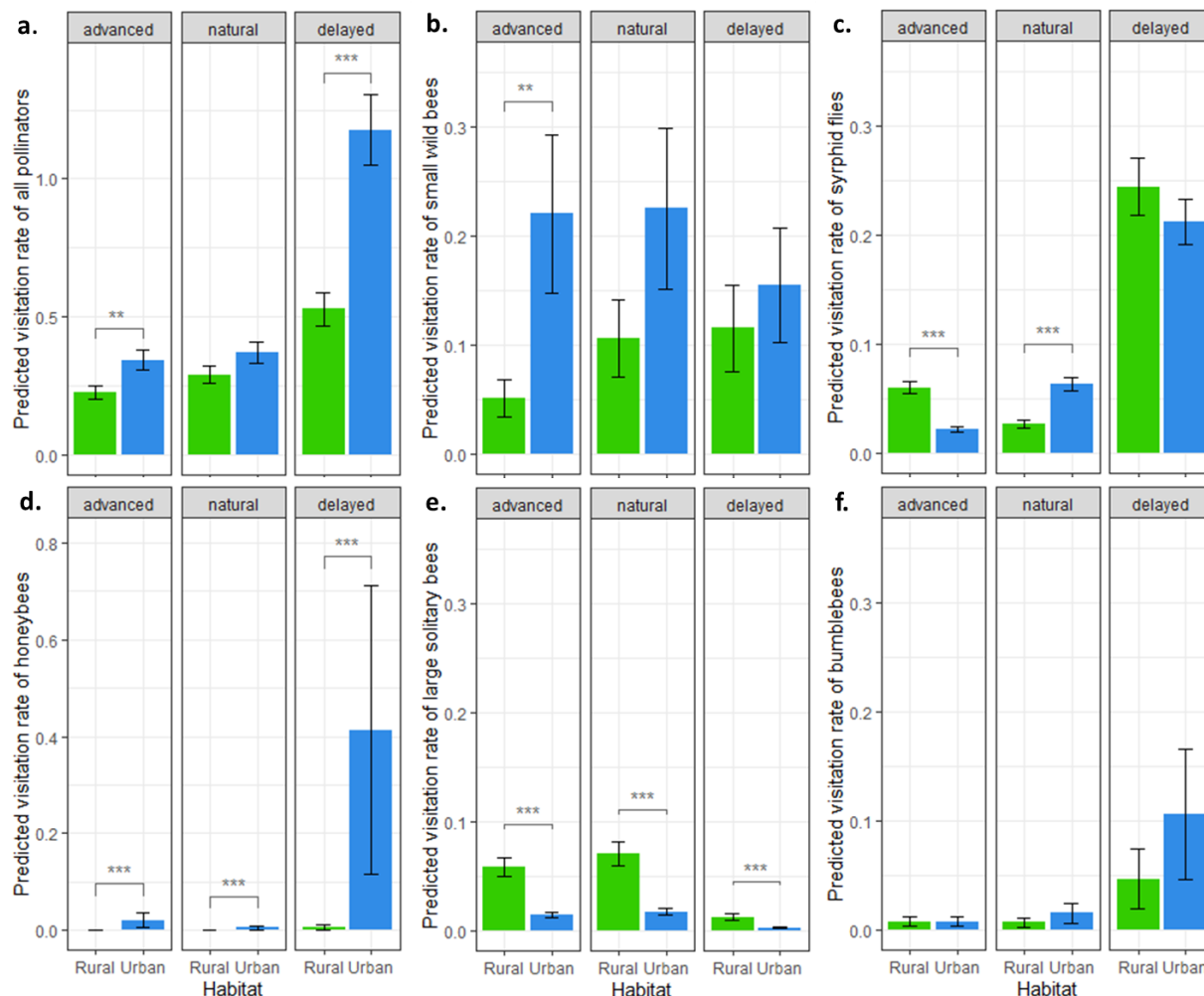


Figure 2. 4. Predicted pollinator visitation rates (number of visits per 5min session) on *Sinapis alba*, per floral round, for all pollinators combined (a.) and major pollinator morphogroups: b. small wild bees, c. syrphid flies, d. honey bees, e. large solitary bees, f. bumble bees. Bars represent estimated marginal means \pm SE (green=Rural; blue=Urban). Stars represent significance levels from Tukey’s post-hoc tests.

Pollinator visits on *L. corniculatus* were more restricted by the natural flowering period of the plant (**Table 2. 3; Figure 2. 5a**), with overall more visits during this natural phenology period compared to the advanced and delayed flowering periods. During this period, bumble bee and large solitary bee visits were the most frequent (**Figure 2. 5b-c**). Overall, pollinator visits were significantly more frequent in the urban habitat during the natural ($t_{df14589}=-3.01$, $p=0.0026$) and delayed ($t_{df14589}=-2.47$, $p=0.014$) flowering periods (**Figure 2. 5a**). This was

mainly driven by bumble bee visitation rates which were significantly higher in the urban habitat for all flowering periods (**Figure 2. 5b**). This might have been compensated in terms of visitation rates by other pollinators in rural sites during the advanced flowering. Yet the other main visitors of *L. corniculatus*, large solitary bees, did not show significantly different visitation rates between habitats during any flowering period (**Figure 2. 5c**). On a smaller scale, butterfly visitation rates were always significantly higher in the rural habitat and increased during the delayed flowering period, albeit remaining scarce over the season (**Figure 2. 5d**).

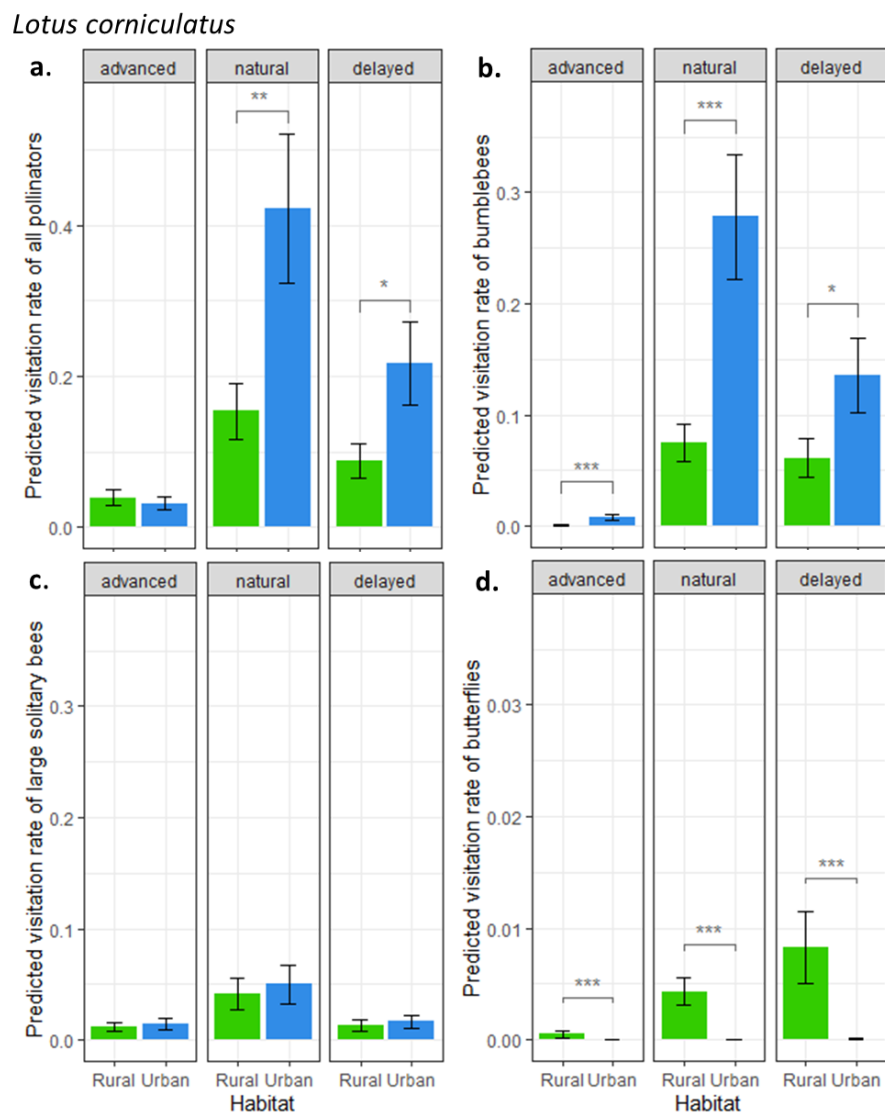
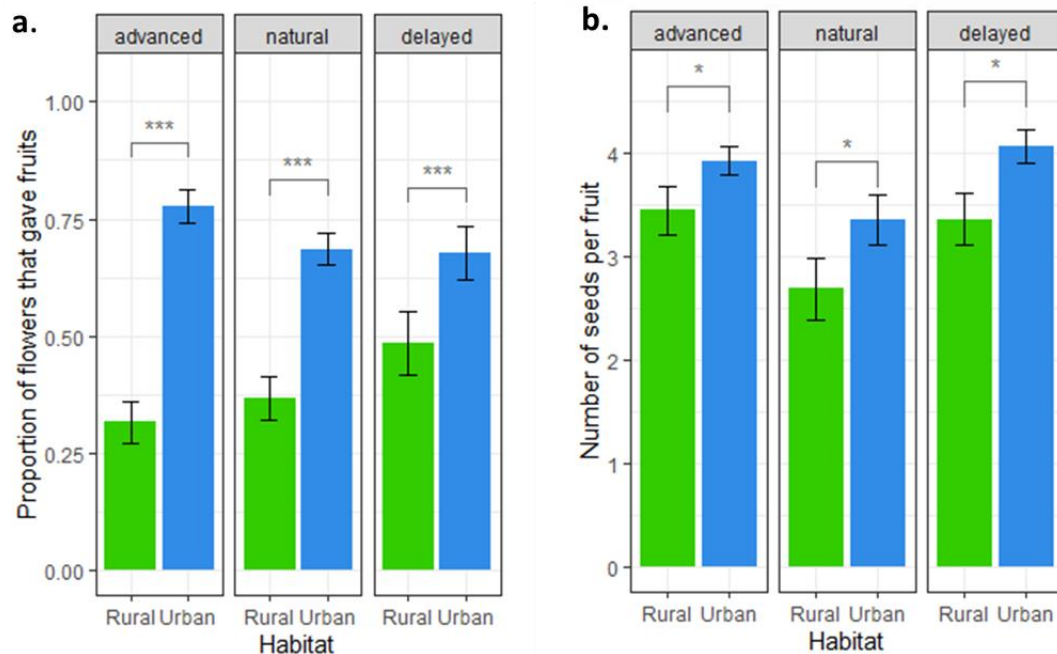


Figure 2. 5. Predicted pollinator visitation rates (number of visits per 5min session) on *Lotus corniculatus*, per floral round, for all pollinators combined (a.) and major pollinator morphogroups: b. bumble bees, c. large solitary bees, d. butterflies. Bars represent estimated marginal means \pm SE (green=Rural; blue=Urban). Stars represent significance levels from Tukey's post-hoc tests.

5.2. Plants reproductive success

In the urban habitat, the fruit set rate of *S. alba* remained elevated for the three experimental phases and was not restricted to the natural flowering time (**Table 2. 4; Figure 2. 6a**).

Sinapis alba



Lotus corniculatus

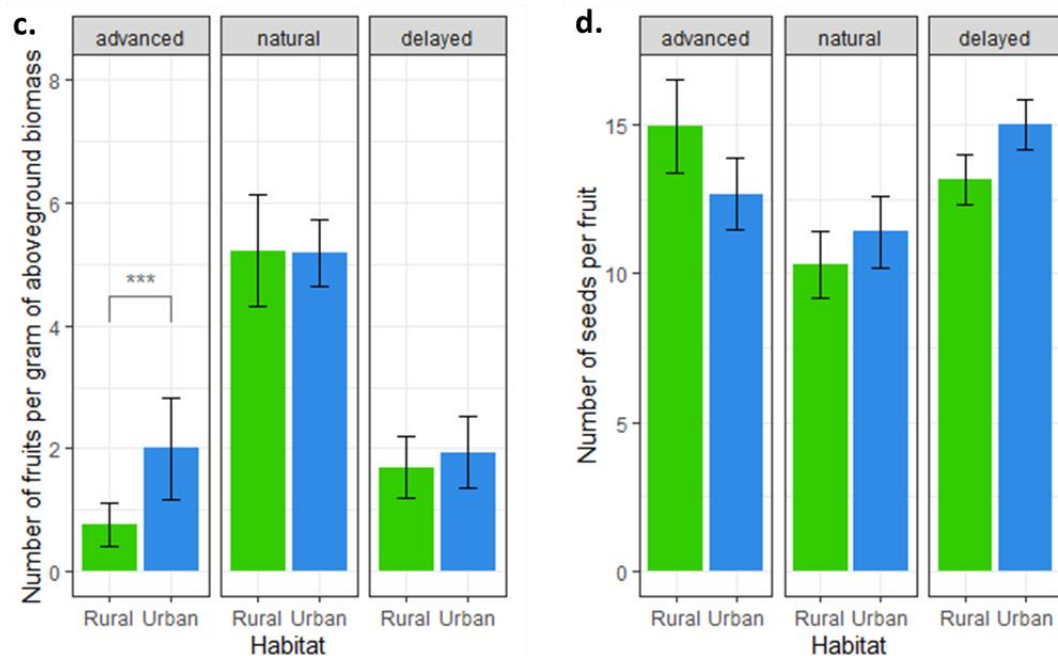


Figure 2. 6. Reproductive success estimators, per flowering period and for the two plant species: a. and b. respectively fruit set and seed set rates of *S. alba*; c. and d. respectively fruit set and seed set rates of *L. corniculatus*. Bars represent mean value \pm SE. Stars represent significance levels from Tukey's post-hoc tests.

In particular, the fruit set rate of *S. alba* during the advanced period was already as high as than during the natural flowering period (mean percentage of flowers that gave fruits \pm SE: advanced period, 78 ± 3.0 %; natural period, 69 ± 3.0 %; delayed period, 68 ± 6.0 %). In contrast, rural fruit set rates were always significantly lower (**Figure 2. 6a**; advanced period: $t_{df352}=-10.2$, $p<0.0001$; natural period: $t_{df352}=-6.81$, $p<0.0001$; delayed period, $t_{df352}=-4.22$, $p<0.0001$), but they seemed to slowly increase throughout the season (advanced period, 32 ± 4.0 %; natural period, 37 ± 5.0 %; delayed period, 49 ± 7.0 %).

Last, mean fruit set rates of the control plants were significantly lower than mean fruit set rate of plants exposed to pollinators (6.0 ± 2.0 % and 3.0 ± 1.0 % of fruit set for 2017 and 2018 controls respectively; no significant difference between these two values, whereas mean overall fruit set of plants exposed to pollinators in both years was 55 ± 2.0 % SE, $W=1702$, $p=1.4e-13$). This indicates that differences in fruit set between habitats are not due to higher selfing rates because of differences in other biotic or abiotic characteristics of the environment. Not only was the fruit set rate of *S. alba* higher in the urban habitat, but the fruits also contained more seeds during each of the periods studied (**Figure 2. 6b**; for each period: $t_{df259}=-2.56$, $p=0.011$). This resulted in an overall higher reproductive success of the plant in the urban habitat than in the rural habitat.

For *L. corniculatus*, the fruit set showed the same dynamics as pollinators' visits frequencies, and was consequently higher during the natural flowering period in both habitats (**Table 2. 4**; **Figure 2. 6c**). However, this fruit set was significantly higher in the urban than in the rural habitat during the advanced flowering period ($t_{df68}=-4.07$, $p=0.0001$), though well below the value during the natural flowering time. Last, mean fruit set rates of the two types of control plants were significantly lower than mean fruit set rates of plants exposed to pollinators (no fruit has ever been observed on 2017 or 2018 controls, whereas mean overall fruit set of plants exposed to pollinators in both years was 3.11 ± 0.35 fruits per gram of dry aboveground biomass, $W=260$ $p=1.5e-14$). This also strongly suggests that differences in fruit set between habitats are not due to higher selfing rates because of differences in other biotic or abiotic characteristics of the environment. As for seed set rates, there seemed to be no difference between the two habitats throughout the season (**Figure 2. 6d**).

Table 2. 4. Summary table of the best-fitting glmm models of fruit set and seed set of the two plant species. For each term, χ^2 and p-value of the Type III Wald chisquare tests are presented, as well as the estimates of each coefficient (\pm SE) ('urb.' = urban, 'adv.' = advanced, 'del.' = delayed; rural habitat, normal flowering period and year 2017 were taken as references).

Response var.	Predictors	df	χ^2	P	Estimates
<i>Sinapis alba</i>					
Proportion of flowers that gave fruits AIC=2793	Year	1	31	2.5e-08	0.51 \pm 0.09 (2018)
	Habitat	1	65	7.3e-16	1.37 \pm 0.20 (urb.)
	Flowering period	2	3.6	0.17	-0.28 \pm 0.12 (adv.) NS (del.)
	Habitat x Flowering period	2	36	1.5e-08	0.73 \pm 0.17 (urb. adv.) -0.39 \pm 0.20 (urb. del.)
Number of seeds per fruit AIC=999	Habitat	1	6.6	0.011	0.18 \pm 0.07 (urb.)
	Flowering period	2	7.6	0.022	0.19 \pm 0.08 (adv.) 0.21 \pm 0.08 (del.)
<i>Lotus corniculatus</i>					
Number of fruits per plant AIC=2369	Dry mass of the plant	1	139	< 2e-16	0.31 \pm 0.03
	Habitat	1	4.4	0.036	NS (urb.)
	Flowering period	2	632	< 2e-16	-1.84 \pm 0.10 (adv.) -0.97 \pm 0.08 (del.)
	Habitat x Flowering period	2	78	< 2e-16	0.92 \pm 0.10 (urb. adv.) 0.17 \pm 0.10 (urb. del.)
Number of seeds per fruit AIC=1233	Habitat	1	0.3	0.59	NS (urb.)
	Flowering period	2	26	2.2e-06	0.35 \pm 0.10 (adv.) 0.28 \pm 0.08 (del.)
	Habitat x Flowering period	2	5.9	0.052	-0.25 \pm 0.13 (urb. adv.) NS (urb. del.)

6. DISCUSSION

In this study, we used an experimental approach to compare the response of pollinator assemblages and their activity between urban and rural sites within the same geographical region, when confronted with a controlled plant assemblage with constant flowering throughout seasons. Our results show that the phenology of pollination activity differed between the two habitats, with several pollinator morphogroups (small wild solitary bees, bumble bees, honey bees) being significantly more active on the plant assemblage in the urban habitat compared to the rural one, especially during the advanced and the delayed flowering of this plant assemblage. This resulted in contrasted reproductive success of the plants between the two habitats, with an overall reproductive success higher in the urban habitat due to the broadening of the pollinator activity season in this habitat compared to the rural one.

The phenology of visits on *S. alba* did not seem to be restricted to the natural flowering period of the plant. In particular, in the urban habitat, abundant early visits of small wild bees, and intense honey bee activity late in the season might be responsible for the high and stable measured fruit set and seed set rates of the plants, beyond the range of the natural flowering period. In contrast, *L. corniculatus* visits were predominantly carried out by bumble bees,

whose visitation rates were more limited to the natural flowering period of the plant. As a result, fruit set rates, and by extension reproductive success of the plant, was more restricted to this period than in *S. alba*. This can be associated with a higher degree of specialization in the pollination ecology of *L. corniculatus*, with deep and hard-to-reach floral resources that are nevertheless accessible to bumble bees (**Figure 2. 1**). Since these pollinators seem to be determinant to the pollination of *L. corniculatus* (Fontaine et al., 2006; Jones & Turkington, 1986), the synchronization between the natural flowering period of this plant and the activity of bumble bees was expected. Before that, during the advanced blossom, we registered greater bumble bee activity in urban sites, though visits remained scarce in both habitats. This may explain why plants achieved a better fruit set in urban sites at that time, which could result in better reproductive success.

Previous recent work (Harrison et al., 2018; Leong et al., 2016; Wray & Elle, 2015) highlighted different phenological patterns of bee abundance and diversity in urban versus semi-natural habitats. Bee pollinating peak was reached in early spring in the forest (natural) habitat whereas it was delayed to mid-summer in the city (late-summer in arable land for Leong et al. 2016). Both Harrison et al. (2018) and Wray and Elle (2015) found differences in traits representation linked with phenology among forest and city pollinator communities: in an urban habitat, they recorded more bees in general, with later emergence time and/or longer flight periods. Furthermore, Theodorou et al. (2020) also found that Hymenoptera diversity was negatively affected by the presence of arable/agricultural lands, thus leading to a higher diversity in the city. Here we indeed observed a higher abundance of pollinator visits during the late season in the urban habitat. This was mainly driven by the late abundance of domesticated honey bees and bumble bees. However, we also observed higher activity of small wild bees on *S. alba* and bumble bees on *L. corniculatus* in the city early in the season. Overall, this suggests different phenological adaptations to the urban habitat for different groups of pollinators.

As for syrphid flies, few studies are available. Luder et al. (2018) showed that syrphid flies are less abundant in the city than in the rural habitat, but their phenology seemed broader in the city, with an earlier appearance and a later peak. Here, we did not observe a similar phenological

pattern. Hoverflies on *S. alba* showed more pronounced activity in rural sites during the advanced flowering period, but the contrary was found in the urban habitat during the natural flowering period. Last, during the delayed flowering period, hoverfly activity strongly increased in both the urban and the rural habitats, although no significant difference was detected between the two habitats.

Here, the observed urban phenological patterns might arise from different, although nonexclusive, processes. It might be the result of a plastic adaptation to broader phenology in a warm environment with little temporal limitation of floral resources. Such a plastic adaptation of phenology could happen at the species level. Pollinators would have to shift their emergence date or extend their flight period. Multivoltine species such as bumble bees could also benefit from a longer favorable period by producing additional generations during the year Stelzer et al. (2010).

At the community level, the broad urban phenological pattern could also be a consequence of environmental filtering of pollinator species in favor of generalist species (Geslin et al., 2013; Wray & Elle, 2015). As these generalist species have particularly broad phenologies, the resulting urban assemblage would have a longer flight period. Besides, environmental filtering in the city could lead to the replacement of species by others whose traits better match the phenology of plants in the urban habitat. Previous studies showed this seems to be the case with small bee species of the genus *Lasioglossum* (Geslin et al., 2016). Species replacement may also be artificially enhanced by the introduction of managed honey bee colonies in the city, as the different pollinator morphogroups investigated showed variable responses to increased apiary densities (Ropars et al., 2019).

It is very unlikely that the observed differences in fruit set and seed set between habitats were due to varying selfing rates between localities or between habitats. Furthermore, *S. alba* is an obligate outcrossing species (Olsson, 1960) and such is also the case for *L. corniculatus* (Ollerton & Lack, 1998). Here we used three proxies of reproductive success (percentage of flowers that set fruits for *S. alba*, fruit production per unit of aboveground biomass for *L. corniculatus*, and the number of seeds per fruit for both plants) to account for the influence of different pollinator assemblages and phenologies on the reproductive success of the

experimental plant assemblage. However, other factors are involved in this reproductive success, that might have various impacts outside the natural phenology ranges of plants. For example, Parsche et al. (2011) found that advanced flowering strongly enhanced the reproductive success of a close species to *S. alba*, *Sinapis arvensis*. Although advanced-flowering plants were less visited by pollinators, they also less suffered from pollen grazing beetles. Parsche et al. thus hypothesized that enhanced reproductive success during advanced flowering may result from a trade-off between weaker pollination and an escape from pollen grazing. We found a similar trend concerning the fruit set and the seed set of *S. alba*, which were elevated during the advanced flowering period, especially in the city. Considering the impact of pollen grazing beetles on fruit set might provide another hypothesis for the weak fruit set of *S. alba* in the rural habitat: these plants might have suffered more from this grazing pressure than the urban ones. Indeed, the intensity of plant damage caused by pollen beetle herbivory was found to be positively associated with the proportion of crops in the landscape (Thies et al., 2003), and in our case, agricultural landscapes were more common in the vicinity of the rural sites (mean share of agricultural lands in a 5km radius were respectively 23% and 0% around rural and urban sites, **Figure 2. 2**).

In turn, Theodorou et al. (2020) also witnessed a higher seed set of their ‘pollinometer’ species (*Trifolium pratense*) in urban habitats, apparently driven by high visitation rates of *Bombus sp.* and domesticated honey bees. This resonates with the high fruit set and seed set achieved in our urban habitat by *S. alba* and *L. corniculatus*. The same morphological groups of pollinators seemed involved here: respectively domesticated honey bees on *S. alba* during delayed flowering; and bumble bees on *L. corniculatus* during natural, delayed, and to a lesser extent advanced flowering. On the other hand, Pellissier et al. (2012), while monitoring the reproductive success of *Lotus corniculatus* along an urbanization gradient, observed a greater fruit set in suburban areas than in dense urban sites. Since their study was conducted during the natural flowering period of the plant, this result is not at odds with our present work: here we did not observe a significant difference in fruit set between urban and rural sites during the natural flowering period of the plant.

Overall, our results suggest that a flowering phenology broadening might be beneficial to *S. alba*, as elevated reproductive success rates were not limited to its natural flowering time. This positive impact of phenological broadening on reproductive success was weaker for *L. corniculatus*, even though it was detected in the urban habitat where bumble bees displayed a longer, and especially an earlier starting flight period. Besides, this plant species needs strict photoperiod conditions to initiate flowering (Steiner, 2002).

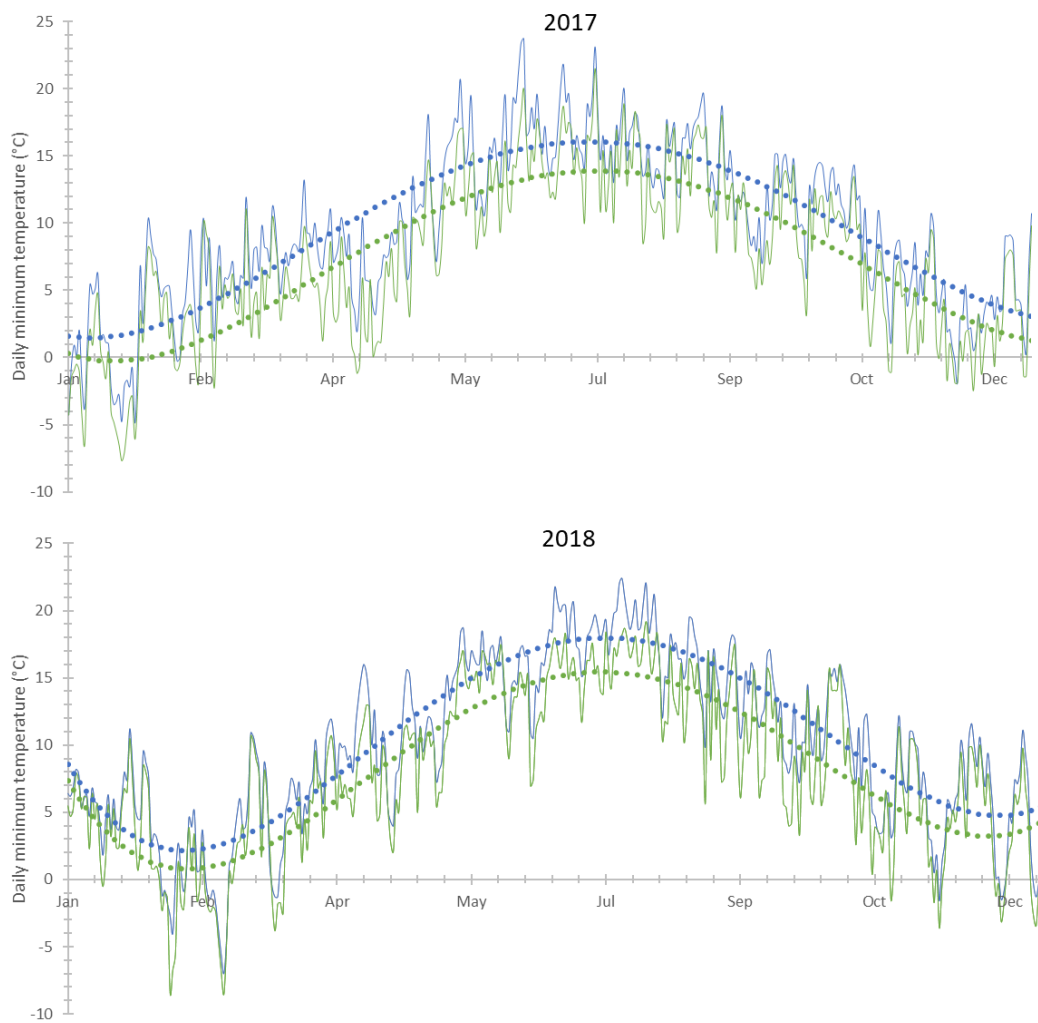
Here we witnessed different phenological patterns of pollinator activity between an urban and a rural habitat. Still, we cannot explain the underlying causes of these differences with our experimental setting alone. The two habitats differ in several factors, including temperature. Indeed, through meteorological data, we detected an UHI effect, with a mean difference of about 2°C in daily minimum temperatures between our urban and rural habitats (**Appendix 2. 1**). Adaptation to UHI might contribute to shaping the phenology of the pollinator community in the city, with earlier activity of pollinator morphogroups such as small wild bees and bumble bees (Stelzer et al., 2010). Besides, other phenomena might be involved. The temporal availability of floral resources differs substantially between the two habitats, not only because of the advanced phenology of spontaneous plants in response to UHI. Thus we cannot exclude a “honeypot effect” (Theodorou, Radzevičiūtė, et al., 2020) of our experimental plant assemblage, which might represent an important trophic resource in an otherwise resource-poor environment, especially during early- and late-season, and even more during droughts. Indeed, water-stressed plants were shown to provide less nectar sugar content per flower, and consequently attract fewer flower visitors (Descamps et al., 2018). The “honeypot effect” might have concentrated the local urban pollinator community on our plants, thus increasing visitation rates and ultimately reproductive success. This phenomenon may be just as intense in the rural habitat, where proximity to massively flowering crops (**Figure 2. 2**) could induce strong variations in the availability of floral resources, with alternating high and low-food supply periods (Requier et al., 2015); whereas flower resources are more stable all-year-round in the city (Tasker et al., 2020) thanks to the presence of ornamental plants. Indeed, in the city, abundant managed flowering plants are set in green spaces, private gardens, balconies. Though

ornamental plant species' attractiveness to pollinators is highly variable, they are suspected to lessen temporal resources limitations for pollinators (Garbuzov et al., 2015).

We found differences in pollinator assemblages visiting the two focal plant species used in our experimental design. This emphasizes the need to carry such experimental approaches on several plant species with contrasting floral morphologies. Indeed, it is necessary to monitor the responses of a large range of pollinator groups – with various mouthparts morphologies enabling them to visit contrasted corolla shapes – in order to assess the response of the pollination function to plant phenological changes within and among environments. Here, the assemblage of pollinators we witnessed was shaped by our choice of plant models, and also by the timing of observation. Hence, it is not a comprehensive survey of all the pollinators present in the two habitats studied.

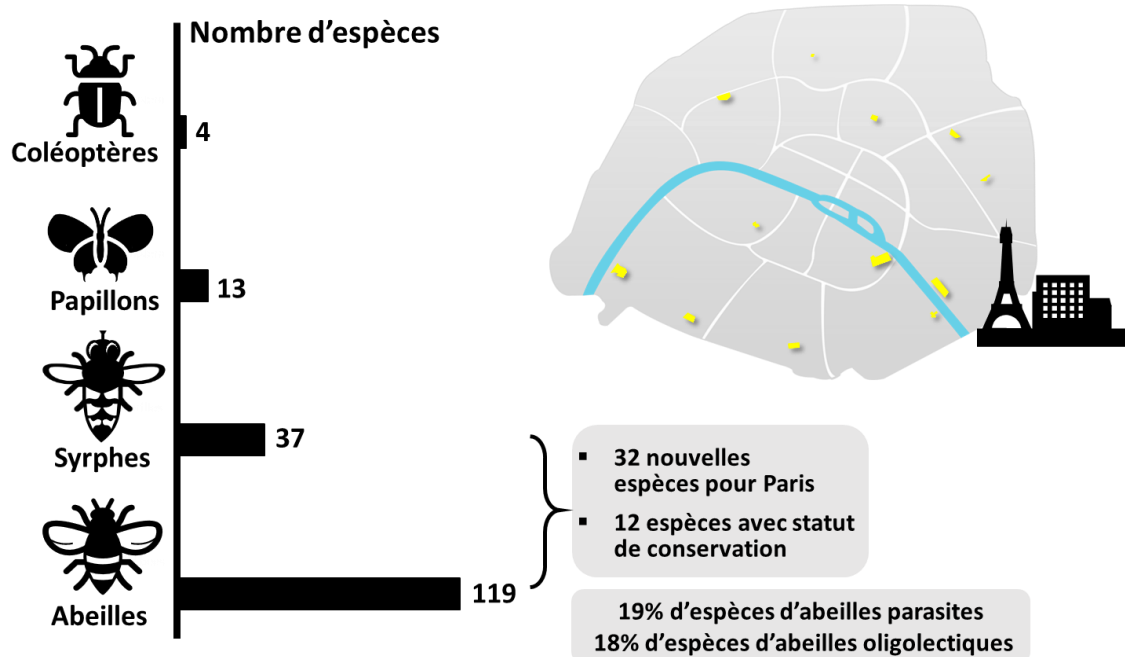
The high temporal resolution of our experiment, with two weekly monitoring sessions spanned over several months, together with the high level of maintenance required to set up the plant assemblage in the different localities surveyed, made it difficult to multiply geographical replicates. Overall, we are aware that future research on the response of the pollination function to phenological and habitat changes would benefit from a wider set of geographical replicates, especially if they could encompass an urban-rural gradient (Fisogni et al., 2020).

7. APPENDIX



Appendix 2. 1. Daily minimum temperatures in urban (blue) and rural (green) habitats during both years of monitoring. Dotted lines represent polynomial fitted curves. (RADOME network public data, ‘Melun-Villaroche’ and ‘Paris-Montsouris’ stations, available at: <https://www.meteo60.fr/stations-relevés/station-mois>)

CHAPITRE 3 : À la rencontre des insectes pollinisateurs à Paris



CHAPITRE 3 : Résumé graphique

Nous présentons ici les résultats d'un nouvel inventaire des espèces de pollinisateurs dans les espaces verts de Paris, issus d'un suivi standardisé dans douze espaces verts de la capitale depuis le printemps jusqu'à l'automne pendant deux années consécutives.

- Quelles informations peut apporter la mise à jour des listes d'espèces d'abeilles et de syrphes à Paris ? Ce milieu urbain dense est-il aussi appauvri qu'on pourrait le supposer ?
- Quelles sont les particularités des assemblages d'espèces, notamment en termes de préférences florales, de complexité des interactions, de rareté, et de successions saisonnières ?

Malgré sa densité de bâti et de population, Paris abrite des communautés de pollinisateurs relativement riches et fonctionnellement diversifiées. Il ne faut donc pas négliger les environnements urbains denses dans les stratégies de conservation des insectes pollinisateurs.

Keeping up with insect pollinators in Paris

published in Animals in 2022

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1. ARTICLE DETAILS

Acknowledgments: We gratefully acknowledge all the greenspace management services for allowing access to the sites. We also thank the specialists who helped identify the insects: D. Genoud (genus *Andrena*), E. Dufrêne (genus *Nomada*), and R. Rudelle (other bees and hoverflies); as well as all those who contributed to the field work.

Funding: This project was partially funded by the CITY OF PARIS through a CIFRE scholarship n°2018/0699, by the Institut de la Transition Environnementale – Sorbonne University (“Yapud-saison” 2019 and 2020), and by the Société Centrale d’Apiculture (« Pollinisateurs sauvages et communautés végétales urbaines », 2019).

Authors’ contributions: Conceptualization, V.Z. and I.D.; methodology, V.Z.; investigation, V.Z.; data curation and visualization, V.Z.; writing—original draft preparation, V.Z.; writing—review and editing, I.D.; supervision, project administration, and funding acquisition, I.D. All authors have read and agreed to the published version of the manuscript.

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

Complete Reference: Zaninotto V., Dajoz I. (2022). Keeping up with Insect Pollinators in Paris. *Animals*, 12(7):923. <https://doi.org/10.3390/ani12070923>

2. ABSTRACT

There is growing interest in urban pollinator communities, although they may be subject to biotic homogenization in densely artificial landscapes. Paris (France) is one of the densest cities in the world, yet over the years many insect pollinator species have been reported there. We conducted in-depth surveys of Parisian green spaces for two years, to improve our knowledge of these assemblages. We explored several types of green spaces, monitoring pollinators throughout their activity season. We listed 118 species of wild bees and 37 species of hoverflies, updating pre-existing lists with 32 additional species. Bee assemblages showed functional diversity with 18.5% parasitic species and 17.7% oligolectic species. We also found several bee and hoverfly species under special conservation status. Over the study period, we observed seasonal succession of species, with diversified phenological niches. The greatest taxonomic and functional diversity was found in green spaces combining several habitats with ecological management. Despite its very dense urbanism, Paris is home to diverse pollinator communities. As a result, nearly half of the wild bee species of the wider Ile-de-France administrative region can be found within the city. This highlights the need to also consider dense urban environments in insect pollinator conservation strategies.

Keywords: urban pollinators; urban ecology; wild bees; hoverflies; pollinator functional diversity; greenspace management practices; urban biodiversity

3. INTRODUCTION

Urban pollinator communities are receiving increasing attention, and many studies have revealed the potential of urban environments to host a diversity of insect pollinators (Wenzel et al., 2020). More specifically, low-density urban environments are often described as pollinator-friendly (Fortel et al., 2014), especially when they encompass private gardens and allotments (Baldock et al., 2019; Wenzel et al., 2020). As a result, pollinator abundance and diversity can be equally high in urban and rural areas across European landscapes (Baldock et al., 2015; Banaszak-Cibicka & Żmihorski, 2020). However, urban pollinators are mainly relegated to green spaces, not all of which provide suitable habitat (Baldock et al., 2019). In green spaces, pollinator communities are under the influence of both local and landscape environmental

factors (Ayers & Rehan, 2021). As demonstrated in Austria (Lanner et al., 2020) and Germany (Theodorou, Herbst, et al., 2020), local factors seem to be most relevant, foremost among them flower diversity and abundance. Sufficient floral resources are essential to maintaining functionally diverse bee communities, but are impaired by land artificialization. As a result, in densely built cities, pollinators must cope with a fragmented habitat and scattered resources (Harrison & Winfree, 2015).

Accordingly, in the literature, dense urban areas are often considered as an endpoint of landscape artificialization gradients, and are supposedly not suitable for pollinator diversity. Such is the case of several studies measuring the effects of urbanization on bees across France. Although urbanized areas were found to support relatively diverse bee communities (Geslin et al., 2020; Le Féon et al., 2020; Villalta et al., 2021), these communities are poorer than those of surrounding suburban and semi-natural areas (Fisogni et al., 2020; Fortel et al., 2014; Levé et al., 2019). Besides, within dense urban habitats, pollinator assemblages may be subject to community homogenization. As seen in several cities of Poland, the overall urban bee community may only consist of a subset of the rural one, and be identical across all urban landscapes (Banaszak-Cibicka & Żmihorski, 2020). Such biotic homogenization has also been recorded in France based on a nationwide dataset from participatory science (Deguines et al., 2016). These results show that the functional composition of pollinator communities is affected by the urban environment, with a shift toward more generalist insect species. Indeed, urban settings are known to apply an environmental filter on pollinators, bees in particular. In the city, species with certain traits seem to be at a disadvantage: such is the case for specialist species, ground-nesting species, large-sized species and early-emerging species (Ayers & Rehan, 2021; Buchholz & Egerer, 2020). These filtering effects of the urban environment on specialist and ground-nesting bee species have also been observed in the Paris region (Geslin et al., 2016; Zaninotto et al., 2021).

Given its very dense urban landscape, one may expect the city of Paris (France) to be a hostile environment for pollinators. However, over the years of monitoring in the French capital, the assemblage of bee species has proven to be relatively rich. Indeed, from 2011 to 2018, bee monitoring in Parisian green spaces combining two sampling methods (pan traps and

nets) has resulted in a list of 119 bee species (91 in peer-reviewed studies: Geslin et al., 2015; Ropars et al., 2017, 2018; Zaninotto et al., 2021; and an additional 28 species in ecological assessment reports: Ferrand et al., 2014; Stallegger, 2015). In contrast, other pollinator taxa have received less attention. Such is the case for hoverflies, with only 47 recorded species in recent studies (17 in published papers: Speight et al., 2018; Zaninotto et al., 2021; and 30 additional species in ecological assessment reports: Ferrand et al., 2014).

Here we present the results of a new inventory of pollinator species in the green spaces of Paris, France. By setting up standardized monitoring of insect pollinators in 12 green spaces from spring to fall during two consecutive years (2019 and 2020), we aim to: 1/ Update the list of bee and hoverfly species in Paris, describing their diversity in several types of green spaces within a high density urban environment; 2/ Provide a description of the floral preferences of these species and their conservation status; 3/ Assess the diversity of seasonal activity patterns of pollinators from March to October in Paris, to demonstrate the need for extended inventories throughout the year.

4. MATERIALS AND METHODS

4.1. Features of the city of Paris and the selected green spaces

This inventory of pollinator species was conducted in the city of Paris, one of the most densely populated cities in the world (INSEE, 2021). Paris covers 105.4 km² and is part of the Ile-de-France administrative region (12,012 km²). Insect collection was carried out in 12 green spaces of different sizes (vegetated areas ranging from 2,960 to 116,102 m²) evenly distributed throughout the city (**Figure 3. 1**). These 12 green spaces were integrated into a dense urban matrix, characterized by a high proportion of impervious surfaces (70 to 90% within a 1-km radius) (APUR, 2016). They had various management practices, but were always free of pesticides. They were classified into four categories: 1/ restricted areas, intended to serve as biodiversity reservoirs (MT, SV, JP), managed using ecological practices (no intensive mowing, little pruning, no weeding, only native plant species); 2/ small parks open to the public, maintained using the same ecological practices as above, and combining several vegetation layers (AP, PE); 3/ large parks with differentiated management including dedicated refuge spaces to accommodate biodiversity (BL, CT, MC, BR); 4/ classical gardens with a

predominantly ornamental style (preference for horticultural plants and frequent weeding) (BS, LB, VL). The 12 green spaces are managed by diverse stakeholders (for the most part the Paris City Council) and have different histories: some are large historical parks that have undergone transformations over the centuries (MC, JP); other former convents or private mansions (VL, LB, ST); though most are recent parks built on formerly residential or industrial land (AP, BL, BR, BS, CT, PE). MT is located above a buried hydraulic structure dating from 1873. Further information on these green spaces can be found in **Appendix 3. 1**.



Figure 3. 1. Distribution of the 12 green spaces surveyed in 2019-2020 in the city of Paris. Green: greenspace; grey: built environment; blue: Seine river. Triangles: biodiversity reservoirs with restricted access; diamonds: small ecological parks; squares: biodiversity refuges within large parks; circles: classical gardens. Insert: light grey represents continental France, dark grey represents the Ile-de-France region, which comprises Paris (black dot); the scale bar represents 100 km. Background map: E. Gaba (data: IAU IdF - ODbL, CC BY-SA 4.0, <https://commons.wikimedia.org/w/index.php?curid=38508343>)

4.2. Standardized sampling protocol

We completed a two-year (2019-2020) standardized sampling of insect pollinators with two complementary capture methods. In each green space, we first conducted an active collection of pollinators visiting flowers along a 50 m transect, with two runs at least 10 minutes apart.

All flower visitors were collected within one meter of the transect line using insect nets and plastic boxes. The transect covered several vegetation habitats: grasslands, shrubs, and ornamental flowerbeds; in proportions representative of these respective habitat surfaces in each green space. In addition, we conducted passive insect collection using two sets of colored traps (pan traps - blue/white/yellow cups filled with slightly soapy water) per green space. During each sampling session, these traps were set for two hours.

Sampling sessions were repeated once a month from March to October, in order to get a comprehensive overview of the seasonal successions of pollinator species. April 2020 was skipped due to the COVID-19 crisis. All twelve green spaces were sampled in alternating order during the first two weeks of the month, between 8:00 a.m. and 3:00 p.m. (solar time), under favorable weather conditions (no rain, low wind, temperature > 10°C). While distinctly recognizable specimens were identified in the field, most catches were euthanized with ethyl acetate and then carried back to the laboratory. We identified them down to the genus level before sending them to specialists for further identification. The insect specimens are now kept in the collection of the iEES-Paris institute.

4.3. Species traits and conservation status

We assessed species conservation statuses from the European red list of bees (Nieto et al., 2014), but also regional lists of bee and hoverfly species that define areas of ecological interest (Dufrêne et al., 2020; Gadoum et al., 2020). We used several databases to document the bee traits (BWARS, 2020; Gérard et al., 2018; Geslin et al., 2018; Rasmont et al., 2021; Ropars et al., 2018; SwissBeeTeam, 2021), and hoverfly species (Speight et al., 2020).

5. RESULTS

5.1. Updated lists of bees and hoverflies in Paris

We found a total of 3,142 wild bee individuals, belonging to 118 species. Among these wild bee species, 26 had not been documented in Paris before (**Table 3. 1**), at least in recent published reports. Hence we completed the list of bee species in Paris from recent reports of 119 wild species (Ferrand et al., 2014; Geslin et al., 2015; Ropars et al., 2017, 2018; Stallegger, 2015; Zaninotto et al., 2021), to an updated list of 145 wild species (**Annexe 1**). We also

encountered 1,168 domesticated honey bee individuals. Concerning hoverflies, we collected 394 individuals representing 37 taxa (**Table 3. 2**). Of these, 6 were new species compared to previous inventories (Ferrand et al., 2014; Speight et al., 2018; Zaninotto et al., 2021). We have therefore compiled an updated list of 53 species of hoverflies for the city of Paris (**Annexe 2**).

Table 3. 1. Report on the 2019-2020 sampling of bee species in the 12 Parisian green spaces, with numbers of captures for each species. ‘Type’ describes the method of acquiring pollen (“P”: Polylectic; “O”: Oligolectic; “C”: Cleptoparasitic). Species in bold are those which are recorded for the first time in Paris. Superscript numbers indicate possible conservation status: ¹ Regional ZNIEFF characterizing species; ² IUCN NT conservation status.

Species	Pollen	AP	BL	BR	BS	CT	JP	LB	MC	MT	PE	SV	VL
ANDRENIDAE													
<i>Andrena bicolor</i> (Fabricius 1775)	P	2		12	13	5	7		4	1		4	
<i>Andrena carantonica</i> (Pérez 1902)	P		1	1		1							
<i>Andrena chrysoseles</i> (Kirby 1802)	P	1									1		
<i>Andrena cineraria</i> (Linnaeus 1758)	P			1						1			
<i>Andrena dorsata</i> (Kirby 1802)	P	2	1	3	2	1	1	1	3	3			1
<i>Andrena flavipes</i> (Panzer 1799)	P		6	3	1	3	4	2	2	10			
<i>Andrena florea</i> (Fabricius 1793)	O						10						
<i>Andrena gravida</i> (Imhoff 1832)	P	1	3	1	2		4		1	2	1		
<i>Andrena haemorrhhoa</i> (Fabricius 1781)	P					1							
<i>Andrena lagopus</i> (Latreille 1809)	O									1			
<i>Andrena minutula</i> (Kirby 1802)	P	9	10	39	7	22	24	5	9	5	3	3	4
<i>Andrena minutuloides</i> (Perkins 1914)	P		3		4	1	4						3
<i>Andrena nigroaenea</i> (Kirby 1802)	P		1	1								1	
<i>Andrena nitida</i> (Müller 1776)	P		3		1	2		1	1		1	1	3
<i>Andrena ovatula</i> (Kirby 1802) ²	O					1							
<i>Andrena propinqua</i> (Schenck 1853)	P					1							
<i>Andrena proxima</i> (Kirby 1802)	O						5						
<i>Andrena pusilla</i> (Pérez 1903)	P		7	7	2	10			1				2
<i>Andrena rufula</i> (Schmiedeknecht 1883)	P		1	2		1		1					
<i>Andrena strohmeilla</i> (Stoekherth 1928)	P	1	1				1						
<i>Andrena subopaca</i> (Nylander 1848)	P			2									
<i>Andrena tenuistriata</i> (Pérez 1895)	P		1				1						
<i>Andrena ventralis</i> (Imhoff 1832) ¹	O	1											
<i>Andrena viridescens</i> (Viereck 1916)	O		1				1						
<i>Panurgus dentipes</i> (Latreille 1811)	O					2	3			6	4		
APIDAE													
<i>Anthophora plumipes</i> (Pallas 1772)	P		22	5	8	2		2	4	3	4		4
<i>Anthophora quadrimaculata</i> (Panzer 1789)	P					1	3	3	1				
<i>Apis mellifera</i> (Linnaeus 1758)	P	47	126	154	158	47	159	143	172	24	43	19	76
<i>Bombus hortorum</i> (Linnaeus 1761)	P			1		1							
<i>Bombus hypnorum</i> (Linnaeus 1758)	P			1	1				1				
<i>Bombus lapidarius</i> (Linnaeus 1758)	P		3	1	4		2	1	3	1	3		
<i>Bombus lucorum</i> (Linnaeus 1760)	P		6	9	14	2	1		5		1		1

<i>Bombus pascuorum</i> (Scopoli 1763)	P	19	123	41	41	25	27	48	66	3	27	26	95
<i>Bombus pratorum</i> (Linnaeus 1760)	P				1		1	1	1		1	2	2
<i>Bombus terrestris</i> (Linnaeus 1758)	P		17	16	20	3	5	2	15	5	10	2	6
<i>Bombus vestalis</i> (Geoffroy in Fourcroy 1785)	C		1	1	2				9			3	
<i>Nomada bifasciata</i> (Olivier 1811)	C	1	1			1							
<i>Nomada discrepans</i> (Schmiedeknecht 1882) ¹	C		1										
<i>Nomada distinguenda</i> (Morawitz 1874)	C		1					1					
<i>Nomada fabriciana</i> (Linnaeus 1767)	C	1		2	1			1		1	1	1	
<i>Nomada ferruginata</i> (Linnaeus 1767)	C			1									
<i>Nomada flava</i> (Panzer 1798)	C			1							1		
<i>Nomada flavoguttata</i> (Kirby 1802)	C	2	4	45		2			3	4			2
<i>Nomada fulvicornis</i> (Fabricius 1793)	C					1	1						
<i>Nomada goodeniana</i> (Kirby 1802)	C												1
<i>Nomada lathburiana</i> (Kirby 1802)	C		1				1						
<i>Nomada succincta</i> (Panzer 1798)	C	1									1		
<i>Nomada zonata</i> (Panzer 1798)	C	1	1	2		1							
<i>Xylocopa violacea</i> (Linnaeus 1758)	P		1		10	4	8						1

COLLETIDAE

<i>Colletes cunicularius</i> (Linnaeus 1761)	P									1			
<i>Colletes daviesanus</i> (Smith 1846)	O							1		1			
<i>Colletes hederæ</i> (Schmidt & Westrich 1993)	O										1		
<i>Colletes marginatus</i> (Smith 1846)	P									1			
<i>Colletes similis</i> (Schenck 1853)	O				1		2						
<i>Hylaeus brevicornis</i> (Nylander 1852)	P						1						
<i>Hylaeus communis</i> (Nylander 1852)	P	2	11	2	12	3	2	4	4		2		9
<i>Hylaeus gredleri</i> (Förster 1871)	NA						1				1		
<i>Hylaeus hyalinatus</i> (Smith 1842)	P	1					1		2	1			
<i>Hylaeus incongruus</i> (Förster 1871) ¹	P					3							
<i>Hylaeus pictipes</i> (Nylander 1852)	P		1				1				1		
<i>Hylaeus punctatus</i> (Brullé 1832)	P	2	12	9	1		2	1	11	7	3	1	
<i>Hylaeus signatus</i> (Panzer 1798)	O						18						
<i>Hylaeus variegatus</i> (Fabricius 1798)	P						1			1			

HALICTIDAE

<i>Halictus langobardicus</i> (Blüthgen 1944)	NA					2				1			
<i>Halictus maculatus</i> (Smith 1848)	P									1			
<i>Halictus scabiosae</i> (Rossi 1790)	P	2	2		7	10	4			1	14		2
<i>Halictus simplex</i> (Blüthgen 1923)	P			1	1			1	2		4		
<i>Halictus subauratus</i> (Rossi 1792)	P	3	4	1		3	3	4	3		1		1
<i>Halictus tumulorum</i> (Linnaeus 1758)	P	13	8	7		6	12	5	43	2	2		1
<i>Lasioglossum bluethgeni</i> (Ebmer 1971) ¹	P			2									
<i>Lasioglossum calceatum</i> (Scopoli 1763)	P	1	3	5	5		2	6	1	6	2		1
<i>Lasioglossum cupromicans</i> (Pérez 1903)	P						1						
<i>Lasioglossum fulvicorne</i> (Kirby 1802)	P							1		1			
<i>Lasioglossum glabriusculum</i> (Morawitz 1872)	P			2		1	7		2	59			
<i>Lasioglossum griseolum</i> (Morawitz 1872)	P		1										
<i>Lasioglossum laticeps</i> (Schenk 1868)	P	9	13	7	22	7	30	10	7	58	11	4	1
<i>Lasioglossum leucozonium</i> (Schränk 1781)	O	7	6			11	2		17	3	1		
<i>Lasioglossum limbellum</i> (Morawitz 1876) ¹	P		1	1			3	1					
<i>Lasioglossum malachurum</i> (Kirby 1802)	P	10	6	6	1	6	2	2	1	7	1		1

<i>Lasioglossum marginatum</i> (Brullé 1832)	P					2							
<i>Lasioglossum minutissimum</i> (Kirby 1802)	P	4	1			3	1	2	1				4
<i>Lasioglossum morio</i> (Fabricius 1793)	P	62	39	34	18	8	59	21	24	26	15	20	1
<i>Lasioglossum nitidulum</i> (Fabricius 1804)	P	1	5		3		6	19	2	3	11	3	1
<i>Lasioglossum pallens</i> (Brullé 1832)	P								1			1	
<i>Lasioglossum pauxillum</i> (Schenck 1853)	P	1	41	1	2	1	7		1	16	1		4
<i>Lasioglossum politum</i> (Schenck 1853)	P	2	26	1	3	10	11	4	1	3	2	1	3
<i>Lasioglossum pygmaeum</i> (Schenck 1853) ^{1,2}	P		1	4					1				1
<i>Lasioglossum sabulosum</i> (Morawitz 1891) ^{1,2}	P			1									
<i>Lasioglossum subhirtum</i> (Lepeletier 1841)	P									1			
<i>Lasioglossum villosulum</i> (Kirby 1802)	P	13	16	6	4	73	8	1	46	23	9	4	11
<i>Sphecodes crassus</i> (Thomson 1870)	C								1				
<i>Sphecodes ephippius</i> (Linnaeus 1767)	C		1										
<i>Sphecodes ferruginatus</i> (Hagens 1882)	C		1							1	1		
<i>Sphecodes gibbus</i> (Linnaeus 1758)	C									1			
<i>Sphecodes niger</i> (Hagens 1874)	C			1				1					
<i>Sphecodes pseudofasciatus</i> (Blüthgen 1925)	C					1							
<i>Sphecodes puncticeps</i> (Thomson 1870)	C							1					
MEGACHILIDAE													
<i>Anthidiellum strigatum</i> (Panzer 1805)	P						1		1				
<i>Anthidium manicatum</i> (Linnaeus 1758)	P					9	30	2	1		1		
<i>Anthidium septemspinatum</i> (Lepeletier 1841)	P		12	6	4		17	1			9		4
<i>Chelostoma campanularum</i> (Kirby 1802)	O						1	1	1				
<i>Chelostoma rapunculi</i> (Lepeletier 1841)	O					3	1						
<i>Coelioxys inermis</i> (Kirby 1802)	C								1		1		1
<i>Heriades crenulata</i> (Nylander 1856)	O		1				1						
<i>Heriades truncorum</i> (Linnaeus 1758)	O		2		1	4		1	5		2		
<i>Hoplitis adunca</i> (Panzer 1798)	O								1				
<i>Megachile centuncularis</i> (Linnaeus 1758)	P	4	18	2	7	9	3	2	6		8	4	5
<i>Megachile ericetorum</i> (Lepeletier 1841)	O						2						
<i>Megachile lagopoda</i> (Linnaeus 1760)	P		3		3						1		1
<i>Megachile maritima</i> (Kirby 1802)	P					1					1		
<i>Megachile rotundata</i> (Fabricius 1793)	P	1	1			2	1	1	7		1		
<i>Megachile willughbiella</i> (Kirby 1802)	P	7	9	7	11	1	17	8	7	2	20		10
<i>Osmia bicornis</i> (Linnaeus 1758)	P	1	7	11	1	3		2	7	3	1	4	4
<i>Osmia caerulescens</i> (Linnaeus 1758)	P	1					3		1				
<i>Osmia cornuta</i> (Latreille 1805)	P	3	1		1		3			1	2		
<i>Pseudoanthidium nanum</i> (Mocsáry 1881)	O										1		
<i>Stelis punctulatissima</i> (Kirby 1802)	C		3			1			1				
MELITTIDAE													
<i>Macropis europaea</i> (Warncke 1973)	O			1									
<i>Melitta leporina</i> (Panzer 1799)	O					3							
TOTAL (wild bee individuals)		192	477	316	242	278	383	172	342	288	176	85	191
TOTAL (wild bee species)		35	57	47	38	50	59	39	52	39	44	18	33

Table 3. 2. Report on the 2019-2020 sampling of hoverfly species (Syrphidae, Diptera order) in the 12 Parisian green spaces, with numbers of captures for each species. Larvae feeding type: “H”: Herbivorous; “P”: Predator; “M”: Microphagous; “S”: Saprophytic. Species in bold are those which are recorded for the first time in Paris. Superscript numbers (¹) indicate possible conservation status, as a Regional ZNIEFF characterizing species.

Species	Larvae	AP	BL	BR	BS	CT	JP	LB	MC	MT	PE	SV	VL
<i>Cheilosia grossa</i> (Fallén 1817)	H	1											
<i>Cheilosia</i> sp.	H	1		1		1	1						
<i>Dasysyrphus albostrigatus</i> (Fallén 1817)	P										1		
<i>Epistrophe eligans</i> (Harris 1780)	P	1			2								
<i>Epistrophe nitidicollis</i> (Meigen 1822)	P				1						1		
<i>Episyrphus balteatus</i> (De Geer 1776)	P	4	1	8	7	5	4	10	16	1	11	12	6
<i>Eristalis arbustorum</i> (Linnaeus 1758)	M		2				2						
<i>Eristalis similis</i> (Fallén 1817) ¹	M/S				1	1	1						1
<i>Eristalis tenax</i> (Linnaeus 1758)	M		5		1		1	2	1		1		
<i>Eumerus amoenus</i> (Loew 1848) ¹	H/M						2			1	1	1	1
<i>Eumerus funeralis</i> (Meigen 1822)	H/M										1		2
<i>Eupeodes corollae</i> (Fabricius 1794)	P	1	1	1	1				2		2	3	2
<i>Eupeodes luniger</i> (Meigen 1822)	P	2	1	2	4	1		2	4	4	2	2	4
<i>Eupeodes</i> sp.	P				1								
<i>Helophilus pendulus</i> (Linnaeus 1758)	M			4	1		1			1	2		
<i>Melanostoma mellinum</i> (Linnaeus 1758)	H/P				1	1		1					
<i>Melanostoma scalare</i> (Fabricius 1794)	H/P											1	
<i>Meliscaeva auricollis</i> (Meigen 1822)	P			1		2							2
<i>Merodon equestris</i> (Fabricius 1794)	H/M		6		2		2	1	2		3		
<i>Myathropa florea</i> (Linnaeus 1758)	M/S		3	1		2	5		1		3	1	1
<i>Neoascia podagrica</i> (Fabricius 1775)	M				1		1						
<i>Neocnemodon vitripennis</i> (Meigen 1822)	P						1						
<i>Paragus haemorrhous</i> (Meigen 1822) ¹	P		1										
<i>Paragus pecchiolii</i> (Rondani 1857)	P											1	
<i>Pipiza festiva</i> (Meigen 1822) ¹	P	1									1		
<i>Pipizella</i> sp.	P											1	
<i>Platycheirus scutatus</i> (Meigen 1822)	P	1	1	1	3			1	2			3	2
<i>Platycheirus sticticus</i> (Meigen 1822)	P					1							
<i>Scaeva pyrastris</i> (Linnaeus 1758)	P		1							1			
<i>Sphaerophoria rueppelli</i> (Wiedemann 1830)	P		1										
<i>Sphaerophoria scripta</i> (Linnaeus 1758)	P	3	8	2	5	6	3	8	10	14	10		2
<i>Syritta pipiens</i> (Linnaeus 1758)	M	16	13	2	1	12	4	9	7				2
<i>Syrphus rectus</i> (Osten-Sacken 1877)	P							1					
<i>Syrphus ribesii</i> (Linnaeus 1758)	P	1	1		1		1						1
<i>Syrphus vitripennis</i> (Meigen 1822)	P		1		1		1		1		1		
<i>Volucella zonaria</i> (Poda 1761)	P/M								2				
<i>Xanthogramma dives</i> (Rondani 1857)	P					1							
TOTAL (hoverfly individuals)		32	46	23	34	33	30	35	48	22	40	25	26
TOTAL (hoverfly species)		11	15	10	17	11	15	9	11	6	14	9	12

Additionally, we found 13 species of Lepidoptera (139 individuals), 4 species of Coleoptera (20 individuals), and three species of bee flies (Bombyliidae, Diptera) (16 individuals). All of them were common species (species list can be found in **Appendix 3. 2**). We also encountered other Diptera (1101 individuals), other Apocrita (118 individuals), and Symphyta (50 individuals) that we could not identify to the species level.

5.2. Specialist and/or rare species and their habitats

According to the scientific literature, urbanization has a strong negative influence on specialist and parasitic bee species, making their presence notable in a dense city. Here, we encountered bees that are specialized in collecting pollen from plants that belong to a single particular genus: *Andrena florea* (on plants of the *Bryonia* genus); *Andrena ventralis* (*Salix* genus), *Andrena viridescens* (*Veronica* genus), *Hoplitis adunca* (*Echium* genus), *Hylaeus signatus* (*Reseda* genus), *Macropis europaea* (*Lysimachia* genus). We noted the presence of *Colletes hederæ*, that collects pollen on only one plant species (monolectic), the ivy *Hedera helix*. We also found some oligolectic bees with broader preferences, but limited to a single plant family: Brassicaceae (the bee *Andrena lagopus*), Fabaceae (*Andrena ovatula*, *Megachile ericetorum*, *Melitta leporina*), Apiaceae (*Andrena proxima*), Campanulaceae (*Chelostoma campanularum* and *Chelostoma rapunculi*), and especially the Asteraceae (*Colletes daviesanus*, *Colletes similis*, *Heriades truncorum*, *Lasioglossum leucozonium*, *Panurgus dentipes*, *Pseudoanthidium nanum*). Furthermore, the hoverfly assemblage also shows a diversity of feeding types, most notably concerning larvae foraging behavior. Thereby we report the presence of herbivorous, predatory, saproxylic, and microphagous species (**Table 3. 2**).

Besides, our sampling includes several genera of brood parasite bees, that deposit their eggs in the nests of the host species, thus appropriating the resources allocated to the larvae (cleptoparasitism). Here, we found brood parasite species covering all major bee nesting types: the bumble bee *Bombus vestalis*, which deposits its eggs in the ground-nesting eusocial *Bombus terrestris* colonies; the bees of the genera *Nomada* (12 species here) and *Sphecodes* (7 species here), which parasitize small non-eusocial ground-nesting bees belonging to the genera *Andrena*, *Halictus* and *Lasioglossum*; and the species *Coelioxys inermis* and *Stelis punctulatissima*, which respectively parasitize the stem-nesting bees of the genus *Megachile*

and *Anthidium*. Moreover, the presence of three species of bee flies (Bombylidae, Diptera) should be mentioned. While the adult bee flies feed on nectar and participate in pollination, the maggots are parasitoids of the bee larvae. The eggs are deposited in mid-flight by females directly in the burrows of ground-nesting solitary bees (Kastinger & Weber, 2001). We also note the presence of commensals such as the hoverfly *Volucella zonaria*, whose detritiphagous and microphagous larvae reside in the nests of eusocial Hymenoptera. Since honey bees and bumble bees seem to thrive in urban areas (Bennett & Lovell, 2019), such commensal species may have the opportunity to prosper in these environments.

Although most of the collected pollinator species are common, some have special conservation status. We recorded 3 bee species under “near-threatened” (NT) status from the European IUCN red list (**Table 3. 1**). Additionally, 7 bee species (including two of the three NT-European status species) and 4 hoverfly species had special regional statuses in the Ile-de-France, characterizing areas of high ecological interest (ZNIEFF) (**Table 3. 2**).

Sites that hosted the most specialist bee species were dedicated biodiversity refuge areas within large public parks (BL, CT, MC, BR), followed by the small ecological parks (PE, AP). Results from the natural sites with restricted access were highly variable: the fewest specialist species were found in the SV woodland site; they were more numerous in the MT grassland site; but most were found in JP which combines both habitats and is also integrated into a larger park (**Appendix 3. 1**). Species with special conservation status were found at all twelve sites. Nevertheless, most of those conservation status species were found at sites BL and BR, which have high functional diversity of plant assemblages.

5.3. Seasonal distribution of species

Though most bee individuals were collected during late spring and summer, we observed active bees throughout all seasons from March to October. Indeed, we assessed a seasonal succession of species that resulted in a high temporal complementarity (**Figure 3. 2**).

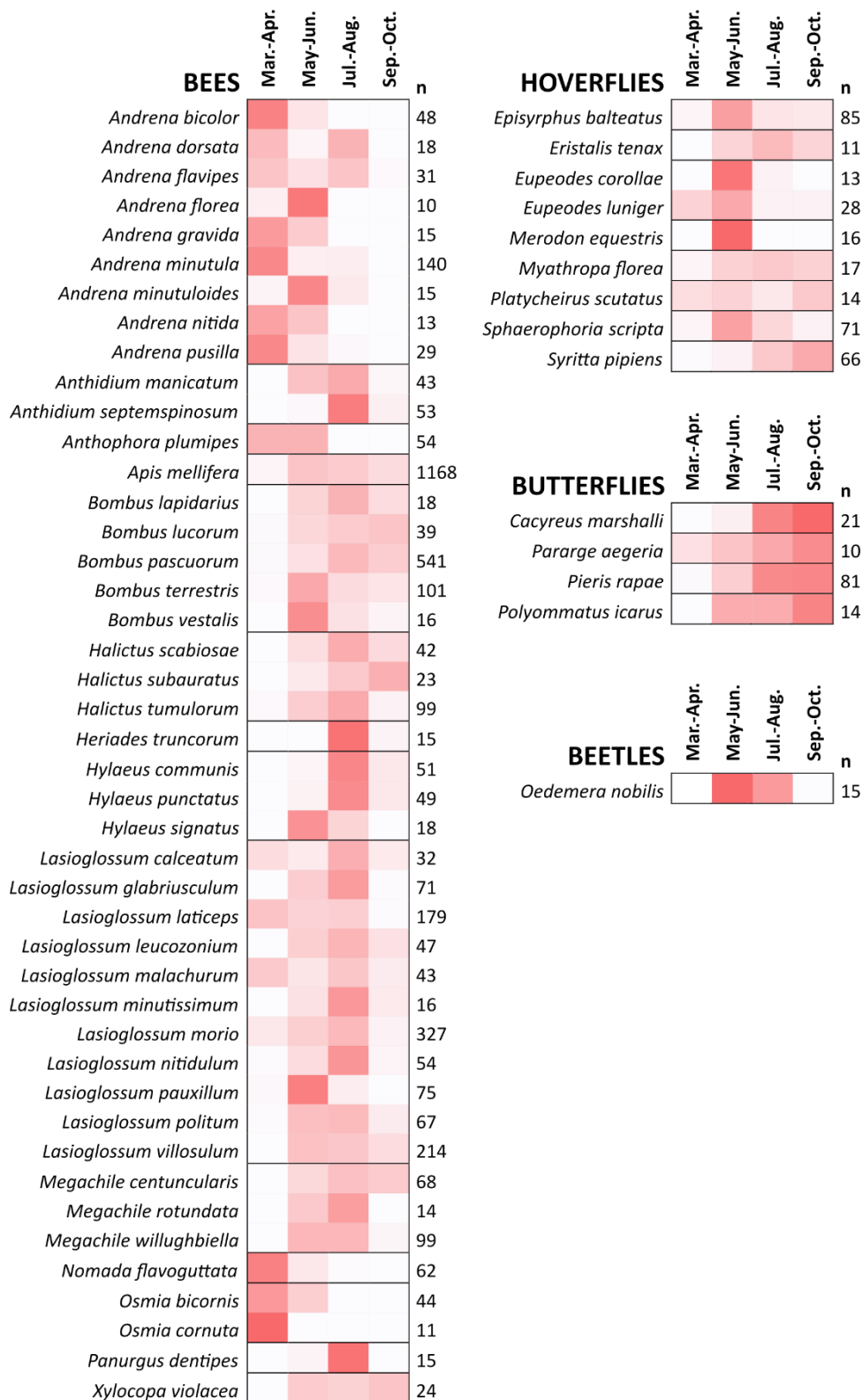


Figure 3. 2. Seasonal distribution of insect occurrence in all twelve green spaces and both years combined. The color intensity gradient represents the distribution of catches for each species over the study period, which is divided into two-month intervals (redder means more catches). Only bee, hoverfly, butterfly, and beetle species collected in large numbers are represented (total number of individuals per species $n \geq 10$).

Some bee taxa displayed broad phenologies of activity, with continuous presence over several months. This is especially true for social species whose colony life cycles last several months, with an increasing number of workers (Goulson, 2010; Kocher & Paxton, 2014), such as bumble bees (*Bombus* genus), and primitively social Halictid species (most notably *L. calceatum*, *L. laticeps*, *L. malachurum*, and *L. morio*). *Apis mellifera*, the managed honey bee, is present all the time, being the only bee species with a colony cycle that covers all year. Other bee species are only active during a single limited period. Some of them emerge during early spring, such as most of the species in the genus *Andrena*, but also in the genera *Anthophora*, *Nomada*, and *Osmia*. Others emerge later, during the summer: this is the case of the genera *Anthidium*, *Heriades*, *Hylaeus*, and *Panurgus*. Besides, we collected bivoltine species from different generations within the year, such as *Andrena dorsata* and *Andrena flavipes* (with the first generation in March-April and another in July-August, Pauly et al., 2019). This pairing of species with either short or long activity periods was also found in hoverflies. In contrast, the butterfly species we commonly found all had rather long and late activity periods (**Figure 3. 2**).

6. DISCUSSION

Our new sampling extended the list of wild bee species (Anthophila) recently occurring in the city of Paris to 145 species, covering the six bee families found in France and representing 43% of the 340 wild bee species lately found in the wider Ile-de-France region (Dufrêne et al., 2020) (**Annexe 1**). We also present a more comprehensive view of the diversity of hoverflies (Syrphidae) in the French capital, with a list of 53 species, representing 25% of the 216 species known in the region (Gadoum et al., 2020) (**Annexe 2**).

Thanks to repeated surveys over the last decade, and despite the small area of Paris and its high density of urbanization, such pollinator richness is noteworthy compared to other cities. In France, reports often list about a hundred bee species within a city (Marseille: 114 species, Geslin et al., 2020; Angers: 91 species, Nantes: 134 species, La Roche-sur-Yon: 120 species, Le Féon et al., 2020). In the Lille urban area, Fisogni et al. (2020) recorded 102 bee species, as well as 52 hoverfly species. Here, the number of bee species is slightly lower than in other large European cities such as Poznan (206 species) (Banaszak-Cibicka, 2014) and Zurich (164 bee species) (Fournier et al., 2020), but higher than in North American metropolises (Chicago: 83

bee species, Gruver & Caradonna, 2021; New York City: 98 species, Matteson et al., 2008), although some variation is likely to arise from climate differences. Furthermore, bee species lists grow considerably larger when surveys are conducted over broader areas encompassing low-density suburbs (Lyon region, France: 291 species, Fortel et al., 2014; Bydgoszcz region, Poland: 242 species, Twerd et al., 2021).

The Parisian assemblage of wild bee species shows a functional complementarity in trophic resources. Indeed, it includes many generalist species, but also species with specific preferences for various plant families. These communities also suggest complex interactions between pollinator species. Hence, we noted the presence of various brood parasite species, taking advantage of ground-nesting and stem-nesting bees. Parasitic interactions were also recorded between insect orders, as several species of Diptera can parasitize bee species. We recorded 22 parasitic bee species, accounting for 18.5% of the total bee species. Yet, parasitic species remained rare as they numbered only 125 individuals (4.0% of the total wild bee abundance). Previous studies in the city of Paris reported a lower percentage of parasitic species (4.5%), suggesting a functionally depleted bee community (Geslin et al., 2015). Our results, obtained over a wider range of green spaces, rather demonstrate a high occurrence of parasitic species in the French capital, a little below the overall rate in France (21%) (Fortel et al., 2014). This now strong representation of parasitic bees in Paris could be a sign of success in recent management practices favoring biodiversity. Here, the percentage of parasitic bee species is higher than in reports from Lyon (17%) (Fortel et al., 2014), Poznan (12%) (Banaszak-Cibicka & Żmihorski, 2012), and across New York City (15%) (Matteson et al., 2008).

By monitoring the pollinator assemblages over the seasons, we were able to observe a phenological complementarity among species. Some had long flight periods, while others had short flight periods spread throughout the year. The literature suggests that late-emerging species and species with long flight periods may have an advantage in urban settings (Wenzel et al., 2020), perhaps because exotic garden plants are mainly providing late-season flower resources (Staab et al., 2020). Indeed, patterns of activity at the community level differ between the city of Paris and the surrounding semi-natural rural areas, with a broader period of activity in the city (Zaninotto et al., 2020). It is therefore important to consider the phenology of insect

pollinators to better assess their functional diversity, but also to examine the effects of urbanization on communities. This also underlines the value of conducting pollinator surveys with standardized protocols covering the entire pollination season.

Our results also suggest a positive effect of the ecological management of some Parisian green spaces on pollinator functional diversity. Specifically, small biodiversity refuges within large parks seem to be particularly effective in supporting specialized and rare bee species. Leaving wild unmanaged areas with native flora is one of the key management solutions for promoting pollinator conservation in public green spaces; alongside reducing mowing and increasing the quantity and diversity of floral resources (Baldock, 2020).

7. CONCLUSIONS

Conservation policies for insect pollinators are developing in France and in the Ile-de-France region where the city of Paris is located (Schatz et al., 2021). Given the surprising diversity of pollinator communities in a dense urban landscape like Paris, these conservation policies could be strengthened by considering urban spaces. In Paris, 15 years after the total ban on the use of pesticides in public spaces, managers are committed to increasing vegetation cover and maintaining ecological management areas to support biodiversity. Such management practices have proven to enhance the diversity of insect pollinators, as well as plants and birds (Shwartz et al., 2013). They entail favoring the development of wild plant species, among which so-called "weeds", which can be highly attractive to wild pollinators (Baldock et al., 2019). Even in a dense urban matrix such as Paris, green spaces can accommodate diverse pollinator communities with remarkable functional diversity. Providing biodiversity refuges within public parks seems to be an effective solution to support these communities.

8. APPENDIX

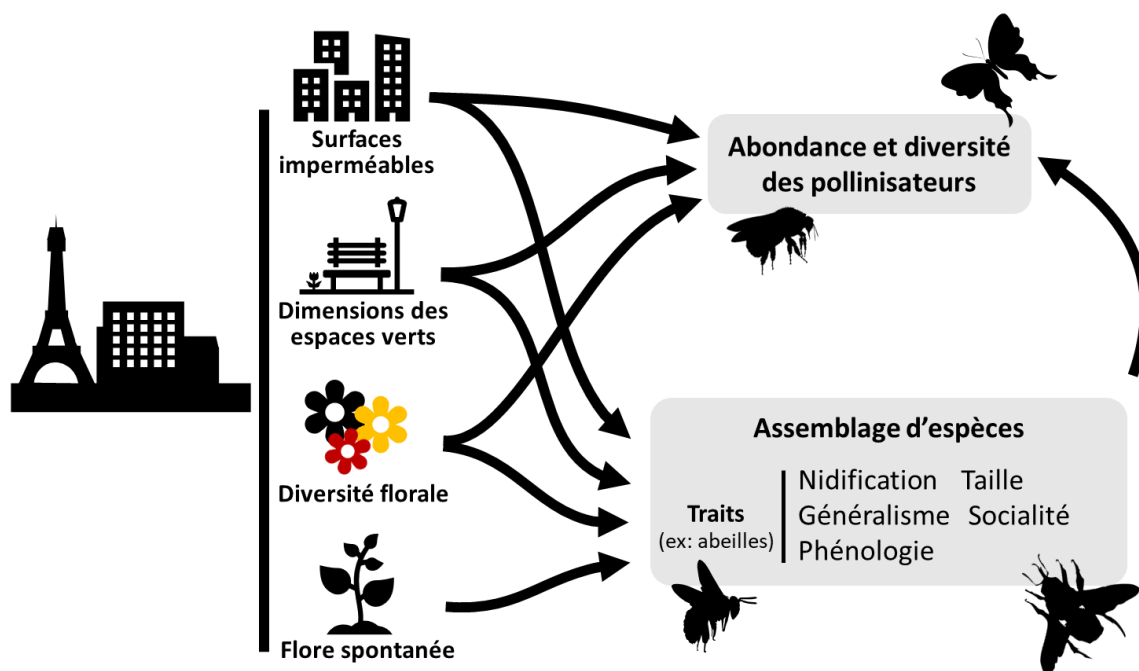
Appendix 3. 1. Additional information on the twelve green spaces surveyed, as presented in Figure 3. 1. Habitats describes the relative areas of four plant habitats in the green spaces: G, grasslands; S, shrubs; F, flowerbeds; T, tree-covered habitat. The dates in brackets are renovation dates.

ID	Greenspace name	Coordinates	Vegetated area (m ²)	Creation date	Habitats (%)			
					G	S	F	T
Biodiversity reservoirs with restricted access								
JP	Jardin écologique (MNHN)	48.844°, 2.3614°	11,610	XVII th c. (1932)	25	20	0	55
MT	Réservoir Montsouris	48.8247°, 2.3326°	29,592	1873	100	0	0	0
SV	Jardin Saint-Vincent	48.8882°, 2.3413°	2,960	1988	0	25	0	75
Small ecological parks								
AP	Jardin Abbé-Pierre	48.8289°, 2.3803°	11,321	2009	37	52	0	11
PE	Jardin Pierre Emmanuel	48.8587°, 2.3989°	5,539	1995	8	8	0	84
Biodiversity refuges within large parks								
BL	Parc de Belleville	48.8714°, 2.385°	37,509	1988	14	18	4	64
BR	Parc de Bercy	48.8358°, 2.3827°	116,102	1993	27	14	4	55
CT	Parc André Citroën	48.8419°, 2.2746°	77,651	1986	34	22	2	42
MC	Parc Monceau	48.8791°, 2.3091°	72,209	XVIII th c. (1852)	32	14	1	53
Classical gardens								
BS	Parc Georges Brassens	48.8315°, 2.2996°	53,951	1985	24	18	1	57
LB	Jardin Catherine Labouré	48.8513°, 2.3208°	4,961	1977	57	21	5	17
VL	Jardin Villemin	48.875°, 2.3611°	14,702	1977	34	19	6	41

Appendix 3. 2. Species lists of flower visitors from the Lepidoptera, Coleoptera and Diptera (Bombyliidae family) orders.

Species	AP	BL	BR	BS	CT	JP	LB	MC	MT	PE	SV	VL
COLEOPTERA												
<i>Cetonia aurata</i> (Linnaeus 1758)			1	1	1							
<i>Coccinella septempunctata</i> (Linnaeus 1758)						1						
<i>Oedemera nobilis</i> (Scopoli 1763)			1		3				1	10		
<i>Trichius fasciatus</i> (Linnaeus 1758)						1						
DIPTERA (Bombyliidae)												
<i>Bombylius discolor</i> (Mikan 1796)		1								1		
<i>Bombylius major</i> (Linnaeus 1758)		2	1	1		1				3		1
<i>Villa hottentotta</i> (Linnaeus 1758)	1		1			2				1		
LEPIDOPTERA												
<i>Aglais urticae</i> (Linnaeus 1758)				1								
<i>Cacyreus marshalli</i> (Butler 1898)	2	4			1		4	1		7		2
<i>Lampides boeticus</i> (Linnaeus 1767)							1					
<i>Lasiommata maera</i> (Linnaeus 1758)				1								
<i>Lasiommata megera</i> (Linnaeus 1767)		2								1		
<i>Lycaena phlaeas</i> (Linnaeus 1761)										1		
<i>Macroglossum stellatarum</i> (Linnaeus 1758)						1						
<i>Pararge aegeria</i> (Linnaeus 1758)	2					4		1		3		
<i>Pieris rapae</i> (Linnaeus 1758)	2	10	6	18	3	11	4	7	2	7	6	5
<i>Polygonia c-album</i> (Linnaeus 1758)								1				
<i>Polyommatus icarus</i> (Rottemburg 1775)		1			1	7			3	2		
<i>Pyrgus malvae</i> (Linnaeus 1758)		1										
<i>Vanessa atalanta</i> (Linnaeus 1758)			2					1				

CHAPITRE 4 : Conséquences de l'aménagement et de la gestion des espaces verts sur les communautés de pollinisateurs dans un paysage densément urbanisé : la ville de Paris



CHAPITRE 4 : Résumé graphique

Ici, nous examinons comment se distinguent les communautés de pollinisateurs au sein des espaces verts intégrés dans le paysage urbain dense de Paris, en fonction des facteurs environnementaux.

- Quels facteurs environnementaux, à l'échelle locale ou paysagère, influencent l'abondance et la richesse spécifique des insectes pollinisateurs ?
- En ce qui concerne les abeilles sauvages, certains facteurs environnementaux déterminent-ils la distribution des espèces selon leurs traits fonctionnels ?

L'abondance et la richesse spécifique des pollinisateurs, mais aussi l'assemblage fonctionnel des abeilles sauvages, sont influencés par l'aménagement urbain et la gestion de la végétation dans les espaces verts. Ces résultats, cohérents avec la littérature, peuvent guider des pratiques vertueuses pour la biodiversité et la fonction de pollinisation, même dans les paysages urbains denses.

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

submitted to Urban Ecosystems in October 2021 (under review),

revised in March 2022

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1. ARTICLE DETAILS

Acknowledgments: We wish to thank the Jardin des Plantes of the MNHN (Philippe Barré), Eau de Paris (Ludovic Robilliard), and all greenspace management services of the DEVE – City of Paris for kindly providing access to the sites. We thank all the specialists who identified the insects at the species level: David Genoud, Rémi Rudelle, and Eric Dufrêne. We also thank Nicolas Quaghebeur, Yvan Kraepiel, and Eric Motard for their contribution to field work and 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).

Authors’ contributions: Conceptualization: VZ, ID; Methodology: VZ; Formal analysis and investigation: VZ, AF; Writing - original draft preparation: VZ; Writing - review and editing: ID, AF; Funding acquisition: VZ, ID; Resources: ID; Supervision: ID. All authors read and approved the final manuscript.

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

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

2. ABSTRACT

The response of pollinating insect 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 orders of pollinating insects (Hymenoptera, Diptera, Lepidoptera, Coleoptera). Pollinator abundance and species richness were both positively tied to greenspace size and flowering plants 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 specialist 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

3. INTRODUCTION

Urbanization is among the strongest changes in land use, and thus one of the main drivers of global change. Multiple factors have been shown to drive 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 proven to support a wide variety of bee species in temperate climates (Baldock et al., 2015; Theodorou, Radzevičiūtė, et al., 2020). Although there is no consistent universal effect of urbanization on the number of bee species, moderately urbanized areas appear to support more species than

some rural agricultural areas (Wenzel et al., 2020). Nevertheless, numerous studies have demonstrated that both local and landscape factors influence pollinator communities in an urban context (Majewska et al. 2018; Baldock 2020; Ayers and Rehan 2021, for reviews). Landscape-scale drivers of pollinator abundance, richness, and composition are often studied along rural to urban gradients; they mostly encompass the proportion of impervious surfaces, landscape heterogeneity, nearby green spaces, etc. Local drivers, by contrast, include greenspace size, urban form, plant richness, flower abundance, plant status as native or exotic, etc. In addition, landscape and local environmental factors may interact, as urban fragmentation has been shown to decrease flowering plant richness (Theodorou, Herbst, et al., 2020).

Several studies have highlighted the negative effect of impervious cover at the landscape scale on wild bee abundance and species richness (Burdine & McCluney, 2019; Egerer et al., 2020; Geslin et al., 2016). This negative effect seems consistent across bee guilds with various life-history traits (Birdshire et al., 2020), though in some cases impervious landscapes benefit to *Bombus* and *Apis* abundance (Bennett & Lovell, 2019). High levels of urbanization may also come with higher proportions of non-native bee species (Gruver & Caradonna, 2021). Since moderate levels of urbanization can benefit some wild bees, greater bee species richness and functional 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 bees 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).

At the local scale, bee communities depend on the type of green space, with differences between nurseries and gardens (Egerer et al., 2020), or residential gardens and urban semi-natural areas (Martins et al., 2017). As stressed by Baldock et al. (2019), green spaces encompass a wide variety of land uses that differ in their extent within the urban landscape: allotments, gardens, parks, cemeteries, and even urban nature reserves. Floral resource availability and quality within these areas are often associated with socio-economic factors and drive pollinator diversity. Community gardens host the greatest abundance of pollinators (Baldock et al., 2019; Daniels et al., 2020; Lanner et al., 2020), due to high flower availability,

making them effective tools for sustaining pollinator communities at the city scale. Indeed, high floral richness consistently comes with high bee abundance and/or species richness (Ballare et al., 2019; Birdshire et al., 2020; Burdine & McCluney, 2019; Gruver & Caradonna, 2021; Quistberg et al., 2016). Not only does the number of plant species matter, but also their management and 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 & 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 (Egerer et al., 2020; Quistberg et al., 2016), 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. (2020) 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 (Dylewski et al., 2019; Majewska et al., 2018). In particular, butterfly richness depends on urban green spaces 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 bees 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 (500m 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 form and greenspace design? Local factors are often found to be the best predictors of bee abundance and richness in urban gardens. These local factors, such as flower availability, may be stronger drivers of bee communities than landscape-scale artificialization (Gerner & Sargent, 2022; Lanner et al., 2020; Quistberg et al., 2016). 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 1000m) features such as the proportion of impervious surfaces, the number of entomophilous trees, and microclimate; 2/ local features of green spaces and their management: greenspace size, flowering plant species richness, floral density, the share of spontaneous plant species, 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 that host them. 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 allowed us to have a broader vision of the urban drivers of pollinator communities than just focusing on bees.

4. METHODS

4.1. Site selection

All survey sites were located in Paris (France), within 12 selected green spaces distributed throughout the city (**Figure 4. 1**). These were of varying sizes (see **Table 4. 1**) in order 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.

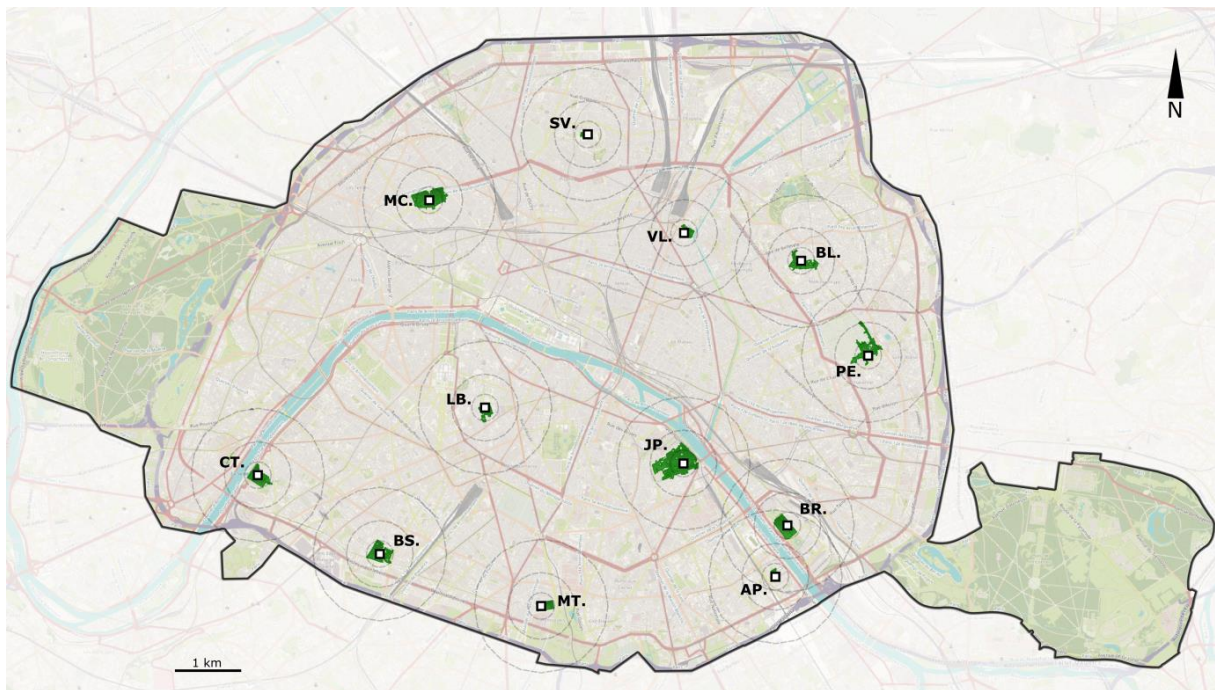


Figure 4. 1. Distribution map of survey sites. We highlighted the administrative boundaries of Paris, including the two main vegetated areas on the outskirts of the city: the Boulogne wood (west) and the Vincennes wood (east). Green spaces that include a survey site are colored in dark green (AP.: Jardin Abbé-Pierre; BL.: Parc de Belleville; BR.: Parc de Bercy; BS.: Parc Georges Brassens; CT.: Parc André Citroën; 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 pollinating insects and flowering plants were carried out. Dashed circles represent the 200m, 500m, and 1000m radii around each site (map base: © OpenStreetMap contributors).

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 very 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 forbidden 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 Citroën; MC.: Parc Monceau; JP.: Jardin des plantes; BL.: Parc de Belleville).

Table 4. 1. Landscape and local environmental characteristics of the survey sites. % Impervious: percentage of impervious surfaces within 200, 500, and 1000 meters-radii around each 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 200m-radius in UHI conditions (August 16, 2016), relative to the city-wide mean 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 200m-radius around each site. A PCA on these variables is available in Annexe 3.

Site	Greenspace size (m ²)	% impervious (200 - 500 - 1000m)	Plant richness (species nb. and % spont.)	Rel. T° (°C)	Floral density (m ² and % spont.)	Trees (200m)
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

4.2. Landscape features

Even though the entire study design was set in a dense urban landscape, there was a marginal variation in the amount of impervious surfaces in the surroundings of each survey site (APUR, 2015). All surfaces that were not covered in vegetation were considered impervious and quantified within 200m, 500m and 1000m of survey sites using QGIS software (QGIS Development Team, 2016) (**Table 4. 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 200m of each survey site and compared it to the city-wide average (the two Parisian woods removed) (**Table 4. 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.

4.3. 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 pollinating insect 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 50m apart from each other. They were left in position for 2 hours, while the active sampling was being carried out. Upon retrieving the traps, insects were collected and preserved in ethanol (70%) before being processed in the laboratory. Active sampling was performed with insect nets and clear plastic boxes to catch foraging insect pollinators. This method was used over 50m transects in each green space.

Sampling was stratified, meaning that 50m 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. Flower visitors were inventoried by walking along each transect and collecting all insects visiting flowers. Sampling extended to 1 m on both sides of the transect line and 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, degree of generalism, and sociality was obtained from several published trait databases (see the list of species and their traits in **Annexe 1**, with detailed sources on the open depository Zenodo). In addition, for each bee species, intertegular 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 < 2mm) or "large" (mean ITD > 2mm) based on the measurements on female bees (or male bees when no females were found). We focused on worker body size for eusocial species, which were all "large" anyway.

4.4. Plant inventory

Flowering plants were inventoried in each green space at each monthly visit in order to describe the resources available to pollinators and to characterize management practices. We identified flowering plants to the species level in five 1m x 1m quadrats, set up regularly along the 50 m insect sampling transect. In addition, we recorded the 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, on a monthly basis between March and October and over the two consecutive years of the study.

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 developed from wild seeds or by vegetative reproduction. We calculated the proportion of inventoried plant species classified as “spontaneous” in each site (**Table 4. 1**). The native status of each plant species in the Ile-de-France region was also considered (Jauzein & Nawrot, 2011).

We also counted the number of floral units in each 1m x 1m quadrat on a monthly basis. 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 1m²-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 4. 1**). 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 meters of all study sites using the open database of the Paris administration (Ville de Paris - DEVE, 2021a) complemented by our own inventories (**Table 4. 1**).

4.5. 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 & 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`) (Oksanen et al., 2019; Vavrek, 2011).

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 (200m, 500m, and 1000m radii), the greenspace size (square root transformed), the relative UHI intensity (200m radius), the number of entomophilous trees (200m 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 pollinating insect communities (based on Bray-Curtis distance, `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 sampling season (March-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 `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). 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 < 2mm; or “large”: ITD > 2mm), nesting habits (either “Above-ground” or “Below-ground”), generalism (either “Specialist” for oligolectic and parasitic species, or “Generalist” for polylectic species), sociality (either “Social” for eusocial and primitively eusocial species, or “Solitary”), and phenology (“Early-emerging” if the first occurrence was before May 1st, or “Late-emerging”). We constructed a GLMM with a binomial error distribution package “`glmmTMB`”) (Brooks et al., 2017). 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. We complemented this approach with a fourthcorner analysis to assess the consistency of the results (**Appendix 4. 2**). For each model, we kept only one scale for the proportion of impervious surfaces, the one that provided the best fit to the data.

5. RESULTS

5.1. Pollinator abundance and species richness

We inventoried 4880 insect pollinators, among which 3142 wild bees (belonging to 118 distinct species), 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 ($\text{Chao}_1=215.1$). Specifically, for bees, which are the dominant pollinator group in our sampling, we inventoried 119 species, accounting for 89.8% of the Chao estimator ($\text{Chao}_1=132.6$) (including honey bees) (**Appendix 4. 1**). This indicates that our sampling method provides an 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 the size of the green space (**Table 4. 2, Figure 4. 2**). However, pollinator abundance and species richness declined with the proportion of impervious surfaces in a 1000m-radius (**Table 4. 2, Figure 4. 3**).

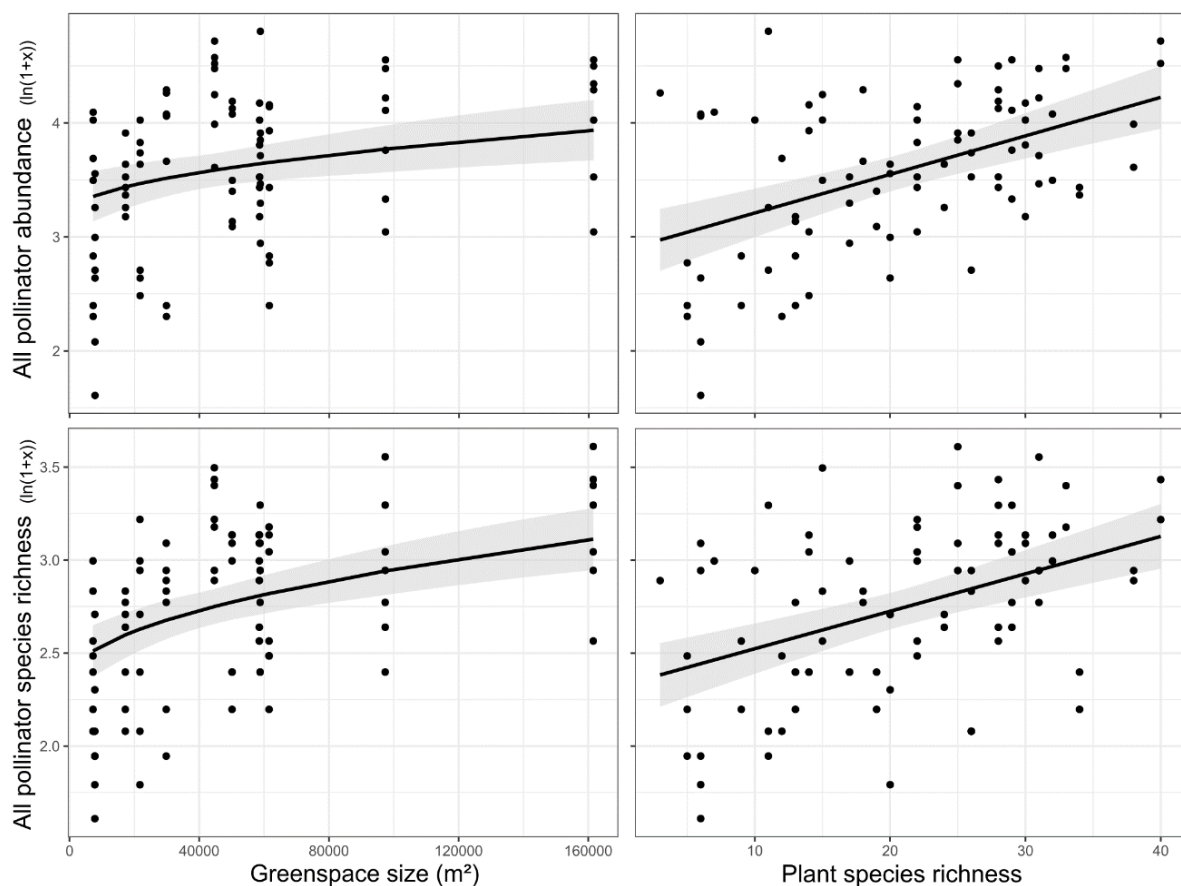


Figure 4. 2. Abundance and species richness of all pollinators in response to local drivers: greenspace size and the number of flowering plant species. Dots represent measures per site per two-month period and per year. Lines and intervals represent the predictions and SE from the linear mixed models.

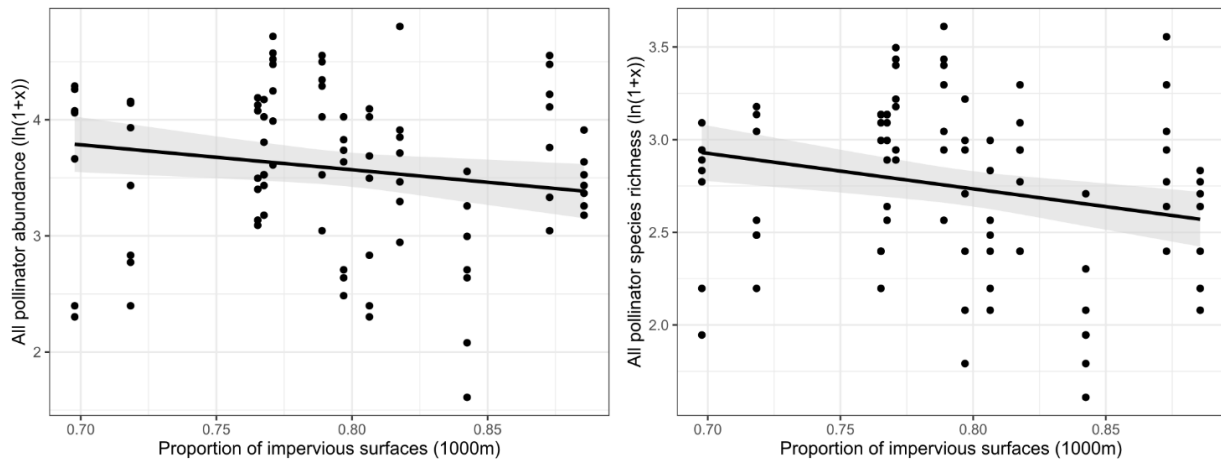


Figure 4. 3. Abundance and species richness of all pollinators in response to a landscape driver: the proportion of impervious surfaces in a 1000m-radius around the survey sites. Dots represent measures per site per two-month period and per year. Lines and intervals represent the predictions and SE from the linear mixed models.

Table 4. 2. Best-fitting linear mixed models of pollinator abundance and species richness. χ^2 and P-values are for Type-II Wald tests. The two-month period nested in the year was an additional random effect in both models. Greenspace size is square root transformed.

Response	Predictor	Coeff. (\pm SE)	χ^2	P	AICc	R ²
All pollinator abundance	% impervious (1000m)	-0.12 \pm 0.06	4.37	0.037	147.60	0.56
<i>Ln(1+x)</i>	Plant richness	0.32 \pm 0.07	23.11	<0.001		
	Greenspace size	0.16 \pm 0.06	7.96	0.005		
All pollinator richness	% impervious (1000m)	-0.10 \pm 0.03	9.42	0.002	67.75	0.66
<i>Ln(1+x)</i>	Plant richness	0.19 \pm 0.04	23.27	<0.001		
	Greenspace size	0.17 \pm 0.03	22.22	<0.001		

5.2. Pollinator community composition

The db-RDA shows that shifts in pollinator community composition across green spaces were associated with only one of the measured habitat variables: the percentage of spontaneous plant species ($F_{1,df}=1.80$, $p=0.017$) (**Figure 4. 4**). However, this variable only explained up to 15.2% of total inertia, leaving most variation unexplained.

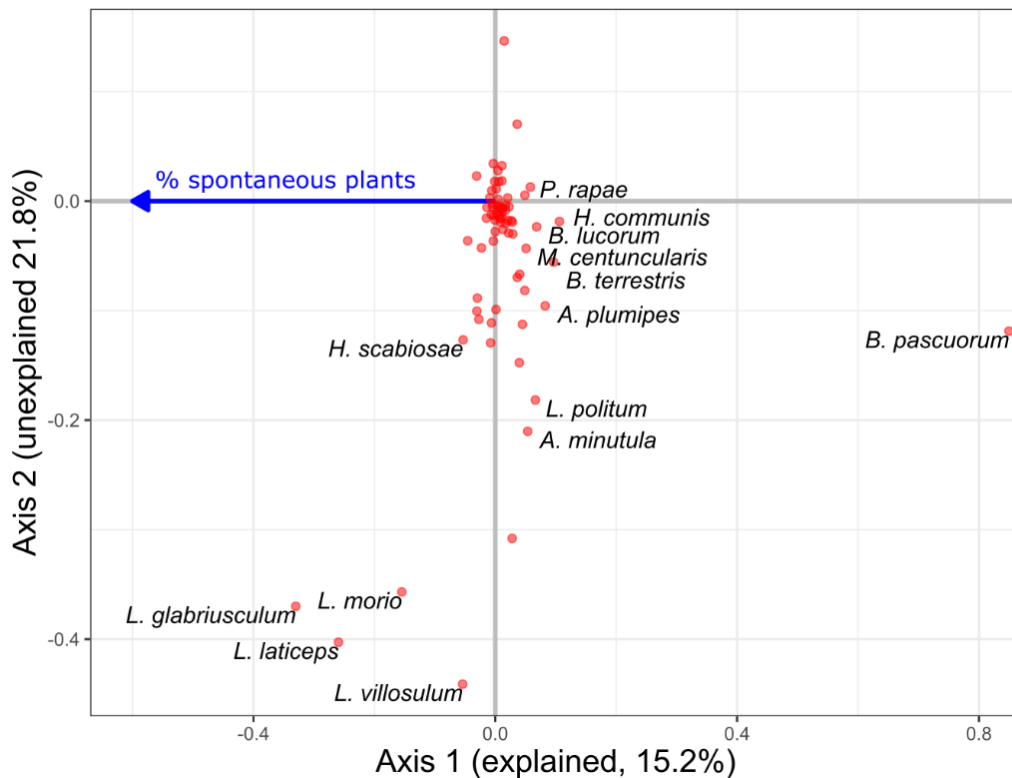


Figure 4. 4. db-RDA ordination of pollinator species, constrained by the percentage of spontaneous plant species within survey sites (blue arrow aligned with Axis 1). Red dots represent pollinator species; labeled species drive the most variation in community composition in response to spontaneous plants (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.

5.3. Wild bee species probability of occurrence

Overall, specialist, solitary, and below-ground nesting bee species had a lesser probability of occurrence than generalist, social, and above-ground nesting species respectively (**Table 4. 3**). Moreover, environmental variables had significant effects on the probability of occurrence of wild bee species (**Table 4. 3**). Pant species richness was positively associated with bee species occurrence, and this effect was more pronounced for large bee species (**Figure 4. 5a**). Also, the negative effect of the proportion of impervious surfaces in the landscape (500m radius) was only detectable on large bee species and not on small ones (**Figure 4. 5b**). In addition, early-emerging species (species encountered as early as March and April) had an overall higher probability of occurrence than late-emerging species. However, this difference disappeared in the largest green spaces, as late-emerging bees seemed to benefit from greenspace size (**Figure 4. 5c**).

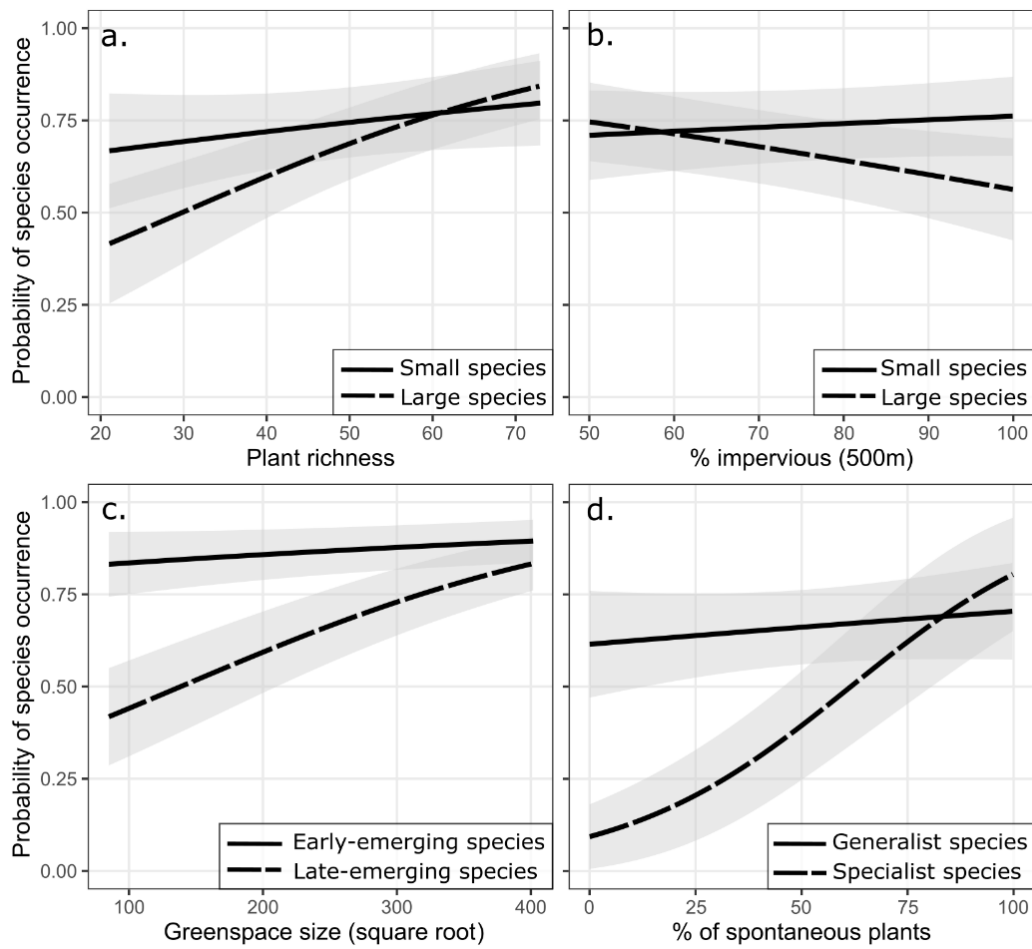


Figure 4. 5. Probability of occurrence of wild bee species in response to environmental variables: a. plant species richness; b. the percentage of impervious surfaces in a 500m radius; c. the greenspace size (square root transformed); d. the percentage of spontaneous plant species. Lines and intervals represent the predictions (\pm SE) from the GLMM presented in Table 4. 3. For a. and b., species are categorized according to their size (“Small” or “Large”); for c., according to their date of emergence (“Early-emerging” or “Late-emerging”); for d., according to their degree of generalism (“Generalist” or “Specialist”).

Finally, the characteristics of available plants appeared to be important, as there was a positive relationship between the presence of specialist bee species (encompassing oligolectic and parasitic bees) and the proportion of spontaneous plant species in each green space (**Figure 4. 5d**). We detected no interannual variation between 2019 and 2020. Similar results were obtained with fourthcorner analysis (**Appendix 4. 2**), except for the interaction between bee size and impervious surfaces at the landscape level.

Table 4. 3. Best-fitting generalized linear mixed model of bee species probability of occurrence (binomial distribution; AICc = 1539.9, R²_{cond.} = 0.43). χ^2 and P-values are for Type-III Wald tests. Additional effects included the Site and Bee species (random effects), and the Year (NS). Greenspace size is square root transformed. NS: non-significant. Spont.: spontaneous. Below: Below-ground, Above: Above-ground. Early: Early-emerging (before May), Late: Late-emerging (from May on).

Predictors of species occurrence (Bee trait x Environmental variable)		χ^2	P	Direction and coefficient
<i>Body size</i>	x Intercept	1.34	0.247	NS
	% impervious (500m)	3.95	0.047	Large (-0.24±0.19) < Small (0.08±0.18)
	Plant richness	5.78	0.016	Large (0.58±0.29) > Small (0.19±0.29)
<i>Generalism</i>	x Intercept	8.04	0.005	Generalist (0.66±0.45) > Specialist (-0.48±0.62)
	% of spont. plants	4.90	0.027	Generalist (0.11±0.25) < Specialist (1.06±0.46)
	Plant richness	2.19	0.139	NS
<i>Sociality</i>	x Intercept	11.36	<0.001	Eusocial (0.66±0.45) > Solitary (-0.57±0.32)
	% impervious (500m)	2.45	0.118	NS
<i>Phenology</i>	x Intercept	12.76	<0.001	Early (1.90±0.56) > Late (0.66±0.45)
	Greenspace size	8.28	0.004	Early (0.16±0.16) < Late (0.55±0.17)
<i>Nesting</i>	x Intercept	3.84	0.050	Below (-0.14±0.40) < Above (0.66±0.45)

6. DISCUSSION

Green patches are known to promote biodiversity in fragmented urban landscapes, provided they are large enough and connected (Goddard et al., 2010). Indeed, there is growing evidence that, in urbanized habitats, the presence of large green spaces supports abundant and diverse pollinator communities (see Wenzel et al. 2020, for a review). Here we investigated the effect of greenspace size on the pollinator communities they support, considering their continuity with other vegetated areas. Indeed, insect mobility in a fragmented environment is strongly constrained by the distance between the favorable habitat patches, as well as by the physical barriers that separate them, such as roads (Fenoglio et al., 2021; Fitch & Vaidya, 2021). As we expected, the extent of continuous green spaces within the Parisian urban landscape is tied to the local species richness of pollinators, with larger ones hosting more pollinator species. Conversely, pollinator abundance and diversity declined with the proportion of impervious surfaces at the landscape scale (1000m-radius), which is an indicator of urban built density. Large greenspace size also favored the occurrence of late-emerging bee species.

Greenspace management was also critical, as evidenced by the relationship between pollinator diversity and the composition of local flowering plant assemblages. Plant species richness was strongly linked with 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). Our results show that the type of flora, and particularly the share of spontaneous plants, played an important role as a driver of shifts in pollinator community composition across survey sites. Functional diversity of bees was higher in "natural" green spaces where management practices were minimal and whose vegetation was dominated by spontaneous plants, as evidenced by a greater presence of specialist bee species. The urban green spaces that are mostly dominated by spontaneous plants are unmanaged wastelands. These areas, which host a significant proportion of native plant species, are known to be highly attractive to pollinators (Twerd & Banaszak-Cibicka, 2019). At the other end of the management intensity gradient, we find the classical French gardens: designed to enhance perspectives, and planted with various ornamental plants. In Paris, intensively managed gardens thus displayed high plant species richness and therefore supported abundant pollinator communities. But these communities might be lacking in functional diversity, as seen with the prevalence of generalist bee species. Then, whether management practices allow for spontaneous plants to grow or not seems determinant for the composition of pollinator communities across green spaces. There is evidence in the literature that native plants maintain the diversity of native flower-visiting insect communities (Mata et al., 2021). Here, we preferred to focus on spontaneous flora, as it better reflects greenspace management. In any case, the proportions of native plant species and spontaneous plant species were strongly correlated ($r_{\text{Pearson}}=0.95$, $p < 0.00001$).

Neither flower density (number of floral units per square meter on the ground), nor the number of entomophilous trees in the vicinity affected pollinator abundance, species richness, and community composition. Rather than flower density, flowering plant species richness seemed to be the best proxy of local floral resources availability. Besides, since we sampled pollinators from 0-2m in height, the insect communities we surveyed may not be customary tree visitors, and thus may not be strongly affected by the presence of trees.

There was also no impact of relative temperatures across green spaces on pollinator communities. Microclimatic 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.

Consistent with some literature (Buchholz & Egerer, 2020), we found that eusocial and generalist bee species respectively had a higher probability of occurrence than solitary and specialist ones in this dense urban landscape. Additionally, studies along urban-rural gradients have shown that below-ground nesting bees were more sensitive to urbanization and impervious surfaces than above-ground nesting bees (Geslin et al., 2016; Zaninotto et al., 2021). Fortel et al. (2014), in particular, reported that cavity-nesting and soil-nesting species probability of occurrence did not respond the same to the extent of impervious surfaces in the landscape. Consistent with this, here we found that ground-nesting bees had an overall lower probability of occurrence in Parisian green spaces than other bee species. We also found a positive effect of the spontaneous flora on the occurrence of specialist bee species, which was expected. Indeed, to fulfill their life-cycle, specialist bees depend on the various resources provided by their specific floral hosts, which are often native and spontaneous plant species (Minckley & Roulston, 2002). However, our results regarding the presence of early- and late-emerging bee species are at odds with some studies that suggest that the urban environment is detrimental to early-emerging species (Banaszak-Cibicka & Żmihorski, 2012; Harrison et al., 2018; Wray & Elle, 2015). Here, in a dense urban landscape, late-emerging bees seem to be filtered out in small green spaces. Because late-emerging bees are primarily active in summer, they may suffer from the effects of urban warming, which are mitigated in large green spaces.

Large bee species appeared to be more sensitive to the extent of impervious surfaces (500m radius) than small ones. These large bees need more floral resources and have higher mobility which allows them to forage across green patches (Buchholz & 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 bumble bees, in turn driving greater within-garden foraging patterns. Moreover, large bee species 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 longer tongue that allows

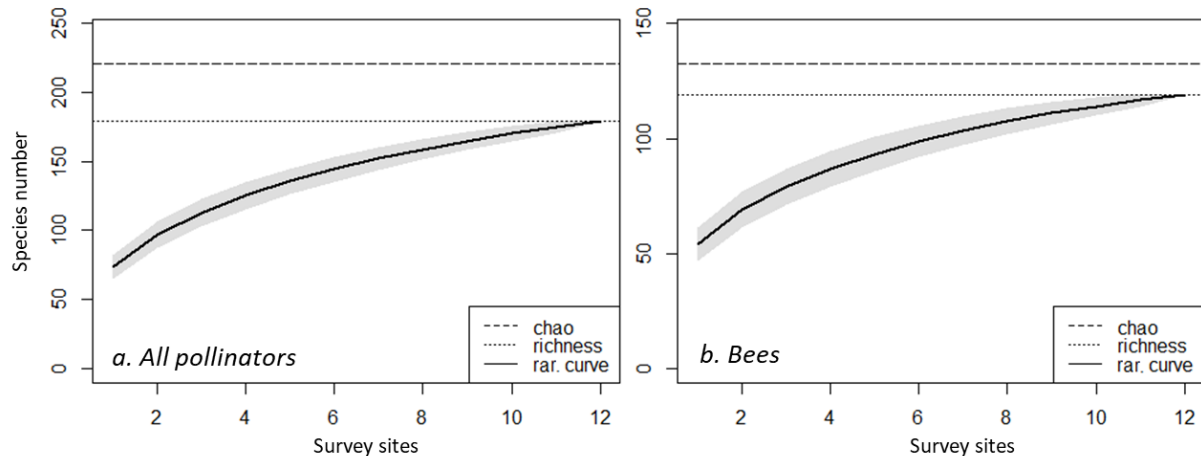
deeper uptake of floral resources (Stang et al., 2009). Larger bees also have greater resource requirements, as they must maintain their massive bodies and provide for their likewise large offspring (Oliveira et al., 2016). For example, in an urban landscape, Hamblin et al. (2018) observed that floral 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.

7. CONCLUSION

Overall, our results indicate that, in a densely urbanized habitat, greenspace size is critical to maintaining pollinator diversity. Since it may be impractical to increase the extent of green spaces 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 abundance and species richness (Quistberg et al., 2016), suggesting that increasing flower availability was the best way to promote pollinator diversity within green spaces. Our data confirm that not only bee diversity, but the overall abundance and richness of all pollinating insects depend on 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 pollinating season (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 and parasitic 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 pollinating insects 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.

8. APPENDIX

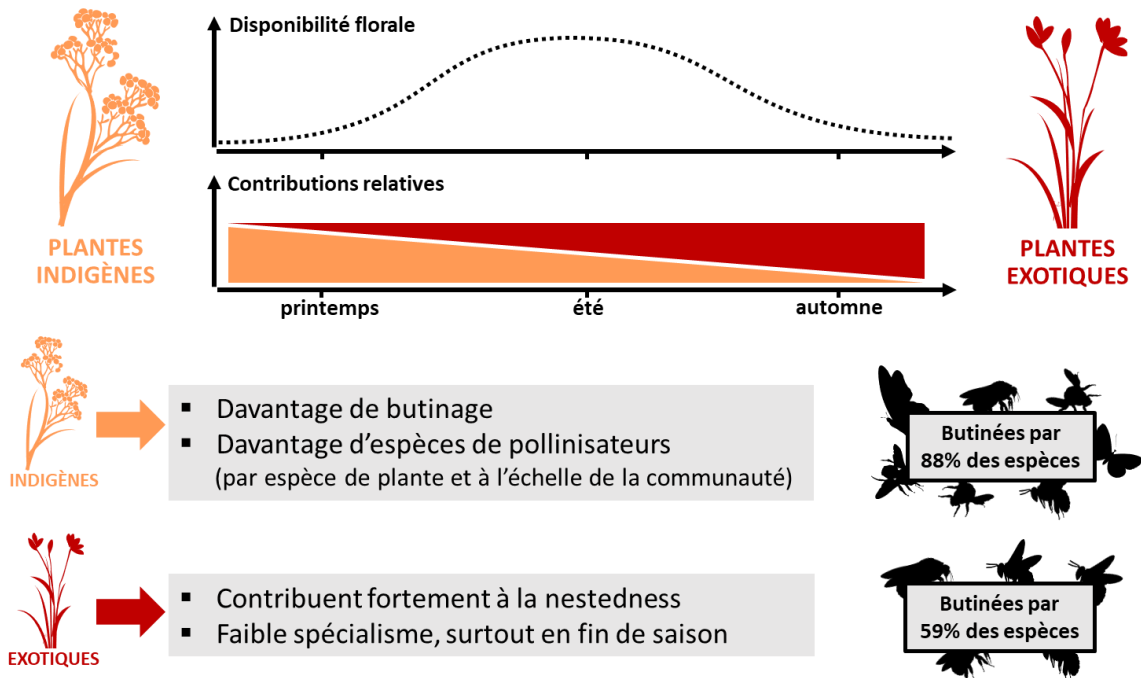


Appendix 4. 1. Rarefaction curves across the 12 survey sites for all pollinators (a.) and for wild bees only (b.). chao: Chao₁ species richness indicator; richness: Total number of species across all sites. Rar. Curve: Rarefaction curve.

Appendix 4. 2. Summary of the fourthcorner analysis assessing the presence-absence of bee species based on their traits (Generalism, Sociality, Nesting, Phenology, Size) and a selection of environmental factors. We report the results of a krantest (Pearson's R between traits and environmental factors, and p-value), with a Monte-Carlo approach (9,999 permutations) and “BH” p-adjustments at trait level (package “ade4”, Thioulouse et al., 2018). We considered bee species with at least 4 occurrences (n=57). Red: positive effect, Blue: negative effect.

Trait	% impervious (500m)		Greenspace size		Plant richness		% Spont. plants	
Specialist	p=0.72	-0.38	p=0.36	0.96	p=0.68	-0.44	p=0.056	1.86
Generalist		0.38		-0.96		0.44		-1.86
Eusocial	p=0.28	-1.15	p=0.78	-0.28	p=0.48	-0.72	p=0.73	0.35
Non-Eusocial		1.15		0.28		0.72		-0.35
Above-ground	p=0.75	-0.35	p=0.55	0.65	p=0.72	0.37	p=0.89	-0.14
Below-ground		0.35		-0.65		-0.37		0.14
Early-emerging	p=0.79	-0.29	p=0.0095 ***	-2.36	p=0.27	-1.15	p=0.53	0.67
Late-emerging		0.29		2.36		1.15		-0.67
Large (ITD≥2mm)	p=0.91	0.12	p=0.34	1.00	p=0.031 *	2.15	p=0.079	-1.74
Small (ITD<2mm)		-0.12		-1.00		-2.15		1.74

CHAPITRE 5 : Rôles respectifs des flores indigène et exotique dans les réseaux de pollinisation urbains au fil des saisons



CHAPITRE 5 : Résumé graphique

Au cours de notre suivi des communautés de pollinisateurs dans les espaces verts parisiens, nous avons examiné les réseaux de pollinisation sur une base mensuelle de mars à octobre, en évaluant les rôles respectifs des flores indigène et exotique.

- La flore exotique et la flore indigène sont-elles équitablement disponibles et attractives pour les pollinisateurs en ville ? Y a-t-il des variations au cours des saisons ?
- Comment ces espèces végétales s'intègrent-elles dans les réseaux de pollinisation et quelles sont les implications pour la dynamique saisonnière des réseaux ?

Les plantes exotiques sont des composantes majeures des interactions plantes/pollinisateurs à Paris, bien que moins attractives pour les pollinisateurs que les plantes indigènes. Ainsi, la plupart des espèces exotiques sont peu visitées par les insectes. Les communautés de pollinisateurs pourraient être favorisées par l'implantation de plus d'espèces indigènes dans les espaces verts.

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

submitted to Oecologia in March 2022 (under review)

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1. ARTICLE DETAILS

Acknowledgments: 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. Dufrière. 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).

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.

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

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

2. 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 green spaces 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. 41% of pollinator species visited only native plants, compared to 12% that visited only exotic plants, with the remainder visiting both types of plants. Pollinator communities may benefit from including more native species, as well as entomophilous varieties of exotic plants when managing urban green spaces.

Keywords: greenspace – nestedness – specialization – phenology – invasive species

3. 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 green spaces.

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 in 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 (Erickson et al., 2020; Garbuzov et al., 2017; Garbuzov & Ratnieks, 2014). The geographic origin of these garden plant species raises concerns since exotic plants can affect pollinator community composition (Pardee & Philpott, 2014; Threlfall et al., 2015), whereas native plants are key elements to sustain rich and functionally diverse insect communities (Cecala & Wilson Rankin, 2021b; Mata et al., 2021). Yet, the relative contribution of native and exotic plants to urban pollinator communities remains debated (Majewska & Altizer, 2020). Exotic flowering plants contribute substantially to the supply of nectar and pollen in urban landscapes (Casanelles-Abella et al., 2022; Tew et al., 2021), thus potentially supporting pollinator communities by increasing overall resources (Staab et al., 2020; Tasker 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 (da Rocha-Filho et al., 2021; Lowenstein et al., 2019). In addition, most of the mentioned studies were conducted in private gardens, allotments, and nurseries; but seldom in public green spaces 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 & Kowarik, 2019). This issue has yet to be assessed in the context of public green spaces 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 (Thébault & 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., 2020). Looking at invasive plants, some studies have shown that these species often successfully integrate pollination networks, occupying a central place therein (Thompson & Knight, 2018; Vilà et al., 2009). The consequences on insect communities vary greatly depending on the context (Davis et al., 2018; Stout & Tiedeken, 2017). Invasive plants tend to attract more generalist pollinator species, while specialist pollinators are more strictly dependent on native plants (Parra-Tabla & 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 & Waser, 2020). Interestingly, the seasonal dynamics of exotic plants in pollination networks may be different from those of native plants (Arroyo-Correa et al., 2020; Larson et al., 2016; 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, which can be kept constant by gardening practices (Erickson et al., 2020, 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 green spaces 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 the 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.

4. METHODS

4.1. 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 green spaces of varying size (from 7,245 to 161,540 m²) and management practices, leading to distinct plant communities. In particular, intensively managed green spaces hosted abundant and diverse garden plant species. In contrast, lightly managed areas contained a majority of spontaneous plants. Details on sampled sites can be found in **Appendix 5. 1**.

4.2. Insect sampling

Surveys were conducted in each site for two consecutive years (2019 and 2020), every month 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).

An 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 green space. 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.

4.3. 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 & 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 exotic, whereas a majority of spontaneous and subspontaneous plants species (83%) were native (**Annexe 5**).

4.4. 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).

4.5. 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 modeled 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 modeled 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 modeled the seasonal variations of the network-level nestedness (NODF) and specialization (H_2' , 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 (**Figure 5. 1**, the complete network over the whole year is in **Annexe 4**).

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 modeled with Poisson error distributions. Meanwhile, the species contribution to nestedness (*nestedcontribution* function, bipartite package) followed a continuous distribution centered on zero (positive values representing a positive contribution to nestedness) and was modeled with a gaussian error distribution. Finally, d' is comprised between 0 and 1 (*specieslevel* function, bipartite package; high values indicating high specialization), and was modeled 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 & Weisberg, 2019). Normality of residues and homoscedasticity were verified using DHARMA package (Hartig, 2021).

5. RESULTS

5.1. Overview of plant-pollinator interactions

Over the two years and across the 12 sites, we recorded a total of 3667 plant-pollinator interactions (**Figure 5. 1**, **Annexe 4**). 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.

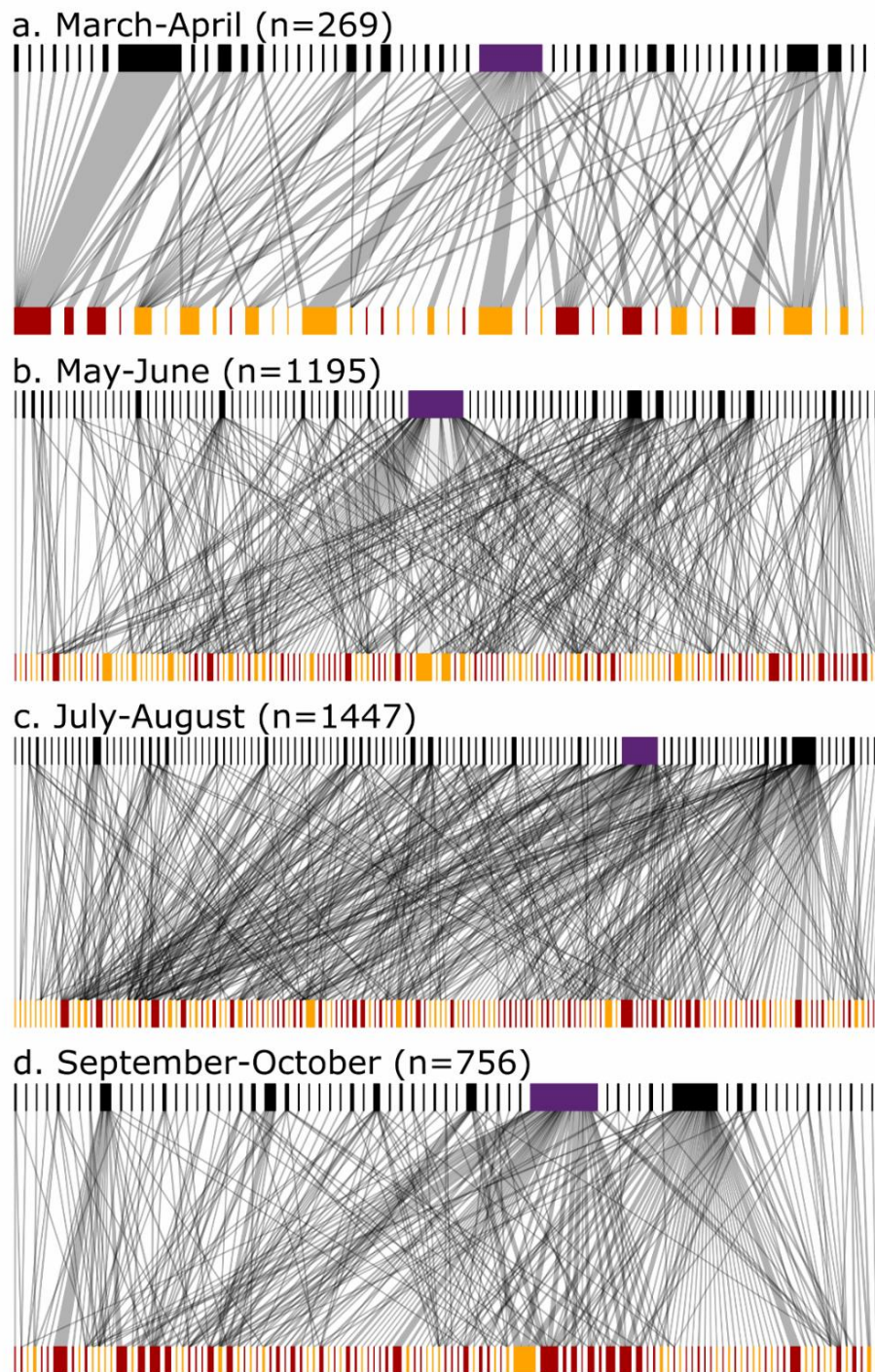


Figure 5. 1. Representation of the bipartite plant-pollinator networks over seasons. Data are pooled across all sites and per two-month period. Upper boxes represent pollinators, width is proportional to the number of interactions performed by each species (n: total number of interactions per period) (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. The complete aggregated network is available in Annexe 4.

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 (**Annexe 5**). 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*). 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.

5.2. 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 (**Figure 5. 2**). As revealed by the significant interaction “Day² x Origin”, exotic and native plants followed different unimodal seasonal patterns (**Table 5. 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 (**Figure 5. 2a**), whereas the peak of floral species richness came in July for native flora and in September for exotic flora (**Figure 5. 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 **Figure 5. 1**).

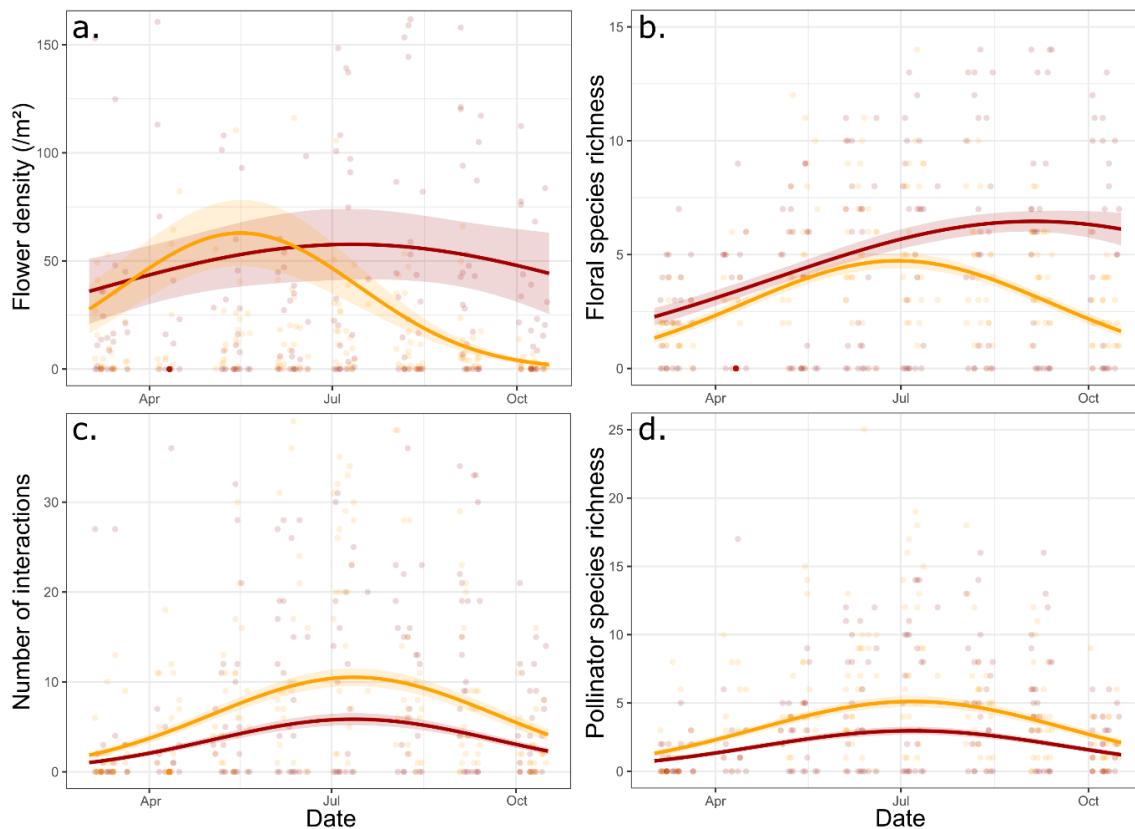


Figure 5. 2. Seasonal variations in flower resources (a. flower density per m² and b. floral species richness per site), and their attractiveness to pollinators (c. number of interactions and d. number of pollinator species) at the community level, for native and exotic plants (native: orange, exotic: red). Lines indicate predictions from the GLMM presented in Table 5. 1 (\pm SE), points represent observed values. The number of interactions and pollinator species richness (c. and d.) are modeled accounting for the variations of flower resources (a. and b.).

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 5. 1**; and **Appendix 5. 2**). 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 (**Figure 5. 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 in network size (**Figure 5. 1**).

Table 5. 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 (<i>Negative binomial</i>)	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 (<i>Negative binomial</i>)	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 (<i>Quasi-Poisson</i>)	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 (<i>Quasi-Poisson</i>)	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	

5.3. Network properties at the plant species level

At the plant species level, we also observed significant differences based on plant origin (**Table 5. 2**). Native plant species individually received more visits than exotic ones, here reaching a peak in late May (**Figure 5. 3a**). Besides, the number of interacting pollinator species (degree) was higher for native plants than for exotic plants, especially in the early season (**Figure 5. 3b**). The number of interactions per plant species and the degree were also positively influenced by flower density (**Appendix 5. 2**).

Plant contribution to monthly network nestedness, at the species level, followed a similar seasonal pattern with a maximum occurring in summer (late July, **Figure 5. 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 5. 2**). Meanwhile, network-level nestedness (NODF) followed a unimodal seasonal pattern with a peak in July, coinciding with the maximum size and diversity of the networks (**Appendix 5. 3** and **Appendix 5. 4**).

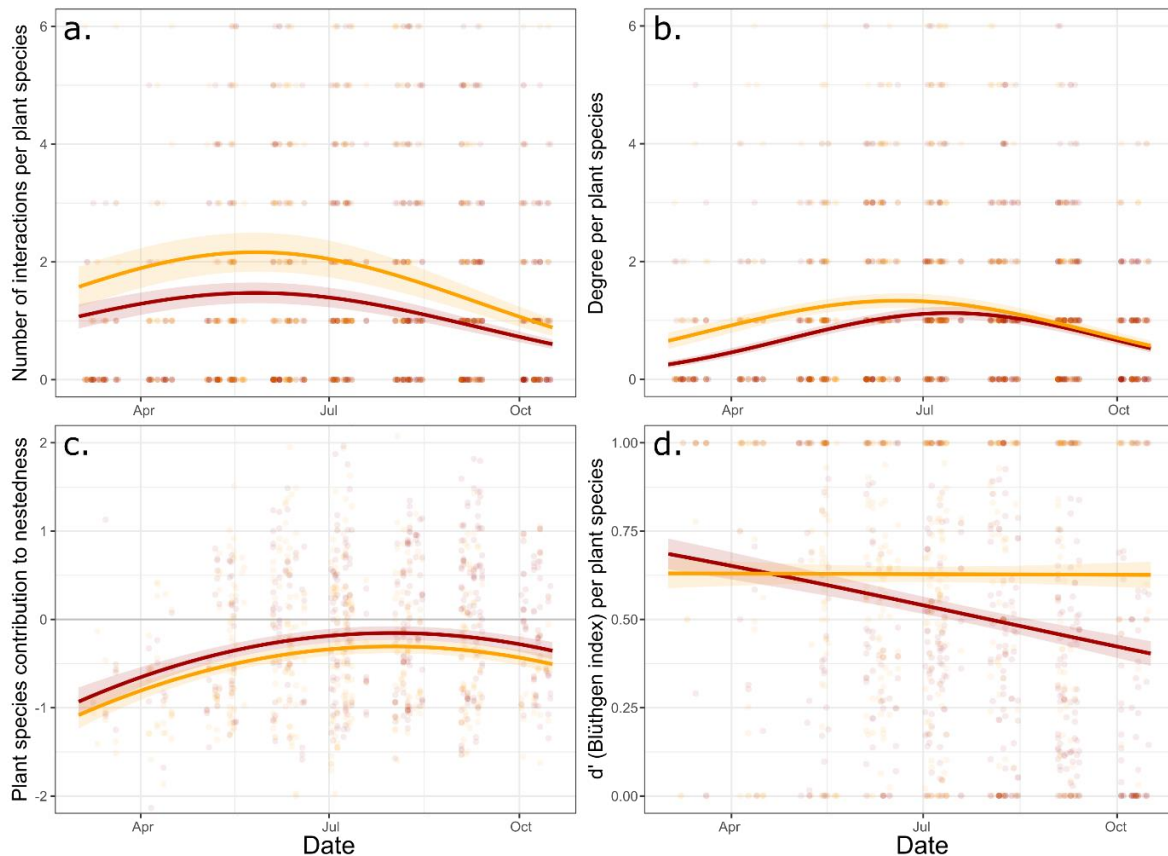


Figure 5. 3. Seasonal variations in plant-pollinator interactions at the plant species level, for native and exotic plants (native: orange, exotic: red): a. Number of interactions per plant species, b. number of interacting pollinator species per plant species (degree), c. contribution to monthly network nestedness per plant species, d. specialization index d' per plant species. Lines indicate predictions from the GLMM presented in Table 5. 2 (\pm SE), points represent observed values. Indices are modeled also accounting for the variations of flower density per plant species.

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 (**Figure 5. 3d**). Thus, exotic plant species were more generalist than native species in the late season, whereas there was no difference between them in the early season. Overall network-level specialization ($H2'$), encompassing both native and exotic flora, similarly decreased over time (**Appendix 5. 3**).

Table 5. 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	χ^2	p	AICc
Number of interactions (<i>Poisson</i>)	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 (<i>Poisson</i>)	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 (<i>Gaussian</i>)	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') (<i>Beta-regression</i>)	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	

6. DISCUSSION

Despite being overall more abundant than natives in urban green spaces, especially in the 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.

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

Our results bring further support to the importance of native plants for urban pollinators, as found previously in urban private gardens (Lowenstein et al., 2019; Salisbury et al., 2015). In the context of a densely-populated city, native plants attracted more pollinator individuals and species than exotic plants, both at the 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. Overall, this is illustrated by the large share of pollinator species that visited only native plants (41%), while few (12%) visited only exotic plants, and the

remainder (47%) visited both. Given such preferences, promoting native flora in green spaces 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 (Banaszak-Cibicka et al., 2018; Harrison et al., 2018), possibly relying more on native plants. This would explain why visitors of exotic flowers are much less diverse in the early season.

6.2. 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 & Wilson Rankin, 2021b). The observed seasonal trend could be due to higher proportions of generalist pollinators in the 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., 2022), as also demonstrated in Paris (Geslin et al., 2015). 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 & 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.

6.3. Guidelines to greenspace managers

In urban green spaces, 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 **Figure 5. 1** (and **Annexe 4**), they are core contributors to Parisian pollination networks. As such, they may enhance network stability, much like exotic plants. However, in Paris, a high density of honey bee hives has been shown to drive a decrease in wild pollinator visitation activity (Ropars et al., 2019). Honey bees could also facilitate the integration of exotic plants into pollination networks, as they visit them abundantly (Parra-Tabla & Arceo-Gómez, 2021; Urbanowicz et al., 2020). In return, the dominance of exotic plants in urban green spaces may benefit honey bees but hinder more specialized bees (Threlfall et al., 2015).

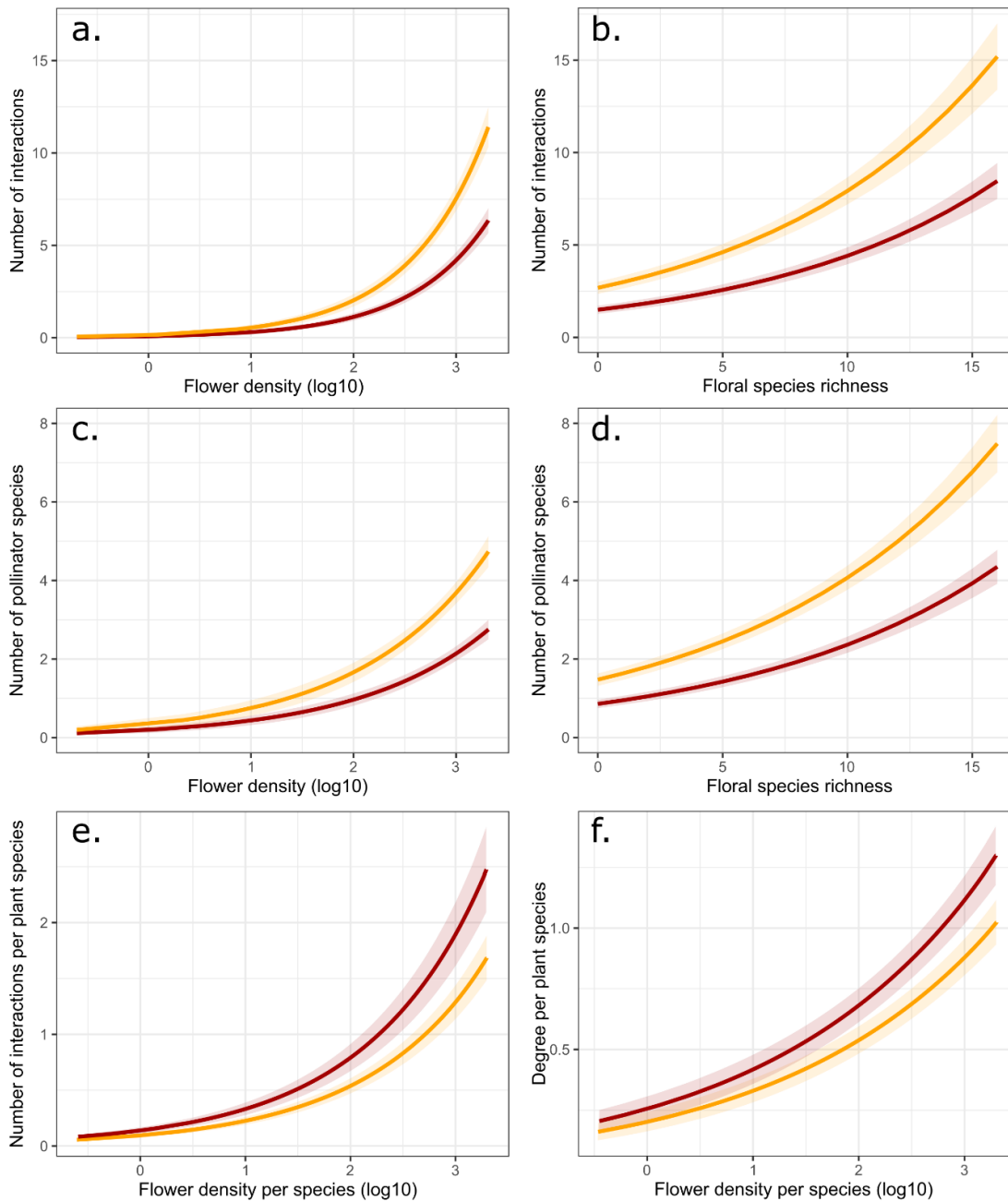
In British cities, Baldock et al. (2019) took note of native and exotic plant species that attracted more pollinators than expected based on their flower densities. Here we recovered most of the plants they recorded as attractive, and again found that they were visited abundantly. Our most visited plants, 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 green spaces (Buckley & 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 green spaces.

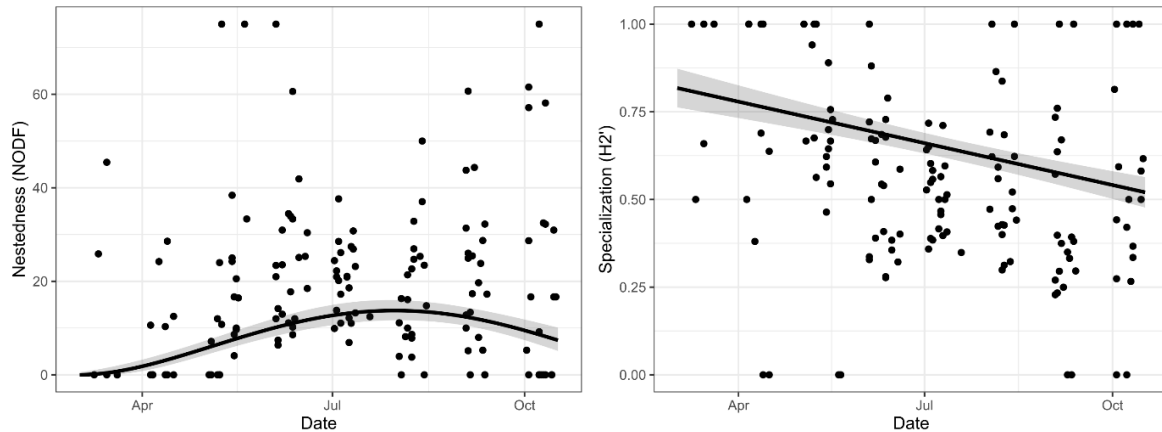
7. APPENDIX

Appendix 5. 1. Detailed information on the 12 selected green spaces and their flower resources. Plant species richness is aggregated over the two years of the survey. Mean flower density is the average number of floral units per m² calculated per month.

Green space name	Coordinates	Greenspace size (m ²)	Plant species richness (% native)	Mean flower density (/m ²) (% native)
Jardin Abbé-Pierre	48.8289°, 2.3803°	7,245	30 (93%)	31.2 (99%)
Parc de Belleville	48.8714°, 2.385°	44,665	75 (31%)	43.8 (23%)
Parc de Bercy	48.8358°, 2.3827°	58,786	56 (50%)	74.8 (64%)
Parc G. Brassens	48.8315°, 2.2996°	58,540	72 (36%)	40.0 (9%)
Parc A. Citroen	48.8419°, 2.2746°	50,126	58 (55%)	71.3 (8%)
Jardin des Plantes	48.844°, 2.3614°	161,540	54 (67%)	90.3 (91%)
Jardin C. Labouré	48.8513°, 2.3208°	21,715	54 (33%)	31.6 (10%)
Parc Monceau	48.8791°, 2.3091°	97,361	65 (37%)	28.6 (35%)
Réservoir Montsouris	48.8247°, 2.3326°	29,828	21 (95%)	8.1 (100%)
Jardin P. Emmanuel	48.8587°, 2.3989°	61,547	39 (97%)	14.7 (98%)
Jardin Saint-Vincent	48.8882°, 2.3413°	7,809	29 (97%)	7.5 (100%)
Jardin Villemin	48.875°, 2.3611°	17,212	57 (25%)	44.4 (36%)



Appendix 5. 2. Variations of plant attractiveness to pollinators according to flower resource availability, for native and exotic plants (orange: native, red: exotic): number of interactions at the community level as a function of (a.) flower density and (b.) floral species richness; number of pollinator species at the community level as a function of (c.) flower density and (d.) floral species richness; and number of interactions (e.) and number of pollinator species (degree, f.) at the plant species level. The lines indicate predictions from the GLMM presented in Table 5. 1 (a., b., c. and d.) and Table 5. 2 (e. and f.) (\pm SE). Predictions are modeled also accounting for seasonal variations presented in Figure 5. 2 and Figure 5. 3.



Appendix 5. 3. Seasonal variations in plant-pollinator interactions properties at the network level: a. network-level nestedness (NODF), b. network-level index of interaction specialization $H2'$. The lines indicate predictions from the GLMM presented in Table 5. 2 ($\pm SE$), points represent observed values. Predictions of both indices are modeled also accounting for the variations of flower density at the community level.

Appendix 5. 4. GLMM of the network-level seasonal variations in plant-pollinator interaction nestedness (NODF) and specialization index ($H2'$). 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
NODF (square-root) (<i>Poisson</i>)	Flower density (log)	14.9 (1df)	0.0001	648.0
	Day ²	19.8 (2df)	<0.0001	
	Year	8.3 (1df)	0.004	
Specialization $H2'$ (<i>Gaussian</i>)	Flower density (log)	11.5 (1df)	0.0002	3.5
	Day	13.9 (1df)	0.0007	
	Year	10.9 (1df)	0.001	

DISCUSSION GÉNÉRALE

Le travail réalisé au cours de cette thèse a permis de conjuguer plusieurs approches innovantes dans le suivi des insectes pollinisateurs, en utilisant des dispositifs simples. Ce suivi a été mené principalement à l'échelle des communautés d'insectes floricoles. Pour cela, tous les taxons d'insectes ont été considérés : hyménoptères, diptères, lépidoptères, coléoptères etc. Nombreuses sont les études qui se limitent aux seules abeilles sauvages. Ici, bien que les abeilles aient bénéficié d'une attention particulière car majoritaires, c'est toute la diversité des pollinisateurs qui a suscité notre attention. En nous ouvrant à un spectre taxonomique large, il s'agissait d'interroger la place de la diversité des insectes dans un environnement extrême et peu étudié, le centre-ville dense.

Par ailleurs, notre première étude, focalisée sur des parcelles de plantes contrôlées, constitue une démarche originale pour étudier les communautés de pollinisateurs au cours du temps (Zaninotto et al., 2020). Par un apport constant de ressources florales uniformes, elle a assuré une comparaison urbain/rural de façon standardisée dans l'espace et dans le temps. Cette approche a également été associée à une analyse du succès reproducteur des plantes, via le succès de fructification. Le succès reproducteur des plantes est un indicateur crucial de l'efficacité de la pollinisation, qui n'est malheureusement que rarement considéré dans les études. Il s'agit néanmoins d'une procédure lourde, nécessitant la mise en culture régulière d'un grand nombre de plantes et la maîtrise de leur cycle de croissance et de floraison. Il est donc délicat de multiplier les répliques géographiques.

Une autre approche innovante est la prise en compte, tout au long de nos travaux, de la variabilité temporelle saisonnière. Nous avons adopté cette démarche dans le but d'évaluer les dynamiques saisonnières d'assemblage et d'activité des pollinisateurs, avec l'hypothèse que le milieu urbain conduit à leur atténuation. La prise en compte de la dimension temporelle a nécessité un effort d'échantillonnage supplémentaire, à travers un suivi prolongé (mars – novembre), et fréquent (bihebdomadaire à mensuel). Cependant, la résolution temporelle fine ainsi obtenue nous a permis de saisir un aspect des interactions plantes-pollinisateurs peu pris en compte : les variations saisonnières dans la structure des réseaux de pollinisation.

1. UN MILIEU URBAIN RELATIVEMENT FAVORABLE

1.1. *Un assemblage de pollinisateurs diversifié*

Le milieu urbain dense parisien semble abriter des communautés d'insectes pollinisateurs riches et abondantes. Ainsi, dans le **Chapitre 1**, nous n'avons pas observé de différence significative en termes de richesse spécifique et de diversité fonctionnelle entre les visiteurs des assemblages végétaux expérimentaux urbains et ruraux. Si les résultats suggèrent une distribution moins équitable des espèces en zone urbaine qu'en zone rurale, cela est dû à la présence de certaines espèces communes qui sont très abondantes en ville. En effet, nous avons constaté des abondances de pollinisateurs parfois plus élevées dans les espaces verts parisiens que dans les milieux ruraux d'Ile-de-France, notamment en ce qui concerne certaines abeilles des familles des Apidae, Megachilidae et Andrenidae. Ces fortes abondances se traduisent par des fréquences de butinage considérables en ville (**Chapitre 2**). Par ailleurs, dans le **Chapitre 3**, en considérant les communautés d'insectes visitant l'ensemble de la flore disponible dans les espaces verts parisiens, nous avons confirmé la diversité inattendue que recèlent les espaces verts de la ville de Paris. Ainsi, avec 146 espèces d'abeilles et 53 espèces de syrphes, et malgré sa forte densité de bâti et de population, Paris se place parmi les métropoles européennes les plus riches. L'assemblage de pollinisateurs témoigne également d'une diversité fonctionnelle non négligeable. On note en particulier la présence de nombreuses espèces spécialistes et cleptoparasites (ici, parasites de couvée).

1.2. *Une fonction de pollinisation efficace*

De plus, nous avons constaté, dans le **Chapitre 2**, que le milieu urbain dense parisien est compatible avec un succès de reproduction considérable pour certaines plantes. En effet, du fait de fréquences de visites élevées en ville, nos plants expérimentaux de *Sinapis alba* et *Lotus corniculatus* ont manifesté des succès de fructification importants en milieu urbain, souvent davantage qu'en milieu rural semi-naturel. Ce résultat était particulièrement prononcé au cours des périodes qui précédaient et qui suivaient la saison de floraison naturelle des plantes, témoignant de la capacité des communautés urbaines à assurer une pollinisation efficace hors-saison.

Ces observations tendent à démontrer que les communautés de pollinisateurs intégrées dans les espaces verts d'une ville dense sont capables d'assurer une fonction de pollinisation efficace. Néanmoins, il convient d'être prudent quant à la généralisation de ces résultats à l'ensemble des communautés végétales. Si les espèces végétales expérimentales que nous avons utilisées ont bien été choisies pour leurs morphologies florales complémentaires, elles ne sont pas suffisantes pour représenter l'ensemble de la diversité végétale. Aussi, l'efficacité de la fonction de pollinisation que nous avons mesurée à Paris n'est pas généralisable à l'ensemble de la flore, sauvage ou cultivée. Au sein même de notre assemblage végétal de deux espèces, des disparités s'observent entre *S. alba* et *L. corniculatus*. Si la moutarde blanche cultivée en ville bénéficie d'un nombre de fruits et de graines plus élevé qu'en milieu rural en toute saison, ce n'est pas le cas du lotier corniculé. Celui-ci ne présente un surplus de fruits en ville qu'en période de floraison précoce, et jamais de surplus de graines par fruit. De fait, il a déjà été montré que le succès de fructification de *L. corniculatus* pouvait être réduit en milieu urbain dense (Pellissier et al., 2012).

En outre, en conditions réelles, des réponses adaptatives des populations végétales face à l'environnement urbain pourraient avoir des répercussions sur l'efficacité de la pollinisation. Par exemple, toujours en région parisienne, Desaezgher et al. (2017) ont constaté que des plants de *Cymbalaria muralis* issus de graines d'origine urbaine produisaient davantage de fleurs et attiraient davantage de pollinisateurs que ceux issus de graines d'origine rurale.

1.3. Un apport de ressources grâce à la flore ornementale

Nous avons relevé, dans le **Chapitre 4**, que l'un des déterminants principaux de l'abondance et de la richesse spécifique des insectes pollinisateurs est la diversité de la flore disponible dans les espaces verts. Or, parmi les espèces végétales visitées par les insectes au cours de cette étude, 61% étaient des plantes ornementales, implantées par des jardiniers (163 espèces ornementales, dont 31 espèces arbustives ; contre 104 espèces spontanées). Comme nous l'avons approfondi dans le **Chapitre 5**, la plupart de ces espèces ornementales (80%) étaient de surcroît des espèces exotiques. En comparaison, 83% des espèces végétales spontanées et subsponanées étaient indigènes à la région Ile-de-France.

Cet apport de ressources florales ornementales et/ou exotiques dans les parcs et jardins de la ville de Paris semble jouer un rôle important pour les communautés d'insectes pollinisateurs. En effet, les ressources florales exotiques sont présentes en plus grande quantité et en plus grande diversité dans les espaces verts que les ressources indigènes ; et ce d'autant plus en fin de saison. Bien qu'individuellement moins visitées que les fleurs indigènes, les fleurs exotiques participent abondamment aux interactions plantes-pollinisateurs à Paris. On peut donc penser que les pratiques de jardinage mises en place dans les espaces verts de Paris sont propices au maintien de communautés de pollinisateurs riches et abondantes, en leur apportant des ressources supplémentaires et variées.

2. MILIEU URBAIN ET FILTRE FONCTIONNEL

Les espaces verts de la ville de Paris semblent donc relativement favorables aux insectes pollinisateurs, au regard du niveau d'urbanisation du paysage qui les entoure. Mais ce milieu est tout de même caractérisé par des facteurs environnementaux qui contraignent les communautés d'insectes floricoles. Ces communautés manifestent des disparités à travers le territoire parisien. De plus, elles montrent les conséquences d'un filtrage fonctionnel.

2.1. Des différences avec les communautés des milieux semi-naturels

Dans le **Chapitre 1**, les assemblages de pollinisateurs observés à Paris et en milieu semi-naturel d'Ile-de-France étaient sensiblement différents. Ainsi, les ordres d'insectes (hyménoptères, diptères, coléoptères, lépidoptères) ne semblent pas représentés de la même façon dans ces deux milieux. La ville paraît être favorable aux abeilles sauvages, alors que les milieux semi-naturels ruraux présentent en proportion davantage de diptères (dont les syrphes), de coléoptères et de lépidoptères. Cette relative tolérance des hyménoptères à l'urbanisation avait déjà été signalée dans la littérature (Deguines et al., 2012; Fenoglio et al., 2020). Parmi les abeilles sauvages que nous avons répertoriées, les Andrenidae et les Apidae sont plus prépondérantes en ville qu'en milieu rural, où ce sont surtout les Halictidae qui dominent. Les Colletidae, rares en ville, sont plus fréquentes en milieu rural. De plus, comme nous avons pu le confirmer dans les **Chapitre 3 & 4**, en ville, les interactions sont dominées par certaines espèces très abondantes, telles que l'abeille domestique (*Apis mellifera*, 24% des visites

répertoriées en 2019 et 2020), le bourdon des champs (*Bombus pascuorum*, 11% des visites), et certaines Halictidae (telles que *Lasioglossum morio* et *Lasioglossum villosulum*, respectivement 7% et 4% des visites). Ces espèces abondantes, plutôt généralistes, sont observables sur de longues périodes, du printemps à l'automne.

2.2. Des différences avec les assemblages fonctionnels des milieux semi-naturels

En nous focalisant sur les communautés d'abeilles sauvages, nous avons pu mettre en évidence un phénomène de filtrage fonctionnel appliqué par le milieu urbain dense parisien. Ainsi, les abeilles terricoles ou solitaires étaient globalement moins fréquentes dans les espaces verts parisiens que dans les espaces ruraux semi-naturels (**Chapitre 1**). Ce résultat est corroboré par le **Chapitre 4**, avec de plus grandes probabilités d'occurrence des espèces nichant au-dessus du sol que des espèces terricoles à Paris ; et de plus grandes probabilités d'occurrence des espèces eusociales que solitaires. Le filtrage fonctionnel semble s'appliquer également à la morphologie, avec des abeilles globalement plus massives en ville qu'en milieu rural, à l'échelle de la communauté (**Chapitre 1**).

Bien que nous n'ayons pas observé de différence de lectisme dans les communautés d'abeilles rurales et urbaines (**Chapitre 1**), ce sont bien les abeilles généralistes qui dominent en ville. Ainsi les abeilles mono- et oligolectiques n'ont constitué que 17,7% des espèces observées à Paris (2019-2020), ne représentant que 3,2% des individus (**Chapitre 3**). De plus, les espèces cleptoparasites, bien que représentant 18,5% des espèces inventoriées, ne comptaient que pour 2,9% des individus. Dans le **Chapitre 1**, seuls les milieux ruraux semblaient abriter des abeilles parasites. Si nos travaux suivants ont montré que les espaces verts parisiens peuvent effectivement accueillir ces espèces, elles y restent rares (**Chapitre 3**). Il conviendrait d'appliquer un échantillonnage similaire à celui que nous avons mené à Paris, mais dans les milieux semi-naturels d'Ile-de-France, afin de déterminer si les abondances relatives d'abeilles oligolectiques et parasites y sont supérieures.

2.3. Certaines différences fonctionnelles associées à des variables environnementales

L'un des objectifs de nos travaux a été de comprendre les facteurs environnementaux à l'origine du filtrage fonctionnel caractéristique des milieux urbains denses. Pour cela, nous

avons été amenés à évaluer les interactions entre les traits fonctionnels des espèces d'abeilles sauvages et les facteurs locaux et paysagers qui façonnent la biodiversité dans les espaces verts (**Chapitre 4**). Ainsi, il nous est apparu que ces facteurs environnementaux n'influençaient pas de la même façon les abeilles en fonction de leurs traits. Les espèces massives (distance intertégulaire > 2mm) sont davantage affectées que les petites espèces par l'effet délétère de l'imperméabilisation du paysage. Mais elles sont également plus sensibles à la contribution positive de la diversité florale locale. Par ailleurs, ce sont les abeilles à émergence tardive qui dépendent le plus de l'étendue des espaces verts, alors que les abeilles à émergence précoce y sont plus indifférentes. Enfin, au contraire des espèces généralistes, les espèces d'abeilles spécialistes sont fortement dépendantes de la présence de plantes spontanées. Cette sensibilité des abeilles sauvages aux facteurs environnementaux, variable selon leurs traits fonctionnels, pourrait contribuer au filtrage fonctionnel urbain.

2.4. Quelles conséquences sur la fonction de pollinisation ?

L'efficacité de pollinisation varie selon les espèces (Page et al., 2021), notamment en fonction des traits morphologiques, en particulier la taille et la pilosité, mais aussi en fonction du comportement de butinage (Kendall et al., 2022; Layek et al., 2022; Phillips et al., 2018; Solís-Montero & Vallejo-Marín, 2017). Tout porte donc à croire que le filtrage fonctionnel des espèces de pollinisateurs en ville puisse avoir des conséquences sur la fonction de pollinisation. C'est d'autant plus vrai pour les espèces florales dont la pollinisation dépend fortement d'insectes spécialistes. Malgré tout, l'importance fonctionnelle d'une espèce de pollinisateur est parfois davantage influencée par sa fréquence de butinage, que par son efficacité par visite individuelle (Page et al., 2021; Sahli & Conner, 2007).

À l'échelle des communautés, il est communément démontré que la diversité de l'assemblage de pollinisateurs, et surtout sa diversité fonctionnelle, est déterminante pour l'efficacité de la pollinisation (Loy & Brosi, 2022). Ici nous avons constaté une pollinisation efficace en milieu urbain malgré le filtrage fonctionnel des pollinisateurs, mais concernant deux espèces végétales seulement. Or le lotier corniculé (*L. corniculatus*) et la moutarde blanche (*S. alba*) sont des plantes abondamment visitées par des insectes très communs en ville. C'est le cas respectivement de *Bombus pascuorum* et de *Lasioglossum morio*, qui apparaissent parmi

les grands « vainqueurs » du filtrage urbain. En revanche, d'autres espèces de plantes pourraient ne pas susciter le même intérêt pour les insectes pollinisateurs parisiens, et donc souffrir d'une réduction de leur succès reproducteur.

3. MILIEU URBAIN ET HOMOGENÉISATION TEMPORELLE

En ville, les variations saisonnières de plusieurs variables environnementales sont atténuées : climat, photopériode, ressources florales. Ceci pourrait conduire à une dégradation des dynamiques saisonnières des communautés de pollinisateurs. En assurant le suivi de ces motifs saisonniers, nous avons souhaité évaluer si le milieu urbain parisien pouvait induire un phénomène d'homogénéisation temporelle.

3.1. Une période d'activité étendue, au printemps et à l'automne

Au cours du **Chapitre 2**, nous avons observé une activité de butinage intense, hors période de floraison naturelle de nos plantes focales. Cette activité hors-saison était particulièrement importante en ville par rapport aux milieux ruraux, participant ainsi à élargir la phénologie de la pollinisation à Paris. Les insectes à l'origine de ce phénomène étaient principalement les petites abeilles sauvages, les abeilles domestiques et les bourdons.

Cet élargissement de la saison de pollinisation en milieu urbain s'est répercuté dans le succès de fructification des plantes. Ainsi, nos cultures ont bénéficié de succès reproducteur plus élevé en ville qu'en milieu rural, lors d'une floraison précoce ou bien retardée. En ville, les plantes à fleurs pourraient ainsi bénéficier d'une pollinisation efficace, même si leur phénologie est altérée par l'îlot de chaleur ou bien la pollution lumineuse. Cependant, il est probable que toutes les espèces de plantes ne puissent pas tirer profit de ce butinage hors-saison. Encore faudrait-il que des pollinisateurs généralistes, en termes de phénologie, puissent leur garantir une pollinisation efficace. Une telle capacité des communautés de pollinisateurs urbains à assurer la pollinisation des plantes, hors-saison, témoigne d'une atténuation des dynamiques saisonnières d'activité des insectes, par rapport aux espaces semi-naturels ruraux. Ceci pourrait contribuer à une homogénéisation temporelle de l'activité des communautés de pollinisateurs urbains.

3.2. Une modification des dynamiques saisonnières de l'assemblage fonctionnel

Par ailleurs, nous avons souhaité déterminer si cette homogénéisation temporelle se retrouvait également dans l'assemblage fonctionnel des abeilles sauvages. Pour cela nous avons évalué les prévalences de certains traits à l'échelle des communautés d'abeilles en milieu urbain et en milieu rural (**Chapitre 1**).

En ce qui concerne les modes de nidification, nous n'avons pas constaté de différence dans les dynamiques saisonnières des deux milieux. Celles-ci se traduisent, en ville comme en milieu rural, par une diminution saisonnière de la proportion d'espèces terricoles. En revanche, nous avons observé un motif temporel contraire à nos attentes en ce qui concerne le niveau de socialité des abeilles. Ainsi, le milieu urbain présentait une dynamique qui était absente en milieu rural : une augmentation de la proportion d'abeilles eusociales depuis le printemps jusqu'à l'automne. En effet, en ville, les motifs saisonniers de l'assemblage fonctionnel semblent surtout marqués par la prépondérance croissante des espèces eusociales, telles que les bourdons, dont les colonies s'agrandissent au cours de l'été. En outre, et précisément chez les bourdons, nous avons observé une altération de la dynamique saisonnière de la taille corporelle. Pour ces espèces, les variations de taille en milieu urbain sont atténuées par rapport au milieu rural. En revanche, pour les autres espèces d'abeilles sauvages, les motifs saisonniers sont similaires entre les deux milieux.

Enfin, le filtrage fonctionnel sur la phénologie des espèces, remarqué dans le **Chapitre 4**, interroge. À Paris, les abeilles à émergence précoce (mars-avril) sont plus fréquentes que les abeilles à émergence tardive (à partir de mai). Les probabilités d'occurrence de ces dernières sont tributaires des dimensions des espaces verts. Il semblerait donc que le filtrage fonctionnel occasionné par l'habitat urbain fragmenté puisse influencer les variations saisonnières de l'assemblage d'abeilles en sélectionnant les espèces sur la base de leurs traits phénologiques.

3.3. Des variations saisonnières dans les réseaux d'interactions

Afin de rendre compte des variations à court-terme dans les interactions plantes-pollinisateurs, nous avons réalisé un suivi des dynamiques saisonnières de la structure des réseaux de pollinisation dans les espaces verts de Paris (**Chapitre 5**). Ceci nous a permis d'émettre des hypothèses sur la stabilité de ces réseaux et d'y évaluer l'importance de la flore

exotique. Depuis le printemps jusqu'à l'automne, nous avons observé une diminution du niveau de spécialisation des interactions dans les réseaux de pollinisation. Ainsi, en fin de saison, les réseaux sont peu spécialisés, c'est-à-dire que les plantes et les pollinisateurs interagissent sur la seule base de leur co-occurrence, sans préférence particulière entre les espèces. Cette perte de spécialisation saisonnière semble être tributaire de la flore exotique, dont l'abondance relative croît au cours de la saison. En effet, les espèces végétales exotiques contribuent individuellement à des interactions de moins en moins spécialisées en fin de saison. De plus, au cours du printemps, la taille des réseaux augmente, jusqu'à atteindre un maximum en fin d'été. Cette période correspond au pic d'abondance et de richesse spécifique des pollinisateurs dans les espaces verts. C'est aussi à cette période que l'emboîtement (« nestedness ») du réseau est maximal. Or nous avons constaté que les plantes exotiques contribuent davantage à l'emboîtement des réseaux que les plantes indigènes. Il semblerait donc qu'en ville, les variations saisonnières des réseaux soient largement dépendantes des dynamiques des ressources florales exotiques. Ces plantes exotiques pourraient participer à l'atténuation des variations saisonnières caractéristiques des milieux naturels. En effet, elles apportent des ressources complémentaires aux pollinisateurs à des périodes où les fleurs indigènes sont rares, par exemple en début d'automne. À ces dates en revanche, les fleurs exotiques sont exploitées de manière indifférenciée par des pollinisateurs généralistes.

Il serait opportun de comparer ces dynamiques saisonnières avec celles des réseaux de pollinisation dans les milieux ruraux d'Ile-de-France. L'on pourrait alors déterminer si le milieu urbain est véritablement à l'origine d'une altération de la structure des réseaux plantes-pollinisateurs et de leurs dynamiques annuelles.

3.4. Des changements phénologiques au niveau intraspécifique ?

Tout au long de cette thèse, nous avons raisonné à l'échelle des communautés. Ainsi nous avons étudié comment le milieu urbain pouvait contraindre les assemblages d'espèces et les niveaux d'activité des pollinisateurs. Qu'en est-il au niveau intraspécifique ? Le milieu urbain pourrait-il influencer les traits phénotypiques au sein d'une même espèce d'insecte ?

Au regard de la grande diversité d'insectes que nous avons observés en comparant le milieu urbain dense parisien et le milieu rural, nous n'avons pas pu répondre à cette question. En effet,

nous n'avons identifié que peu d'espèces en effectifs suffisants, dans chaque milieu, pour pouvoir comparer leur phénologie (**Chapitre 1**). Seules deux espèces d'abeilles sauvages (*Bombus pascuorum* et *Lasioglossum morio*) et deux espèces de syrphes (*Episyrphus balteatus* et *Eristalis tenax*) ont décompté chacune plus de 10 spécimens capturés dans chaque habitat. Chez ces espèces, aucune différence significative dans les dates d'occurrence ne s'est manifestée entre l'habitat urbain et l'habitat rural (**Figure 6. 1**).

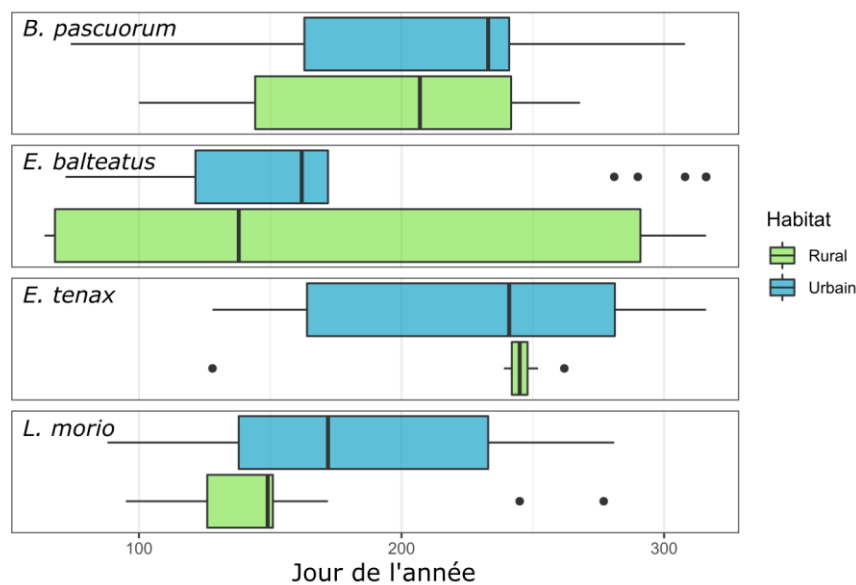


Figure 6. 1. Phénologies à l'échelle intraspécifique pour *B. pascuorum*, *E. balteatus*, *E. tenax* et *L. morio*. Les boîtes représentent la médiane, le 1^{er} et le 3^e quartile ; les « moustaches » intègrent les valeurs comprises autour de la médiane sans dépasser 1,5 x la distance interquartile. Les tests de wilcoxon ne montrent pas de différence dans les dates d'occurrence entre les deux habitats (*B. pascuorum* : $W = 521$, $P = 0.8$; *E. balteatus* : $W = 187$, $P = 0.3$; *E. tenax* : $W = 52.5$, $P = 0.9$; *L. morio* : $W = 238.5$, $P = 0.1$).

Afin de compléter cette comparaison intraspécifique des dates d'occurrences des pollinisateurs à Paris et en milieu naturel, il serait nécessaire de se concentrer sur la capture de certaines espèces abondantes dans les deux milieux. L'effort d'échantillonnage doit être régulier dans le temps et suffisamment important pour obtenir des échantillons statistiques satisfaisants. Si des différences dans les traits phénologiques sont constatées, des expériences en conditions contrôlées, ainsi que des analyses génétiques, pourraient permettre d'établir si l'on a affaire à une réponse adaptative ou de la plasticité phénotypique.

3.5. Quelles sont les conséquences de cette saisonnalité atténuée ?

Les atteintes à la variabilité temporelle des écosystèmes sont une des causes de l'homogénéisation fonctionnelle des communautés et des fonctions écologiques (Alberti, 2015). En ville, l'atténuation des dynamiques saisonnières de l'environnement est ainsi à l'origine d'une homogénéisation temporelle des communautés de plantes et de pollinisateurs, se caractérisant notamment par une réduction du turnover saisonnier des espèces (Uchida et al., 2018). Ici, notre échantillonnage était insuffisant pour observer une différence dans le turnover saisonnier des espèces entre le milieu urbain parisien et le milieu rural semi-naturel.

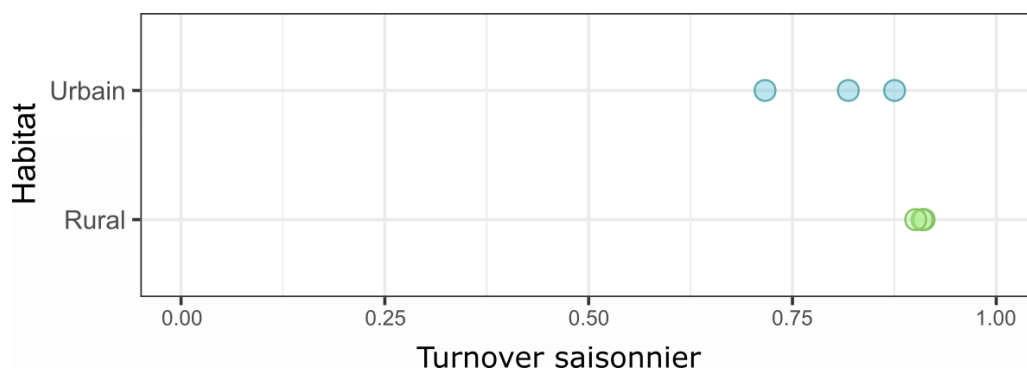


Figure 6. 2. Turnover saisonnier des assemblages de pollinisateurs obtenus en milieu urbain et rural sur *S. alba* et *L. corniculatus* (2017-2018). Points bleus : milieu urbain ; points verts : milieu rural (presque superposés car valeurs très proches). Les assemblages sont comparés sur une base mensuelle, le renouvellement des espèces est estimé par la composante « turnover » de la dissimilarité de Jaccard (Baselga, 2012) : des valeurs proches de 1 témoignent d'un turnover élevé. La différence observée entre habitats n'est pas significative ($W = 9, P = 0.1$).

Comme on le constate sur la **Figure 6. 2**, les sites urbains tendent à manifester un turnover saisonnier des pollinisateurs plus faible que les sites ruraux, mais cette différence n'est pas significative. Il serait pertinent de renouveler l'expérience avec davantage de répliques géographiques pour déterminer si cette tendance se confirme. Toutefois il serait alors préférable d'élargir l'échantillonnage aux insectes pollinisateurs visitant l'ensemble de la flore disponible dans l'habitat, et pas seulement des espèces végétales sélectionnées et contrôlées. Au sein du milieu urbain dense parisien, quelques disparités sont à relever dans le turnover saisonnier des pollinisateurs, au sein des sites échantillonnés en 2019 et 2020 (**Figure 6. 3**), bien que le turnover reste élevé dans tous les sites. Aucune variable environnementale, à l'échelle locale

ou à l'échelle du paysage, n'a présenté de lien manifeste avec le turnover saisonnier des espèces de pollinisateurs.

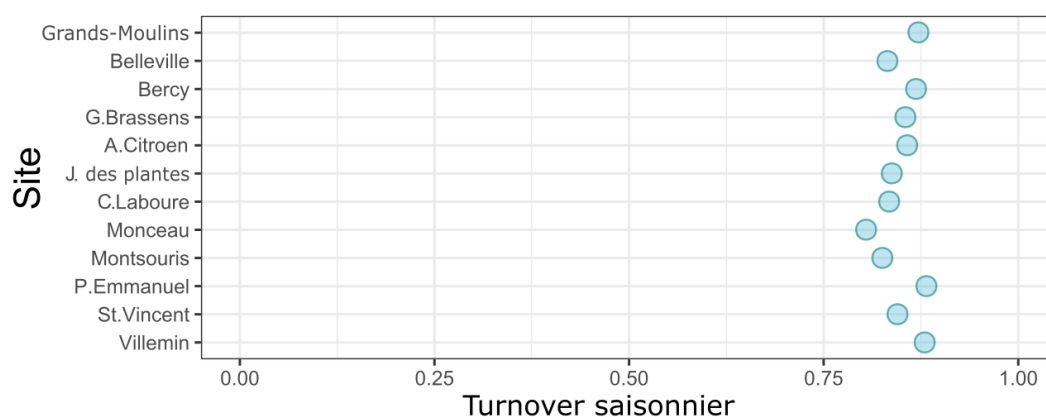


Figure 6. 3. Turnover saisonnier des assemblages de pollinisateurs obtenus dans les espaces verts parisiens sur toute la flore disponible (2019-2020). Les assemblages (comprenant abeilles, syrphes, bombyles, lépidoptères et coléoptères) sont comparés sur une base mensuelle, le renouvellement des espèces est estimé par la composante « turnover » de la dissimilarité de Jaccard (Baselga, 2012) : des valeurs proches de 1 témoignent d'un turnover élevé.

Si nous n'avons pas démontré d'altération du turnover saisonnier des espèces en milieu urbain, nous avons observé une atténuation des schémas saisonniers d'activité des pollinisateurs, à l'échelle des communautés (**Chapitre 2**). De plus, nous avons constaté des différences dans les dynamiques fonctionnelles saisonnières des pollinisateurs entre la ville et le milieu rural (**Chapitre 1**). Dans le paysage dense parisien, ces dynamiques saisonnières sont profondément affectées par les pratiques d'aménagement et de gestion des espaces verts, qui déterminent les variations saisonnières des ressources. En altérant les dynamiques saisonnières florales, le milieu urbain pourrait influencer le niveau de spécialisation des espèces d'abeilles (Glaum et al., 2021). En effet, ces successions florales conditionnent la diversité de ressources disponibles au cours des quelques semaines de vie adulte d'un insecte.

Par ailleurs, nous avons émis l'hypothèse que l'altération des dynamiques saisonnières urbaines impliquerait une modification des traits phénologiques des pollinisateurs à l'échelle intraspécifique. Si ce phénomène était avéré, et qu'il se traduisait par une superposition des niches phénologiques des pollinisateurs, les conséquences sur la structure des réseaux de pollinisation pourraient être importantes. En effet, en limitant la compétition dans les réseaux de pollinisation, les traits phénologiques favorisent la coexistence des espèces (Duchenne et al.,

2021). Ainsi, davantage de chevauchement entre les niches phénologiques pourrait accroître la compétition interspécifique pour les ressources florales. Ce seraient alors les espèces spécialistes, les plus vulnérables, qui présenteraient le plus grand risque d'extinction. L'intégrité de la structure saisonnière des réseaux d'interactions est donc fondamentale dans le maintien de la diversité des communautés de plantes et de pollinisateurs. Le turnover saisonnier des espèces de pollinisateurs étant tributaire de celui des plantes à fleurs (Cecala & Wilson Rankin, 2022), c'est en favorisant la diversité végétale et la complémentarité temporelle des floraisons que l'on pourrait lutter contre l'homogénéisation temporelle des communautés de pollinisateurs.

4. RECOMMANDATIONS D'AMÉNAGEMENT ET DE GESTION

En premier lieu, nous avons confirmé que le niveau d'artificialisation, à l'échelle du paysage, est un déterminant majeur de l'abondance et de la diversité des insectes pollinisateurs. C'est le facteur principal qui différencie le milieu urbain parisien et les milieux ruraux semi-naturels que nous avons étudiés. L'artificialisation se manifeste notamment par l'imperméabilisation des sols. Ainsi, la France compterait près de 10% de sols artificialisés, dont 6% imperméabilisés. Cette proportion augmente continuellement, à raison d'une extension de bâti de 15 000 ha chaque année (Antoni & Kraszewski, 2018). Afin de préserver les zones naturelles de l'artificialisation des sols, les solutions qui s'imposent sont la densification de l'habitat, et le renouvellement urbain (CDC Biodiversité, 2020). Il convient d'atteindre un compromis entre densification et intégration de la nature en ville. Ici, nous avons travaillé dans un habitat déjà extrêmement densifié, qui gagnerait à accueillir davantage d'espaces de nature. À travers les démarches de renaturation, il s'agit d'apporter des services écosystémiques qui font défaut aux Parisiens, tout en rendant la ville perméable à la biodiversité. Ceci permettrait de concilier la densification urbaine, la qualité du cadre de vie et les enjeux liés à la biodiversité (CDC Biodiversité, 2020).

Nos études menées dans les espaces verts de Paris ont révélé une abondance et une richesse taxonomique remarquables pour les communautés d'insectes pollinisateurs, au regard de la densité de la population et du bâti. Ces communautés ont fait preuve d'une activité de butinage suffisante pour assurer un succès reproducteur élevé pour certaines plantes. Cette pollinisation

est restée efficace longtemps au cours de l'année, avec une extension de la période d'activité des pollinisateurs. Nos résultats semblent donc encourageants pour la végétalisation et l'agriculture urbaine, car ils témoignent de la faculté des communautés de pollinisateurs urbains à assurer le service écosystémique de pollinisation. Toutefois, nous avons constaté que certains éléments constitutifs du paysage urbain contraignent l'abondance, la richesse spécifique et l'assemblage des pollinisateurs. De plus, les communautés urbaines subissent un filtrage fonctionnel, ainsi qu'une altération des dynamiques saisonnières de l'activité des pollinisateurs et de l'assemblage fonctionnel. Ceci conduit plus largement à une perte de diversité des communautés, et à leur homogénéisation dans l'espace et dans le temps. Il est donc crucial de considérer des pratiques favorables à la diversité des insectes pollinisateurs. Parmi celles-ci, nous retenons trois solutions principales pour l'aménagement et la gestion des espaces verts.

1/ Les grands espaces verts abritent la plus grande diversité de pollinisateurs. Il s'agit donc de promouvoir le développement d'espaces verts de taille suffisante, tout en participant à la désimperméabilisation des paysages urbains. Néanmoins cette démarche de « renaturation » repose également sur le déploiement d'espaces de tailles plus réduites, qui favorisent la perméabilité de la matrice urbaine et la connectivité entre les habitats végétalisés (Filazzola et al., 2019; Shwartz et al., 2013). Ce rôle peut aussi être assuré par les « infrastructures vertes », telles que les murs et toitures végétalisées. Bien qu'il soit recommandé que les espaces verts soient le plus compacts possible (Su et al., 2015), pour favoriser la biodiversité en leur cœur, de petites parcelles végétalisées participent à la renaturation d'un paysage où la pression foncière est grande.

2/ La diversité des plantes à fleurs sous-tend la diversité des pollinisateurs. Nos expériences ont confirmé l'importance de la diversité et de la densité florale pour soutenir des communautés abondantes et diversifiées de pollinisateurs. Par conséquent, les pratiques de gestion des espaces verts doivent assurer l'implantation de plantes à fleurs variées et en grandes quantités (Baldock, 2020). Afin de couvrir les besoins de tous les insectes, ces plantes doivent être complémentaires en termes de traits floraux (morphologie, couleur, etc.), et en particulier

en termes de phénologie de floraison (Majewska & Altizer, 2020; Salisbury et al., 2015). En effet, il s'agit d'apporter des ressources florales tout au long de l'année en assurant leur succession saisonnière (Hicks et al., 2016). Dans les espaces verts, les assemblages végétaux comportent de nombreuses espèces végétales exotiques. Certaines de ces espèces exotiques sont attractives pour les pollinisateurs et peuvent compléter les ressources apportées par les plantes natives, notamment en fin de saison (Ayers & Rehan, 2021). Pour soutenir ce phénomène, il s'agit de veiller à sélectionner des variétés de plantes exotiques qui sont effectivement porteuses de ressources florales : plus précisément, des variétés entomophiles visitées par des insectes locaux et peu transformées par sélection horticole. Cependant, les plantes natives restent, à disponibilité égale, plus attractives pour les insectes pollinisateurs. Elles sont impliquées dans des interactions plus spécialisées, et soutiennent donc les pollinisateurs spécialistes. Ainsi, il est crucial de promouvoir leur développement et de ne pas se limiter aux seules espèces exotiques (Lowe et al., 2022). Pour cela, des variétés ornementales locales peuvent être préférées pour les plates-bandes et massifs arbustifs, mais aussi dans les semis de plantes nectarifères. Enfin, les végétaux ligneux peuvent apporter des ressources complémentaires, non florales, à certaines espèces d'abeilles : résines, feuilles, fibres, sites de nidification (Requier & Leonhardt, 2020).

3/ La végétation spontanée est essentielle à la diversité des pollinisateurs. En effet, la présence d'espèces végétales spontanées favorise la dissimilarité des communautés à travers le paysage. Les ressources florales qu'elles apportent sont déterminantes pour les pollinisateurs spécialistes, et donc pour la diversité fonctionnelle et la structure des réseaux de pollinisation. De plus, le maintien de leurs floraisons successives pourrait limiter le risque d'homogénéisation temporelle des espèces pollinisatrices, grâce au fort turnover saisonnier des plantes spontanées (Cecala & Wilson Rankin, 2022; Uchida et al., 2018). Enfin, la présence de plantes-hôtes sauvages est indispensable pour le cycle de vie des certains pollinisateurs, dont de nombreux papillons (Majewska & Altizer, 2020). Ainsi, en laissant la végétation spontanée indigène se développer et atteindre la floraison, l'on soutient la diversité des pollinisateurs (Turo et al., 2021). Pour concilier cette démarche avec les différents usages des espaces verts, plusieurs

solutions existent : réduire la hauteur et la fréquence de tonte pour laisser fleurir les pelouses (Lerman et al., 2018; Lowe et al., 2022), dédier des espaces de prairie à la biodiversité etc. Il convient aussi de ne pas abuser des paillages, qui limitent la croissance des plantes spontanées et l'installation des abeilles terricoles (Cohen et al., 2021). Grâce à la place qu'ils laissent à la végétation spontanée, les jardins partagés sont largement reconnus pour accueillir une grande diversité de pollinisateurs (Baldock et al., 2019). Ils conjuguent ainsi agriculture urbaine, lien social, et nature en ville.

Enfin, en marge de nos travaux en milieu urbain, nous avons pu constater un déficit d'éducation du grand public sur les sujets de biodiversité et de pollinisation. Si les gestionnaires et visiteurs des espaces verts, ainsi que les médias, font preuve d'une grande érudition sur le cycle de vie de l'abeille domestique (*Apis mellifera*), l'on déplore une forte méconnaissance de la diversité des abeilles et plus généralement des pollinisateurs (Wilson et al., 2017). Hélas, cette méconnaissance a des conséquences concrètes sur la biodiversité. Il est nécessaire de proposer une vulgarisation au grand public sur ces sujets, en cessant de se focaliser sur les pratiques d'apiculture. Ceci permettrait notamment de limiter l'usage de certains dispositifs, mis en place avec de bonnes intentions, mais dont les apports à la biodiversité sont discutables. C'est le cas de l'apiculture urbaine, mais aussi de l'implantation d'hôtels à insectes, parfois garnis de cocons d'abeilles rubicoles issues d'élevages (Geslin et al., 2022). Ces dispositifs, souvent inefficaces, parfois délétères, bénéficient d'images positives ; mais ils se substituent à des pratiques de gestion éprouvées qui soutiennent effectivement la biodiversité. Face à l'effondrement des populations d'insectes ainsi qu'à l'intensification des changements globaux, il est urgent d'appliquer des efforts de conservation efficaces et ambitieux pour préserver la diversité des pollinisateurs.

PERSPECTIVES

Nous avons mis en évidence un processus de filtrage fonctionnel sur les communautés d'insectes pollinisateurs parisiens. Il conviendrait d'étendre notre perspective aux autres grandes villes françaises, afin d'y comparer les effets de l'urbanisation dense, et d'évaluer le risque d'homogénéisation fonctionnelle à grande échelle. Une telle homogénéisation a déjà été constatée à travers les données de sciences participatives (Deguines et al., 2016), et reste encore à confirmer à l'aide de données d'identification précises, confirmées par des experts.

Ici, nous nous sommes efforcés de décrire les assemblages de pollinisateurs de façon détaillée, mais lacunaire pour certains taxons. Ainsi, de nombreux diptères et hyménoptères n'ont pas pu être identifiés avec précision. De plus, nos échantillonnages ont conservé plusieurs « angles morts ». De fait, par souci de logistique et de sécurité, nous avons uniquement échantillonné au niveau de la strate herbacée et du bas de la strate arbustive (< 2m). Certains insectes floricoles ont alors pu échapper à notre portée, en particulier au niveau de la canopée. Or des travaux démontrent l'importance des ressources florales apportées par les arbres urbains pour les insectes pollinisateurs (Somme et al., 2016; Splitt et al., 2021). Malheureusement, les communautés de pollinisateurs qui butinent dans les arbres sont encore méconnues. Leur étude nécessiterait un échantillonnage au plus près de la cime des arbres, à l'aide d'un équipement adapté (Hausmann et al., 2016). En outre, en échantillonnant en journée, nous n'avons pas pu appréhender la diversité des pollinisateurs crépusculaires et nocturnes. Pourtant, les espèces de Lépidoptères nocturnes sont près de 20 fois plus nombreuses en France que les espèces diurnes, et méritent un suivi adapté (Noé, 2020). De plus, cette faune est au cœur d'enjeux particuliers en milieu urbain, en raison des atteintes aux dynamiques saisonnières occasionnées par la pollution lumineuse (Merckx et al., 2021).

Par ailleurs, et comme abordé précédemment, nos travaux pourraient être enrichis par des études complémentaires, afin d'évaluer l'altération des dynamiques saisonnières des communautés de pollinisateurs en ville. D'une part, il s'agirait d'évaluer les effets du milieu urbain sur le turnover saisonnier des assemblages d'insectes. D'autre part, en se focalisant sur certaines espèces ubiquistes, l'on pourrait déterminer si leurs traits phénologiques diffèrent entre les espaces ruraux, périurbains et urbains.

Enfin quelles sont les perspectives face au réchauffement climatique global ? Les projections parisiennes prévoient des répercussions importantes pour les populations humaines et les écosystèmes (Ville de Paris, 2021). Cette contrainte supplémentaire est susceptible d'accroître les phénomènes de filtrage fonctionnels et d'altération des dynamiques saisonnières, que subissent déjà les pollinisateurs. Il conviendrait de modéliser les effets conjugués du réchauffement global, de l'îlot de chaleur urbain, mais aussi des futurs aménagements envisagés pour les atténuer (ex : « forêts urbaines »), sur les communautés de plantes et de pollinisateurs.

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- Ecology Across Borders – International Conference, Ghent 2017 – *BES & SFE²*: poster
- Rencontres Nationales Apoidea Gallica, Lyon 2018 – *Observatoire des abeilles* : présentation orale
- SFÉcologie – International Conference, Rennes 2018 – *SFE²* : présentation orale
- Rencontres Nationales Apoidea Gallica, Lille 2019 – *Observatoire des abeilles* : présentation orale
- Rencontres Nationales du GDR Pollinéco, Montpellier 2019 – *GDR Pollinéco* : présentation orale
- Assises Nationales des Insectes Pollinisateurs, Lyon 2019 – *ARTHROPOLOGIA* : tables rondes
- Journées scientifiques du laboratoire, Paris 2019 – *iEES-Paris* : poster
- Journée de restitution des projets en partenariat avec la *Ville de Paris*, Paris 2019 : présentation orale
- Rencontres Nationales du GDR Pollinéco, Toulouse 2021 – *GDR Pollinéco* : présentation orale
- Journées scientifiques du laboratoire, Paris 2021 – *iEES-Paris* : présentation orale
- Ecology Across Borders – International Conference, Liverpool 2021 – *BES & SFE²* : présentation orale
(convertie en *e-poster* en distancielle en raison de la crise sanitaire)

ENSEIGNEMENTS

- **2021, Université PSL (Paris Sciences & Lettres) – Licence Sciences pour un Monde Durable :**

Pilote scientifique (projet interdisciplinaire Biodiversité)

- **2022, Université Paris Cité – Licence Sciences de la Vie (et de la Terre) :**

Chargé de TD et TP (Introduction à l'Écologie)

- **2022, Université Paris Cité – Master Risques et Environnement, Écosystèmes et Biodiversité :**

Chargé de TP (Initiation au Diagnostic Écologique)

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ANNEXES

Annexe 1. Liste mise à jour des espèces d'abeilles inventoriées à Paris *intramuros*, au cours de ce travail (« Thèse »), lors d'études récentes publiées dans la littérature scientifique (« Biblio. » : Ropars et al., 2017 & 2018, Geslin et al., 2015) et dans des rapports d'expertise (« Exp. » : Stallegger et al., 2015, Ferrand et al., 2014). Traits : « Lect. », lectisme (Poly.: polylectique, Oligo. : oligolectique, Clepto. : cleptoparasite) ; « Social. », niveau de socialité (Soli. : solitaire, Eusoc. : eusocial, PrEusoc. : primitivement eusocial, ParEusoc. : parasite eusocial) ; « Nid. », mode de nidification (T : terriers, C : cavités diverses, L : litière végétale, R : tiges creuses) ; « Taille » (basée sur la distance intertégulaire des femelles, S : ITD < 2mm, M : 2mm < ITD < 3mm, L : ITD > 2mm) ; « Pheno. », phénologie (préc. : précoce - première occurrence en mars-avril, mi. : mi-saison - première occurrence en mai-juin, tard. : tardive - première occurrence à partir de juillet). Les sources détaillées pour chaque trait et espèce seront disponibles dans la base de traits du Chapitre 4, sur le répertoire ouvert Zenodo.

Species	Thèse	Biblio.	Exp.	Lect.	Social.	Nid.	Taille	Pheno.
ANDRENIDAE								
<i>Andrena anthrisci</i> (Blüthgen 1925)			X					
<i>Andrena bicolor</i> (Fabricius 1775)	X	X	X	Poly.	Soli.	T	S	préc.
<i>Andrena carantonica</i> (Pérez 1902)	X	X	X	Poly.	Soli.	T	M	préc.
<i>Andrena cf. mitis</i> (Schmiedeknecht 1883)			X					
<i>Andrena chrysoseles</i> (Kirby 1802)	X	X	X	Poly.	Soli.	T	S	préc.
<i>Andrena cineraria</i> (Linnaeus 1758)	X	X	X	Poly.	Soli.	T	M	préc.
<i>Andrena curtula</i> (Pérez 1903)		X						
<i>Andrena dorsata</i> (Kirby 1802)	X	X	X	Poly.	Soli.	T	M	préc.
<i>Andrena flavipes</i> (Panzer 1799)	X	X	X	Poly.	Soli.	T	M	préc.
<i>Andrena florea</i> (Fabricius 1793)	X			Oligo.	Soli.	T	M	préc.
<i>Andrena fulva</i> (Müller 1766)			X					
<i>Andrena fulvago</i> (Christ 1791)		X						
<i>Andrena gr. proxima</i> (Kirby 1802)	X	X		Oligo.	Soli.	T	S	mi.
<i>Andrena gravida</i> (Imhoff 1832)	X	X	X	Poly.	Soli.	T	M	préc.
<i>Andrena haemorrhoea</i> (Fabricius 1781)	X	X	X	Poly.	Soli.	T	S	préc.
<i>Andrena lagopus</i> (Latreille 1809)	X			Oligo.	Soli.	T	M	préc.
<i>Andrena minutula</i> (Kirby 1802)	X	X	X	Poly.	Soli.	T	S	préc.
<i>Andrena minutuloides</i> (Perkins 1914)	X	X		Poly.	Soli.	T	S	préc.
<i>Andrena nigroaenea</i> (Kirby 1802)	X	X	X	Poly.	Soli.	T	M	préc.
<i>Andrena nitida</i> (Müller 1776)	X	X	X	Poly.	Soli.	T	M	préc.
<i>Andrena ovatula</i> (Kirby 1802)	X			Oligo.	Soli.	T	S	tard.
<i>Andrena propinqua</i> (Schenck 1853)	X	X	X	Poly.	Soli.	T	S	tard.
<i>Andrena pusilla</i> (Pérez 1903)	X			Poly.	Soli.	T	S	préc.
<i>Andrena rufula</i> (Schmiedeknecht 1883)	X			Poly.	Soli.	T	M	préc.
<i>Andrena semilaevis</i> (Pérez 1903)		X						
<i>Andrena strohella</i> (Stoeckhert 1928)	X	X		Poly.	Soli.	T	S	préc.
<i>Andrena subopaca</i> (Nylander 1848)	X	X		Poly.	Soli.	T	S	préc.
<i>Andrena synadelpha</i> (Perkins 1914)			X					
<i>Andrena tenuistriata</i> (Pérez 1895)	X			Poly.	Soli.	T	S	mi.
<i>Andrena trimmerana</i> (Kirby 1802)		X						

<i>Andrena ventralis</i> (Imhoff 1832)	X			Oligo.	Soli.	T	S	mi.
<i>Andrena viridescens</i> (Viereck 1916)	X		X	Oligo.	Soli.	T	S	mi.
<i>Panurgus calcaratus</i> (Scopoli 1763)		X						
<i>Panurgus dentipes</i> (Latreille 1811)	X	X	X	Oligo.	Soli.	T	S	mi.

APIDAE

<i>Anthophora plumipes</i> (Pallas 1772)	X	X	X	Poly.	Soli.	T	L	préc.
<i>Anthophora quadrimaculata</i> (Panzer 1789)	X	X	X	Poly.	Soli.	T	M	mi.
<i>Apis mellifera</i> (Linnaeus 1758)	X	X	X	Poly.	Eusoc.	C	M	préc.
<i>Bombus hortorum</i> (Linnaeus 1761)	X	X	X	Poly.	Eusoc.	T	L	tard.
<i>Bombus hypnorum</i> (Linnaeus 1758)	X	X	X	Poly.	Eusoc.	C	L	mi.
<i>Bombus lapidarius</i> (Linnaeus 1758)	X	X	X	Poly.	Eusoc.	T	L	mi.
<i>Bombus lucorum</i> (Linnaeus 1760)	X	X		Poly.	Eusoc.	T	L	préc.
<i>Bombus pascuorum</i> (Scopoli 1763)	X	X	X	Poly.	Eusoc.	C-L	L	préc.
<i>Bombus pratorum</i> (Linnaeus 1760)	X		X	Poly.	Eusoc.	T	L	mi.
<i>Bombus sylvestris</i> (Lepeletier 1833)			X					
<i>Bombus terrestris</i> (Linnaeus 1758)	X	X	X	Poly.	Eusoc.	T	L	préc.
<i>Bombus vestalis</i> (Geoffroy in Fourcroy 1785)	X	X	X	Clepto.	ParEusoc.	T	L	mi.
<i>Melecta albifrons</i> (Forster 1771)			X					
<i>Nomada bifasciata</i> (Olivier 1811)	X		X	Clepto.	Soli.	T	S	préc.
<i>Nomada discrepans</i> (Schmiedeknecht 1882)	X			Clepto.	Soli.	T	S	préc.
<i>Nomada distinguenda</i> (Morawitz 1874)	X			Clepto.	Soli.	T	S	mi.
<i>Nomada fabriciana</i> (Linnaeus 1767)	X	X	X	Clepto.	Soli.	T	S	préc.
<i>Nomada ferruginata</i> (Linnaeus 1767)	X			Clepto.	Soli.	T	S	préc.
<i>Nomada flava</i> (Panzer 1798)	X		X	Clepto.	Soli.	T	M	préc.
<i>Nomada flavoguttata</i> (Kirby 1802)	X	X	X	Clepto.	Soli.	T	S	préc.
<i>Nomada fulvicornis</i> (Fabricius 1793)	X			Clepto.	Soli.	T	S	préc.
<i>Nomada goodeniana</i> (Kirby 1802)	X		X	Clepto.	Soli.	T	M	préc.
<i>Nomada lathburiana</i> (Kirby 1802)	X	X	X	Clepto.	Soli.	T	M	préc.
<i>Nomada marshamella</i> (Kirby 1802)			X					
<i>Nomada ruficornis</i> (Linnaeus 1758)			X					
<i>Nomada succincta</i> (Panzer 1798)	X		X	Clepto.	Soli.	T	S	mi.
<i>Nomada zonata</i> (Panzer 1798)	X	X	X	Clepto.	Soli.	T	S	préc.
<i>Xylocopa violacea</i> (Linnaeus 1758)	X	X	X	Poly.	Soli.	C	L	mi.

COLLETIDAE

<i>Colletes cunicularius</i> (Linnaeus 1761)	X			Poly.	Soli.	T	M	préc.
<i>Colletes daviesanus</i> (Smith 1846)	X		X	Oligo.	Soli.	T	S	tard.
<i>Colletes hederæ</i> (Schmidt & Westrich 1993)	X		X	Oligo.	Soli.	T	L	tard.
<i>Colletes marginatus</i> (Smith 1846)	X			Poly.	Soli.	T	M	tard.
<i>Colletes similis</i> (Schenck 1853)	X		X	Oligo.	Soli.	T	M	tard.
<i>Hylaeus brevicornis</i> (Nylander 1852)	X			Poly.	Soli.	R	S	mi.
<i>Hylaeus cf. taeniolatus</i> (Förster 1871)			X					
<i>Hylaeus communis</i> (Nylander 1852)	X	X	X	Poly.	Soli.	R	S	mi.
<i>Hylaeus confusus</i> (Nylander 1852)		X						
<i>Hylaeus gredleri</i> (Förster 1871)	X		X		Soli.	R	S	mi.
<i>Hylaeus hyalinatus</i> (Smith 1842)	X	X	X	Poly.	Soli.	R	S	tard.
<i>Hylaeus incongruus</i> (Förster 1871)	X			Poly.	Soli.	R	S	mi.
<i>Hylaeus leptocephalus</i> (Morawitz 1870)			X					
<i>Hylaeus pictipes</i> (Nylander 1852)	X		X	Poly.	Soli.	R	S	tard.
<i>Hylaeus punctatus</i> (Brullé 1832)	X	X	X	Poly.	Soli.	R	S	mi.

<i>Hylaeus signatus</i> (Panzer 1798)	X		X	Oligo.	Soli.	R	S	mi.
<i>Hylaeus variegatus</i> (Fabricius 1798)	X			Poly.	Soli.	T	S	tard.

HALICTIDAE

<i>Halictus compressus</i> (Walckenaer 1802)			X					
<i>Halictus</i> gr. <i>simplex</i> (Blüthgen 1923)	X	X	X	Poly.	Soli.	T	S	mi.
<i>Halictus langobardicus</i> (Blüthgen 1944)	X		X		Soli.	T	S	tard.
<i>Halictus maculatus</i> (Smith 1848)	X			Poly.	PrEusoc.	T	S	tard.
<i>Halictus scabiosae</i> (Rossi 1790)	X	X	X	Poly.	PrEusoc.	T	M	mi.
<i>Halictus subauratus</i> (Rossi 1792)	X	X	X	Poly.	PrEusoc.	T	S	mi.
<i>Halictus tumulorum</i> (Linnaeus 1758)	X	X	X	Poly.	PrEusoc.	T	S	préc.
<i>Lasioglossum bluethgeni</i> (Ebmer 1971)	X	X		Poly.	Soli.	T	S	mi.
<i>Lasioglossum calceatum</i> (Scopoli 1763)	X	X	X	Poly.	PrEusoc.	T	S	préc.
<i>Lasioglossum cupromicans</i> (Pérez 1903)	X			Poly.	Soli.	T	S	tard.
<i>Lasioglossum fulvicorne</i> (Kirby 1802)	X			Poly.	Soli.	T	S	préc.
<i>Lasioglossum glabriusculum</i> (Morawitz 1872)	X			Poly.	PrEusoc.	T	S	mi.
<i>Lasioglossum griseolum</i> (Morawitz 1872)	X			Poly.	Soli.	T	S	tard.
<i>Lasioglossum laticeps</i> (Schenk 1868)	X	X	X	Poly.	PrEusoc.	T	S	préc.
<i>Lasioglossum leucopus</i> (Kirby 1802)			X					
<i>Lasioglossum leucozonium</i> (Schrank 1781)	X	X	X	Oligo.	Soli.	T	S	mi.
<i>Lasioglossum limbellum</i> (Morawitz 1876)	X	X	X	Poly.	Soli.	T	S	tard.
<i>Lasioglossum malachurum</i> (Kirby 1802)	X	X	X	Poly.	PrEusoc.	T	S	préc.
<i>Lasioglossum marginatum</i> (Brullé 1832)	X			Poly.	Soli.	T	S	préc.
<i>Lasioglossum minutissimum</i> (Kirby 1802)	X	X		Poly.	Soli.	T	S	mi.
<i>Lasioglossum morio</i> (Fabricius 1793)	X	X	X	Poly.	PrEusoc.	T	S	préc.
<i>Lasioglossum nitidiusculum</i> (Kirby 1802)	X	X		Poly.	Soli.	T	S	préc.
<i>Lasioglossum nitidulum</i> (Fabricius 1804)	X	X	X	Poly.	Soli.	T	S	préc.
<i>Lasioglossum pallens</i> (Brullé 1832)	X	X		Poly.	Soli.	T	S	préc.
<i>Lasioglossum pauxillum</i> (Schenck 1853)	X	X	X	Poly.	PrEusoc.	T	S	préc.
<i>Lasioglossum politum</i> (Schenck 1853)	X	X	X	Poly.	PrEusoc.	T	S	préc.
<i>Lasioglossum pygmaeum</i> (Schenck 1853)	X	X	X	Poly.	Soli.	T	S	préc.
<i>Lasioglossum sabulosum</i> (Morawitz 1891)	X	X	X	Poly.	Soli.	T	S	préc.
<i>Lasioglossum sexnotatum</i> (Kirby 1802)			X					
<i>Lasioglossum subhirtum</i> (Lepeletier 1841)	X			Poly.	Soli.	T	S	mi.
<i>Lasioglossum villosulum</i> (Kirby 1802)	X	X	X	Poly.	Soli.	T	S	préc.
<i>Sphecodes crassus</i> (Thomson 1870)	X			Clepto.	Soli.	T	S	tard.
<i>Sphecodes ephippius</i> (Linnaeus 1767)	X			Clepto.	Soli.	T	S	préc.
<i>Sphecodes ferruginatus</i> (Hagens 1882)	X	X		Clepto.	Soli.	T	S	tard.
<i>Sphecodes gibbus</i> (Linnaeus 1758)	X			Clepto.	Soli.	T	S	tard.
<i>Sphecodes monilicornis</i> (Kirby 1802)			X					
<i>Sphecodes niger</i> (Hagens 1874)	X		X	Clepto.	Soli.	T	S	mi.
<i>Sphecodes pseudofasciatus</i> (Blüthgen 1925)	X			Clepto.	Soli.	T	S	tard.
<i>Sphecodes puncticeps</i> (Thomson 1870)	X			Clepto.	Soli.	T	S	tard.

MEGACHILIDAE

<i>Anthidiellum strigatum</i> (Panzer 1805)	X			Poly.	Soli.	C	M	tard.
<i>Anthidium manicatum</i> (Linnaeus 1758)	X	X	X	Poly.	Soli.	C	L	mi.
<i>Anthidium oblongatum</i> (Illiger 1806)	X			Oligo.	Soli.	C	M	tard.
<i>Anthidium septemspinosum</i> (Lepeletier 1841)	X	X	X	Poly.	Soli.	C	L	mi.
<i>Chelostoma campanularum</i> (Kirby 1802)	X	X		Oligo.	Soli.	C-R	S	mi.
<i>Chelostoma florissomme</i> (Linnaeus 1758)			X					

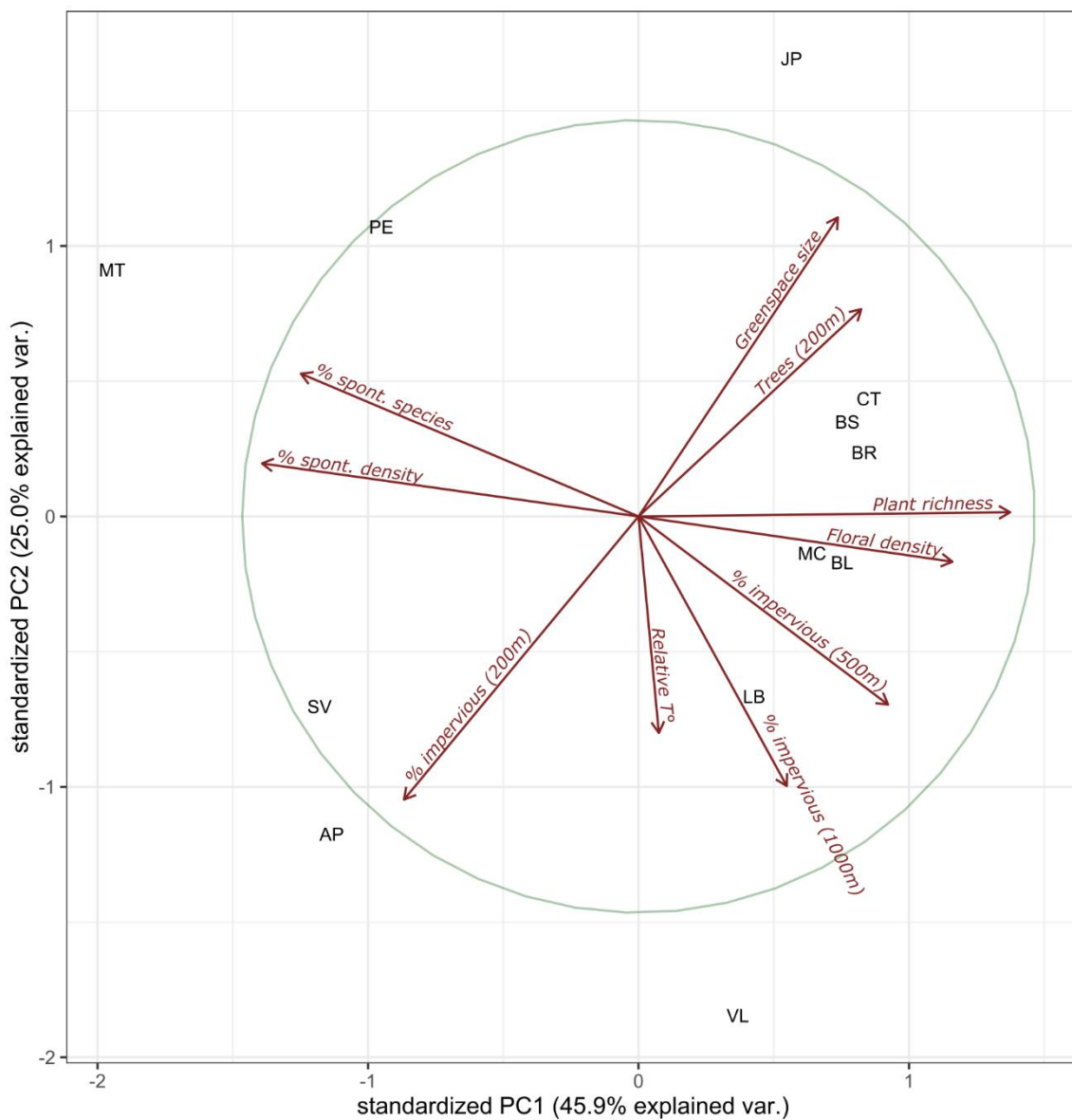
<i>Chelostoma rapunculi</i> (Lepeletier 1841)	X	X		Oligo.	Soli.	C-R	S	mi.
<i>Coelioxys inermis</i> (Kirby 1802)	X		X	Clepto.	Soli.	C	M	mi.
<i>Heriades crenulata</i> (Nylander 1856)	X	X		Oligo.	Soli.	C-R	S	tard.
<i>Heriades truncorum</i> (Linnaeus 1758)	X	X	X	Oligo.	Soli.	C-R	S	tard.
<i>Hoplitis adunca</i> (Panzer 1798)	X	X		Oligo.	Soli.	C-R	S	mi.
<i>Hoplitis leucomelana</i> (Kirby 1802)	X			Poly.	Soli.	R	S	mi.
<i>Megachile centuncularis</i> (Linnaeus 1758)	X	X	X	Poly.	Soli.	C	M	mi.
<i>Megachile ericetorum</i> (Lepeletier 1841)	X	X		Oligo.	Soli.	C	L	mi.
<i>Megachile lagopoda</i> (Linnaeus 1760)	X	X	X	Poly.	Soli.	C	L	mi.
<i>Megachile leachella</i> (Curtis 1828)		X						
<i>Megachile maritima</i> (Kirby 1802)	X			Poly.	Soli.	C	L	mi.
<i>Megachile rotundata</i> (Fabricius 1793)	X	X		Poly.	Soli.	C	M	mi.
<i>Megachile willughbiella</i> (Kirby 1802)	X	X	X	Poly.	Soli.	C	L	mi.
<i>Osmia bicornis</i> (Linnaeus 1758)	X	X	X	Poly.	Soli.	C	L	préc.
<i>Osmia caerulescens</i> (Linnaeus 1758)	X	X	X	Poly.	Soli.	C	M	mi.
<i>Osmia cornuta</i> (Latreille 1805)	X	X	X	Poly.	Soli.	C	L	préc.
<i>Osmia niveata</i> (Fabricius 1804)		X						
<i>Osmia spinulosa</i> (Kirby 1802)			X					
<i>Pseudoanthidium nanum</i> (Mocsáry 1881)	X			Oligo.	Soli.	C	M	tard.
<i>Stelis punctulatissima</i> (Kirby 1802)	X		X	Clepto.	Soli.	C	M	mi.
MELITTIDAE								
<i>Macropis europaea</i> (Warncke 1973)	X			Oligo.	Soli.	T	M	tard.
<i>Melitta leporina</i> (Panzer 1799)	X	X		Oligo.	Soli.	T	M	tard.

Annexe 2. Liste mise à jour des espèces de syrphes inventoriées à Paris *intramuros*, lors d'une étude récente publiée dans la littérature scientifique (« Biblio. » : Speight et al., 2018) et dans des rapports d'expertise (« Exp. » : Ferrand et al., 2014).

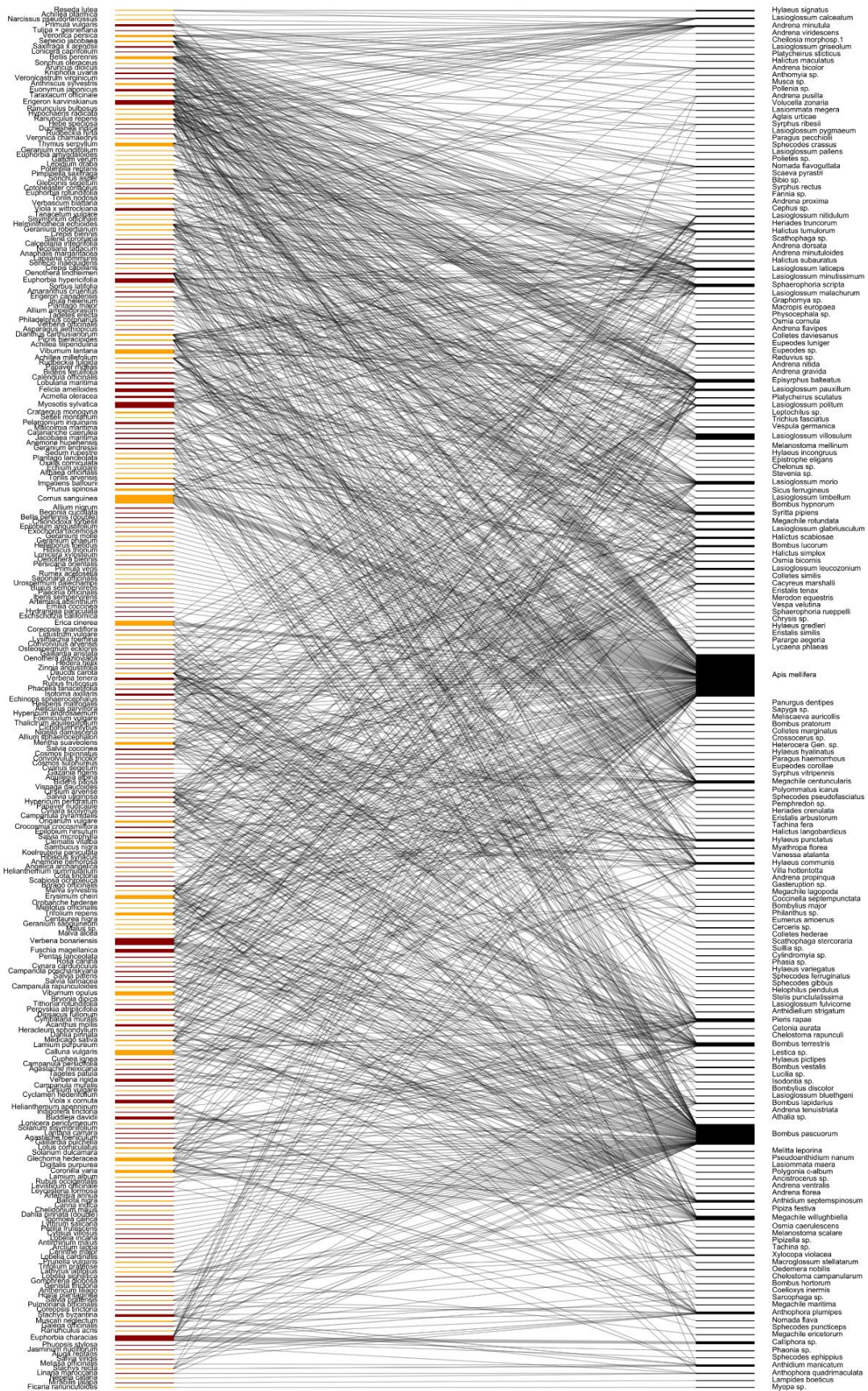
Species	Thèse	Biblio.	Exp.
SYRPHIDAE			
<i>Baccha elongata</i> (Fabricius 1775)			X
<i>Cheilosia caerulescens</i> (Meigen 1822)			X
<i>Cheilosia grossa</i> (Fallén 1817)	X		
<i>Cheilosia latifrons</i> (Zetterstedt 1843)			X
<i>Cheilosia vernalis</i> (Fallén 1817)			X
<i>Cheilosia vulpina</i> (Meigen 1822)			X
<i>Dasysyrphus albostriatus</i> (Fallén 1817)	X		X
<i>Epistrophe eligans</i> (Harris 1780)	X		X
<i>Epistrophe nitidicollis</i> (Meigen 1822)	X		X
<i>Episyrphus balteatus</i> (De Geer 1776)	X		X
<i>Eristalis arbustorum</i> (Linnaeus 1758)	X		X
<i>Eristalis pertinax</i> (Scopoli 1763)			X
<i>Eristalis similis</i> (Fallén 1817)	X		
<i>Eristalis tenax</i> (Linnaeus 1758)	X		X
<i>Eumerus amoenus</i> (Loew 1848)	X		X
<i>Eumerus funeralis</i> (Meigen 1822)	X		X

<i>Eupeodes cf. bucculatus</i> (Rondani 1857)			X
<i>Eupeodes corollae</i> (Fabricius 1794)	X		X
<i>Eupeodes luniger</i> (Meigen 1822)	X		X
<i>Helophilus pendulus</i> (Linnaeus 1758)	X		X
<i>Helophilus trivittatus</i> (Fabricius 1805)			X
<i>Heringia heringi</i> (Zetterstedt 1843)			X
<i>Melanostoma mellinum</i> (Linnaeus 1758)	X		X
<i>Melanostoma scalare</i> (Fabricius 1794)	X		X
<i>Meligramma cincta</i> (Fallén 1817)			X
<i>Meliscaeva auricollis</i> (Meigen 1822)	X		X
<i>Merodon equestris</i> (Fabricius 1794)	X		X
<i>Myathropa florea</i> (Linnaeus 1758)	X	X	X
<i>Neoascia podagrica</i> (Fabricius 1775)	X		X
<i>Neocnemodon vitripennis</i> (Meigen 1822)	X		
<i>Paragus haemorrhous</i> (Meigen 1822)	X		X
<i>Paragus pecchiolii</i> (Rondani 1857)	X		X
<i>Paragus quadrifasciatus</i> (Meigen 1822)	X		X
<i>Pipiza festiva</i> (Meigen 1822)	X		X
<i>Pipizella annulata</i> (Macquart 1829)			X
<i>Pipizella viduata</i> (Linnaeus 1758)			X
<i>Platycheirus albimanus</i> (Fabricius 1781)	X		X
<i>Platycheirus clypeatus</i> (Meigen 1822)			X
<i>Platycheirus scutatus</i> (Meigen 1822)	X	X	X
<i>Platycheirus sticticus</i> (Meigen 1822)	X		
<i>Pocota personata</i> (Harris 1780)		X	
<i>Scaeva pyrastris</i> (Linnaeus 1758)	X		X
<i>Sphaerophoria rueppelli</i> (Wiedemann 1830)	X		
<i>Sphaerophoria scripta</i> (Linnaeus 1758)	X		X
<i>Syritta pipiens</i> (Linnaeus 1758)	X		X
<i>Syrphus rectus</i> (Osten-Sacken 1877)	X		
<i>Syrphus ribesii</i> (Linnaeus 1758)	X		X
<i>Syrphus vitripennis</i> (Meigen 1822)	X		X
<i>Volucella inanis</i> (Linnaeus 1758)			X
<i>Volucella zonaria</i> (Poda 1761)	X		X
<i>Xanthogramma dives</i> (Rondani 1857)	X		X
<i>Xylota ignava</i> (Panzer 1798)		X	
<i>Xylota segnis</i> (Linnaeus 1758)			X

Annexe 3. Analyse en composantes principales des caractéristiques environnementales des douze espaces verts étudiés en 2019-2020, telles que présentées dans la Table 4. 1. La projection représentée, selon les composantes principales 1 et 2, rend compte de 70,9% de la variance. Variables (sens horaire, depuis le haut): surface des espaces verts ; nombre d'arbres entomophiles (rayon de 200m), richesse spécifique des plantes à fleurs ; densité d'unités florales ; pourcentage de surfaces imperméabilisées (rayons de 500m, puis 1000m, puis 200m) ; température relative à la moyenne parisienne lors d'un épisode caniculaire (« nuit tropicale ») ; pourcentage de la densité florale représentée par des plantes spontanées ; pourcentage de la richesse spécifique florale représentée par des plantes spontanées. Une attention particulière a été donnée à la multicolinéarité de certaines variables dans les analyses du Chapitre 4.



Annexe 4. Représentation du réseau d'interaction complet observé en 2019-2020 dans les douze espaces verts étudiés à Paris *intramuros*. Droite : variétés de plantes (rouge : exotique, orange : indigène, cf. Chapitre 5, largeur proportionnelle à l'abondance des fleurs). Gauche : espèces d'insectes pollinisateurs (largeur proportionnelle à l'abondance des interactions).



Annexe 5. Liste des variétés de plantes à fleurs inventoriées à Paris en 2019-2020. Pour chacune est indiquée l'origine (E: exotique, I: indigène ; arch.: archaeophyte, hort.: variété horticole, nat.: naturalisée, inv.: exotique envahissante), son type de gestion (P: plantée, S: spontanée, SubS: subsponnée), le nombre total de visites de pollinisateurs, le nombre total d'unités florales décomptées et le nombre de taxons de pollinisateurs en interaction.

Variété de plante	Origine	Gestion	Nombre de visites	Nombre d'unités florales	Nombre de taxons de pollinisateurs
<i>Acanthus mollis</i>	E	P	13	523	4
<i>Achillea filipendulina</i>	E	SubS	6	14	4
<i>Achillea millefolium</i>	I	S	22	80	17
<i>Achillea ptarmica</i>	I	P	2		1
<i>Acmella oleracea</i>	E	P	9	512	3
<i>Aesculus parviflora</i>	E	P	20	10	6
<i>Agastache foeniculum</i>	E	P	3		2
<i>Agastache mexicana</i>	E	P	6	111	2
<i>Ageratum houstonianum</i>	E	P	0	160	0
<i>Ajuga reptans</i>	I	S	1		1
<i>Alliaria petiolata</i>	I	S	0	53	0
<i>Allium ampeloprasum</i>	E	P	4	1	3
<i>Allium nigrum</i>	E	P	6	115	0
<i>Allium sphaerocephalon</i>	I	P	4		3
<i>Althaea officinalis</i>	I (arch.)	S	7	35	1
<i>Amaranthus cruentus</i>	E	SubS	1	165	1
<i>Amaryllis belladonna</i>	E	P	0	13	0
<i>Anacamptis pyramidalis</i>	I	S	0	8	0
<i>Anaphalis margaritacea</i>	E	P	3		3
<i>Anemone blanda</i>	E	SubS	0	30	0
<i>Anemone hupehensis</i>	E	P	3		2
<i>Anemone nemorosa</i>	I	S	1	1	1
<i>Anemone x blanda</i>	E (hort.)	P	0	2	0
<i>Angelica archangelica</i>	E	P	1		1
<i>Anthemis cotula</i>	I	P	0	6	0
<i>Anthericum liliago</i>	I	P	1	5	1
<i>Anthriscus sylvestris</i>	I	S	20	368	9
<i>Antirrhinum majus</i>	E	P	2		1
<i>Aquilegia alpina</i>	E	P	3	16	1
<i>Aquilegia vulgaris</i>	I	P	0	8	0
<i>Arabis caucasica</i>	E	P	0	41	0
<i>Arctium lappa</i>	I	S	2	2	1
<i>Artemisia absinthium</i>	I (arch.)	S	2		0
<i>Artemisia annua</i>	E (nat.)	S	1		1
<i>Aruncus dioicus</i>	E	P	11		6
<i>Asparagus aethiopicus</i>	E	P	2		1
<i>Ballota nigra</i>	I	S	4	52	1
<i>Begonia cucullata</i>	E	P	1	30	0
<i>Begonia x samperflorens</i>	E	P	0	136	0
<i>Bellis perennis</i>	I	S	46	845	24
<i>Bellis perennis</i> (double)	E (hort.)	P	1	28	0
<i>Berberis aquifolium</i>	E (inv.)	P	0	7	0
<i>Bidens ferulifolia</i>	E	P	15	281	7
<i>Bidens pilosa</i>	E	P	10	100	4
<i>Borago officinalis</i>	E	SubS	64	86	9
<i>Brunnera macrophylla</i>	E	P	0	69	0
<i>Bryonia dioica</i>	I	S	15	15	2
<i>Buddleja davidii</i>	E (inv.)	P	11	978	2
<i>Buxus sempervirens</i>	I (arch.)	S	5		0
<i>Calceolaria integrifolia</i>	E	P	6	35	4
<i>Calendula officinalis</i>	E	P	2	17	1
<i>Calluna vulgaris</i>	I	P	4	2 959	2
<i>Campanula medium</i>	E	P	0	9	0
<i>Campanula muralis</i>	E	P	2		1
<i>Campanula persicifolia</i>	I	P	7	1	3
<i>Campanula poscharskyana</i>	E	P	9	147	2
<i>Campanula pyramidalis</i>	E	P	24		4
<i>Campanula rapunculoides</i>	I (arch.)	S	5	12	4

<i>Canna indica</i>	E	P	1	25	1
<i>Cardamine hirsuta</i>	I	S	0	10	0
<i>Catananche caerulea</i>	E	SubS	12	90	5
<i>Centaurea nigra</i>	I	S	13		5
<i>Centranthus ruber</i>	I (arch.)	SubS	0	112	0
<i>Cerithe major</i>	E	P	2		1
<i>Chaerophyllum temulum</i>	I	S	0	34	0
<i>Chelidonium majus</i>	I	S	1		1
<i>Chionodoxa forbesii</i>	E	P	1	2	0
<i>Cichorium intybus</i>	I	S	6		4
<i>Cirsium arvense</i>	I	S	17	6	11
<i>Cirsium vulgare</i>	I	S	1		1
<i>Clematis vitalba</i>	I	S	5		3
<i>Clematis viticella</i>	E	P	0	7	0
<i>Colchicum autumnale</i>	I	P	0	1	0
<i>Convolvulus arvensis</i>	I	S	14	22	5
<i>Convolvulus tricolor</i>	E	P	1	18	1
<i>Coreopsis grandiflora</i>	E	P	8		3
<i>Coreopsis tinctoria</i>	E	P	2	33	1
<i>Cornus florida</i>	E	P	0	17	0
<i>Cornus kousa</i>	E	P	0	10	0
<i>Cornus sanguinea</i>	I	P	91	10 425	8
<i>Coronilla varia</i>	I	S	41	1 036	7
<i>Cosmos bipinnatus</i>	E	P	11	41	6
<i>Cosmos sulphureus</i>	E	P	1	11	1
<i>Cota tinctoria</i>	E (nat.)	SubS	2		1
<i>Cotoneaster coriaceus</i>	E	P	3	136	1
<i>Crataegus monogyna</i>	I	P	9	287	4
<i>Crepis biennis</i>	I	S	13	1	7
<i>Crepis capillaris</i>	I	S	6	25	4
<i>Crococsmia crocosmiiflora</i>	E	P	8	162	2
<i>Cuphea ignea</i>	E	P	2	94	2
<i>Cyanus segetum</i>	I	S	1		1
<i>Cyclamen hederifolium</i>	E	SubS	1	18	1
<i>Cymbalaria muralis</i>	I	S	3		2
<i>Cynara cardunculus</i>	E	P	9		5
<i>Cynara scolymus</i>	E	P	6		2
<i>Cytisus villosus</i>	E	P	3		1
<i>Dahlia pinnata</i>	E	P	11	8	1
<i>Dahlia pinnata</i> (double)	E	P	1		1
<i>Daucus carota</i>	I	S	52	31	21
<i>Delphinium elatum</i>	E	P	0	6	0
<i>Dianthus barbatus</i>	E	P	0	592	0
<i>Dianthus carthusianorum</i>	I	S	52	281	16
<i>Digitalis purpurea</i>	I	P	5		3
<i>Dipsacus fullonum</i>	I	S	15	4	8
<i>Duchesnea indica</i>	E (nat.)	S	2		2
<i>Echinops sphaerocephalus</i>	E	P	17		7
<i>Echium vulgare</i>	I	S	5	39	2
<i>Emilia coccinea</i>	E	P	2		0
<i>Epilobium angustifolium</i>	I	P	1	2	0
<i>Epilobium ciliatum</i>	E (nat.)	S	0	4	0
<i>Epilobium hirsutum</i>	I	S	6	11	3
<i>Erica cinerea</i>	I	P	9	2 425	2
<i>Erigeron annuus</i>	E (inv.)	S	0	4	0
<i>Erigeron canadensis</i>	E (inv.)	S	27	42	10
<i>Erigeron karvinskianus</i>	E	P	85	2 129	21
<i>Erinus alpinus</i>	E	P	0	3	0
<i>Erodium cicutarium</i>	I	S	0	28	0
<i>Erysimum cheiri</i>	I (arch.)	SubS	12	1 444	6
<i>Eschscholzia californica</i>	E	P	3	1	3
<i>Euonymus japonicus</i>	E	P	20	615	12
<i>Euphorbia amygdaloides</i>	I	P	8		7
<i>Euphorbia characias</i>	E	P	78	3 213	14
<i>Euphorbia hypericifolia</i>	E	P	21	1 946	11
<i>Euphorbia rotundifolia</i>	E	P	5		3
<i>Exochorda racemosa</i>	E	P	1	20	0
<i>Fallopia convolvulus</i>	I	S	0	223	0
<i>Felicia amelloides</i>	E	P	15	1 194	11
<i>Ficaria ranunculoides</i>	I	S	1	1	1
<i>Foeniculum vulgare</i>	I (arch.)	SubS	16	104	7

<i>Fuschia magellanica</i>	E	P	38	1 405	7
<i>Gaillardia aristata</i>	E	P	27	68	2
<i>Gaillardia pulchella</i>	E	P	2	22	2
<i>Galega officinalis</i>	E (inv.)	S	4	34	2
<i>Galium aparine</i>	I	S	0	10	0
<i>Galium verum</i>	I	S	1		1
<i>Gazania rigens</i>	E	P	1	2	1
<i>Genista tinctoria</i>	I	P	2		1
<i>Geranium dissectum</i>	I	S	0	39	0
<i>Geranium endressii</i>	E	P	10	210	8
<i>Geranium molle</i>	I	S	1	25	0
<i>Geranium phaeum</i>	E	P	4	10	0
<i>Geranium robertianum</i>	I	S	14	140	5
<i>Geranium rotundifolium</i>	I	S	2	1	1
<i>Geranium sanguineum</i>	I	P	11	53	8
<i>Geum coccineum</i>	E	P	0	5	0
<i>Geum urbanum</i>	I	S	0	13	0
<i>Glebionis segetum</i>	I	S	4		3
<i>Glechoma hederacea</i>	I	S	24	1 385	7
<i>Gomphrena globosa</i>	E	P	2	27	2
<i>Hebe speciosa</i>	E	P	55		10
<i>Hedera helix</i>	I	S	10	8	6
<i>Helianthemum apenninum</i>	I	S	3		2
<i>Helianthemum nummularium</i>	I	P	2	2	1
<i>Helleborus foetidus</i>	I	P	1	8	0
<i>Helleborus x ericsmithii</i>	E	P	0	94	0
<i>Helminthotheca echioides</i>	I	S	171	168	21
<i>Heracleum sphondylium</i>	I	S	7	9	6
<i>Hesperis matronalis</i>	I (arch.)	S	2	41	2
<i>Heuchera sanguinea</i>	E	P	0	692	0
<i>Hibiscus syriacus</i>	E	P	23		5
<i>Hibiscus trionum</i>	E	P	1	5	0
<i>Himantoglossum hircinum</i>	I	S	0	38	0
<i>Honorius nutans</i>	E	SubS	0	1	0
<i>Hosta plantaginea</i>	E	P	2	14	2
<i>Hyacinthus orientalis</i>	E	P	0	37	0
<i>Hydrangea paniculata</i>	E	P	2	34	0
<i>Hypericum androsaemum</i>	I	P	11		2
<i>Hypericum perforatum</i>	I	S	22	18	13
<i>Hypochaeris radicata</i>	I	S	55	69	16
<i>Iberis sempervirens</i>	E	P	3	18	0
<i>Impatiens balfourii</i>	E (inv.)	P	28	291	6
<i>Impatiens walleriana</i>	E	P	0	21	0
<i>Indigofera tinctoria</i>	E	P	17		4
<i>Inula helenium</i>	I (arch.)	S	5		3
<i>Ipomoea cairica</i>	E	P	1	2	1
<i>Iris germanica</i>	E	P	0	2	0
<i>Isotoma axillaris</i>	E	P	5	440	2
<i>Jacobaea maritima</i>	E	P	29	222	8
<i>Jasminum nudiflorum</i>	E	P	14		2
<i>Kniphofia uvaria</i>	E	P	24	300	3
<i>Koelreuteria paniculata</i>	E	P	7		4
<i>Lactuca serriola</i>	I	S	0	4	0
<i>Lamium album</i>	I	S	9	33	2
<i>Lamium purpureum</i>	I	S	5	23	4
<i>Lantana camara</i>	E	P	5	89	2
<i>Lapsana communis</i>	I	S	11	8	7
<i>Lathyrus latifolius</i>	I (arch.)	S	27	23	7
<i>Lepidium draba</i>	I (arch.)	S	1		1
<i>Levisticum officinale</i>	E	SubS	2		2
<i>Leycesteria formosa</i>	E	P	9	59	1
<i>Ligustrum vulgare</i>	I	P	12	170	2
<i>Linaria maroccana</i>	E	P	4	30	2
<i>Linaria vulgaris</i>	I	S	0	55	0
<i>Lobelia cardinalis</i>	E	P	2	14	1
<i>Lobelia erinus</i>	E	P	0	3	0
<i>Lobelia incana</i>	E	P	3	48	1
<i>Lobelia siphilitica</i>	E	P	2	83	2
<i>Lobularia maritima</i>	E	SubS	2	519	1
<i>Lonicera caprifolium</i>	E (nat.)	SubS	12		4
<i>Lonicera periclymenum</i>	I	S	2		2

<i>Lonicera xylosteum</i>	I	P	1		0
<i>Lotus corniculatus</i>	I	S	47	254	11
<i>Lysimachia arvensis</i>	I	S	0	2	0
<i>Lysimachia foemina</i>	I	P	2	13	2
<i>Lysimachia thyrsoiflora</i>	E	P	0	2	0
<i>Lythrum salicaria</i>	I	P	1		1
<i>Malcolmia maritima</i>	E	P	2		2
<i>Malus</i> sp	I	P	3		0
<i>Malva alcea</i>	I	P	2		1
<i>Malva sylvestris</i>	I	S	38	8	14
<i>Matthiola incana</i>	E	P	0	53	0
<i>Matthiola incana</i> (double)	E (hort.)	P	0	28	0
<i>Medicago arabica</i>	I	S	0	3	0
<i>Medicago lupulina</i>	I (arch.)	S	0	100	0
<i>Medicago sativa</i>	I (arch.)	S	59	206	13
<i>Melilotus officinalis</i>	I	S	15		6
<i>Melissa officinalis</i>	E	P	2		2
<i>Mentha suaveolens</i>	I	P	17	708	10
<i>Mirabilis jalapa</i>	E	SubS	1	9	1
<i>Muscari neglectum</i>	I	S	2	121	2
<i>Myosotis arvensis</i>	I	S	0	21	0
<i>Myosotis sylvatica</i>	E	P	12	3 705	6
<i>Narcissus pseudonarcissus</i>	I	P	4	33	3
<i>Narcissus pseudonarcissus</i> (double)	E (hort.)	P	0	9	0
<i>Nepeta cataria</i>	I	P	2		1
<i>Nicotiana tabacum</i>	E	P	6	199	2
<i>Nicotiana x alata</i>	E	P	0	6	0
<i>Nigella damascena</i>	E	P	4	22	1
<i>Oenothera biennis</i>	E (nat.)	S	4	2	0
<i>Oenothera glazioviana</i>	E (nat.)	S	18	2	7
<i>Oenothera lindheimeri</i>	E	P	68	305	23
<i>Origanum vulgare</i>	I	P	27	472	9
<i>Orlaya grandifolia</i>	I	P	0	1	0
<i>Orobanche hederæ</i>	I	S	4	101	3
<i>Osteospermum ecklonis</i>	E	P	4	47	3
<i>Oxalis corniculata</i>	I (arch.)	S	4	9	4
<i>Paeonia officinalis</i>	E	P	5		0
<i>Papaver nudicaule</i>	E	P	4	17	2
<i>Papaver rhoeas</i>	I	S	3	4	2
<i>Pelargonium inquinans</i>	E	P	11	479	2
<i>Pelargonium x hortorum</i>	E	P	0	45	0
<i>Pentas lanceolata</i>	E	P	4	130	2
<i>Perilla frutescens</i>	E	P	1		1
<i>Perovskia atriplicifolia</i>	E	P	47	535	6
<i>Persicaria orientalis</i>	E	P	1	24	0
<i>Petunia axillaris</i>	E	P	0	26	0
<i>Phacelia tanacetifolia</i>	E	SubS	97	61	11
<i>Philadelphus coronarius</i>	E	P	1	5	1
<i>Phlomis herba venti</i>	E	P	0	18	0
<i>Phuopsis stylosa</i>	E	P	3	17	3
<i>Physostegia virginiana</i>	E	P	0	6	0
<i>Phytolacca acinosa</i>	E	P	0	28	0
<i>Picris hieracioides</i>	I	S	65	98	20
<i>Pimpinella saxifraga</i>	I	S	11		6
<i>Plantago lanceolata</i>	I	S	10	279	1
<i>Plantago major</i>	I	S	2	11	1
<i>Potentilla reptans</i>	I	S	50	94	19
<i>Primula veris</i>	I	S	1	94	0
<i>Primula vulgaris</i>	E (hort.)	P	3	572	3
<i>Primula vulgaris</i> (double)	E (hort.)	P	0	18	0
<i>Prunella vulgaris</i>	I	S	2	167	1
<i>Prunus spinosa</i>	I	P	12	558	5
<i>Pulmonaria officinalis</i>	E	P	3	33	2
<i>Ranunculus acris</i>	I	S	4	22	2
<i>Ranunculus bulbosus</i>	I	S	28	119	13
<i>Ranunculus repens</i>	I	S	31	215	17
<i>Reseda lutea</i>	I	S	20		3
<i>Rosa canina</i>	I	P	9	4	3
<i>Rubus fruticosus</i>	I	P	27	11	8
<i>Rubus occidentalis</i>	E	P	4	15	2
<i>Rudbeckia fulgida</i>	E	P	1	4	1

<i>Rudbeckia hirta</i>	E	P	27	52	12
<i>Rumex acetosella</i>	I	S	1		0
<i>Salvia coccinea</i>	E	P	28	246	6
<i>Salvia farinacea</i>	E	P	27	338	7
<i>Salvia involucrata</i>	E	P	0	27	0
<i>Salvia microphylla</i>	E	P	84	255	10
<i>Salvia patens</i>	E	P	25	42	3
<i>Salvia pratensis</i>	I	S	8	18	4
<i>Salvia splendens</i>	E	P	0	163	0
<i>Salvia uliginosa</i>	E	P	62	189	11
<i>Salvia viridis</i>	E	P	1	33	1
<i>Sambucus nigra</i>	I	P	2	541	1
<i>Sanguisorba minor</i>	I	S	0	12	0
<i>Saponaria officinalis</i>	I	S	1	8	0
<i>Saxifraga x arendsii</i>	E	P	1	254	1
<i>Scabiosa atropurpurea</i>	E	P	0	9	0
<i>Scabiosa ochroleuca</i>	E	P	4		3
<i>Sedum rupestre</i>	I	P	3	38	3
<i>Senecio inaequidens</i>	E (inv.)	S	4		2
<i>Senecio jacobaea</i>	I	S	47	185	24
<i>Seseli montanum</i>	I	S	1		1
<i>Silene coronaria</i>	E	P	2	47	2
<i>Sinapis arvensis</i>	I	S	0	4	0
<i>Sisymbrium officinale</i>	I	S	12	29	5
<i>Solanum dulcamara</i>	I	S	20	28	2
<i>Solanum nigrum</i>	I	S	0	1	0
<i>Solanum pimpinellifolium</i>	E	P	0	5	0
<i>Solanum sisymbriifolium</i>	E	P	16	22	5
<i>Sonchus asper</i>	I	S	5	9	3
<i>Sonchus oleraceus</i>	I	S	12	33	5
<i>Sorbus latifolia</i>	I	P	1		1
<i>Spergularia rubra</i>	I	S	0	2	0
<i>Stachys byzantina</i>	E	P	14	692	7
<i>Stachys recta</i>	I	S	37		5
<i>Sternbergia lutea</i>	E	P	0	2	0
<i>Symphyotrichum novi-belgi</i>	E	P	0	6	0
<i>Tagetes erecta</i>	E	P	2	23	1
<i>Tagetes patula</i>	E	P	4	87	2
<i>Tanacetum vulgare</i>	I	S	4		2
<i>Taraxacum officinale</i>	I	S	20	29	14
<i>Thalictrum aquilegifolium</i>	E	P	4	2	1
<i>Thymus serpyllum</i>	I	P	96	1 361	9
<i>Tithonia rotundifolia</i>	E	P	7		4
<i>Torilis arvensis</i>	I	S	9	227	7
<i>Torilis nodosa</i>	I (arch.)	S	6	330	4
<i>Trifolium dubium</i>	I	S	0	7	0
<i>Trifolium pratense</i>	I (arch.)	S	2	3	1
<i>Trifolium repens</i>	I (arch.)	S	116	879	8
<i>Tristagma uniflorum</i>	E	P	0	39	0
<i>Tropaeolum majus</i>	E	P	0	13	0
<i>Tulipa x gesneriana</i>	E	P	3	8	2
<i>Tulipa x gesneriana</i> (double)	E (hort.)	P	0	1	0
<i>Urospermum dalechampii</i>	E	SubS	1		0
<i>Urtica dioica</i>	I	S	0	12	0
<i>Verbascum blattaria</i>	I	P	8	9	4
<i>Verbascum thapsus</i>	I	P	0	27	0
<i>Verbena bonariensis</i>	E	P	116	5 087	15
<i>Verbena officinalis</i>	I	S	1		1
<i>Verbena rigida</i>	E	P	8	869	3
<i>Verbena tenera</i>	E	P	6	656	1
<i>Veronica chamaedrys</i>	I	S	1		1
<i>Veronica hederifolia</i>	I	S	0	10	0
<i>Veronica persica</i>	I (arch.)	S	20	421	12
<i>Veronicastrum virginicum</i>	E	P	27	130	13
<i>Viburnum lantana</i>	I	P	3	2 054	1
<i>Viburnum opulus</i>	I	P	2	1 680	1
<i>Viburnum tinus</i>	E	P	0	15	0
<i>Vicia sativa</i>	I	S	0	8	0
<i>Vicia sepium</i>	I	S	0	33	0
<i>Vinca minor</i>	I	S	0	3	0
<i>Viola x cornuta</i>	E (hort.)	P	12	1 289	4

<i>Viola x wittrockiana</i>	E (hort.)	P	9	719	8
<i>Visnaga daucooides</i>	E	SubS	16	6	7
<i>Zinnia angustifolia</i>	E	P	4	15	2
<i>Zinnia elegans</i>	E	P	0	6	0

TABLE DES FIGURES

Figure 0. 1. Carte mondiale des dépendances de l'agriculture à la pollinisation d'origine animale	6
Figure 0. 2. Réseau d'interaction plantes-pollinisateurs.....	10
Figure 0. 3. Réduction de la diversité des insectes pollinisateurs selon le niveau d'urbanisation.....	12
Figure 0. 4. Diversité des pollinisateurs en milieux naturel, agricole, périurbain, et urbain dense.	14
Figure 0. 5. Conséquences progressives de la fragmentation de l'habitat sur les pollinisateurs	16
Figure 0. 6. Filtrage fonctionnel des communautés d'abeilles sauvages en milieu urbain.....	17
Figure 0. 7. Désynchronisation entre un pollinisateur et ressources florales successives	19
Figure 0. 8. Diminution du turnover des espèces de plantes et de papillons en milieu urbanisé.....	21
Figure 0. 9. Répartition du couvert végétal et de l'îlot de chaleur urbain à Paris.....	25
Figure 0. 10. Histogramme des dimensions des espaces verts gérés par la Ville de Paris	26
Figure 1. 1. Plant-pollinator interaction networks in both habitats	40
Figure 1. 2. Traits variations throughout the year in both habitats.....	44
Figure 2. 1. Detail of the flowers of each focal plant species: <i>S. alba</i> and <i>L. corniculatus</i>	58
Figure 2. 2. Distribution of rural and urban sites	59
Figure 2. 3. Overall pollinator visitation rates.....	66
Figure 2. 4. Predicted pollinator visitation rates on <i>Sinapis alba</i>	68
Figure 2. 5. Predicted pollinator visitation rates on <i>Lotus corniculatus</i>	69
Figure 2. 6. Reproductive success estimators.....	70
Figure 3. 1. Distribution of the 12 surveyed green spaces in 2019-2020.....	84
Figure 3. 2. Seasonal distribution of insect occurrence	92
Figure 4. 1. Distribution map of survey sites	104
Figure 4. 2. Abundance and species richness of all pollinators in response to local drivers	111
Figure 4. 3. Abundance and species richness of all pollinators in response to a landscape driver	112
Figure 4. 4. db-RDA ordination of pollinator species	113
Figure 4. 5. Probability of occurrence of wild bee species in response to environmental variables	114
Figure 5. 1. Representation of the bipartite plant-pollinator networks over seasons.....	129
Figure 5. 2. Seasonal variations in flower resources and their attractiveness to pollinators	131
Figure 5. 3. Seasonal variations in plant-pollinator interactions at the plant species level	133
Figure 6. 1. Phénologies à l'échelle intraspécifique.....	150
Figure 6. 2. Turnover saisonnier des assemblages en milieu urbain et rural	151
Figure 6. 3. Turnover saisonnier des assemblages dans les espaces verts parisiens.....	152

TABLE DES TABLEAUX

Tableau 0. 1. Nombre estimé d'espèces de pollinisateurs.....	8
Table 1. 1. List of species in the two habitats.....	41
Table 1. 2. Equations of the models of traits variations through time	45
Table 2. 1. Proportions of land-use categories within a radius of 500m around the sites.....	60
Table 2. 2. Summary table of flowering periods <i>S. alba</i> and <i>L. corniculatus</i>	62
Table 2. 3. Summary table of visitation rates on the two plant species	67
Table 2. 4. Summary table of fruit set and seed set of the two plant species	72
Table 3. 1. Report on the 2019-2020 sampling of bee species in Parisian green spaces	86
Table 3. 2. Report on the 2019-2020 sampling of hoverfly species in Parisian green spaces	89
Table 4. 1. Landscape and local environmental characteristics of the survey sites	105
Table 4. 2. Best-fitting linear mixed models of pollinator abundance and species richness	112
Table 4. 3. Best-fitting generalized linear mixed model of bee species probability of occurrence	115
Table 5. 1. Seasonal variations in flower resources and attractiveness to pollinators at community level.....	132
Table 5. 2. Seasonal variations in plant-pollinator interactions structure at the plant species level.	134

TABLE DES ANNEXES

Appendix 1. 1. Rarefaction curves of insect pollinator species on both plant species, in both habitats.....	52
Appendix 1. 2. Mean comparison of diversity indices and Tukey post hoc test between habitats.....	52
Appendix 2. 1. Daily minimum temperatures in the urban and rural habitats.....	78
Appendix 3. 1. Additional information on the twelve surveyed green spaces	96
Appendix 3. 2. Species lists of Lepidoptera, Coleoptera and Diptera	97
Appendix 4. 1. Rarefaction curves across the 12 survey sites.....	119
Appendix 4. 2. Fourthcorner analysis assessing the presence-absence of bee species.....	119
Appendix 5. 1. Detailed information on the green spaces and their flower resources.	138
Appendix 5. 2. Variations of plant attractiveness to pollinators according to flower resource availability ...	139
Appendix 5. 3. Seasonal variations in plant-pollinator interactions properties at network level.	140
Appendix 5. 4. GLMM of the network-level seasonal variations in plant-pollinator interactions	140
Annexe 1. Liste mise à jour des espèces d'abeilles inventoriées à Paris intramuros.	183
Annexe 2. Liste mise à jour des espèces de syrphes inventoriées à Paris intramuros.....	186
Annexe 3. Analyse en composantes principales des douze espaces verts étudiés en 2019-2020	188
Annexe 4. Représentation du réseau d'interaction complet observé en 2019-2020 à Paris.....	189
Annexe 5. Liste des variétés de plantes à fleurs inventoriées à Paris en 2019-2020	190

Écologie et fonctionnement des communautés plantes-pollinisateurs en milieu urbain dense: l'exemple de la ville de Paris à travers les saisons

L'urbanisation est une des causes principales de l'érosion de la biodiversité. Ainsi, en ville, les organismes, et notamment les insectes pollinisateurs, sont soumis à de multiples contraintes. Au cours de cette thèse, nous avons caractérisé les communautés de pollinisateurs et leurs dynamiques saisonnières dans un paysage urbain dense, la ville de Paris, à travers des approches empiriques et standardisées. Nous avons d'abord exploré ce qui distingue ces communautés urbaines des communautés rurales, en nous intéressant à leurs diversités taxonomique et fonctionnelle, ainsi qu'à leur activité de butinage et l'efficacité de la pollinisation. Puis, nous avons approfondi la connaissance des pollinisateurs parisiens, en détaillant les facteurs environnementaux qui en déterminent l'abondance et la diversité. Enfin nous avons examiné la dynamique des interactions plantes-pollinisateurs et de leur structure au fil des saisons. Malgré sa densité, Paris abrite des communautés de pollinisateurs relativement riches et abondantes, capables d'assurer une pollinisation efficace de certaines plantes. Cependant, ces communautés sont contraintes par l'environnement urbain, et témoignent d'un filtrage fonctionnel. De plus, en ville, on assiste à l'atténuation des dynamiques saisonnières naturelles, en termes d'activité des pollinisateurs et d'assemblage fonctionnel. Les ressources florales jouent un rôle primordial dans le maintien de la diversité des pollinisateurs, en particulier grâce à la flore indigène et spontanée. Nous proposons des solutions, basées sur l'aménagement et la gestion des espaces verts, afin de promouvoir la biodiversité et la pollinisation en ville.

Mots clés : écologie urbaine ; pollinisation ; phénologie ; réseaux plantes-pollinisateurs ; îlot de chaleur ; gestion des espaces verts

Ecology and functioning of plant-pollinator communities in a dense urban environment: the city of Paris throughout the seasons

Urbanization is one of the main causes of biodiversity loss. Hence, organisms in the city, in particular insect pollinators, are subject to multiple constraints. In this thesis, we characterized pollinator communities and their seasonal dynamics in a dense urban landscape, the city of Paris, through empirical and standardized approaches. We first explored what distinguishes these urban communities from the rural ones, focusing on their taxonomic and functional diversity, as well as their foraging activity patterns and pollination efficiency. Then, we expanded our knowledge of Parisian pollinators, providing details on the environmental factors that determine their abundance and diversity. Finally, we investigated the dynamics of plant-pollinator interactions and their structure throughout the seasons. Despite its high density, Paris is home to relatively rich and abundant pollinator communities, which can provide efficient pollination of some plants. However, these communities are constrained by the urban environment, and undergo functional filtering. Moreover, in the city, natural seasonal dynamics are weakened both in terms of pollinator activity and functional assemblage. Flower resources play a key role in maintaining pollinator diversity, particularly through native and spontaneous flora. We provide design and management guidelines for green spaces, in order to promote biodiversity and pollination in cities.

Keywords: urban ecology ; pollination ; phenology ; plant-pollinator networks ; urban heat island ; greenspace management