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► To cite this version:

Alessandro Fisogni, Nina Hautekèete, Yves Piquot, Marion Brun, Cédric Vanappelghem, et al.. Seasonal trajectories of plant-pollinator interaction networks differ following phenological mismatches along an urbanization gradient. *Landscape and Urban Planning*, 2022, 226, pp.104512. 10.1016/j.landurbplan.2022.104512 . hal-04275135

HAL Id: hal-04275135

<https://hal.science/hal-04275135>

Submitted on 8 Nov 2023

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Title: Seasonal trajectories of plant-pollinator interaction networks differ following phenological mismatches along an urbanization gradient

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31 **1. Introduction**

32 Urbanization is one of the major global threats to pollinators and a main driver of plant-pollinator
33 interactions (Harrison and Winfree 2015; Nieto et al. 2015), although cities can be important
34 hotspots for pollinators (Baldock et al. 2015; Theodorou et al. 2020). Local microclimate variability
35 (Hamblin et al. 2018), the availability of nesting sites (Wray and Elle 2014), and the type and
36 availability of foraging resources (Hülsmann et al. 2015) can shape pollinator communities in urban
37 areas. Moreover, modifications of the urban climate and urban landscapes can drive changes of
38 plant phenophases and species distribution (Roetzer et al. 2000; Godefroid and Koedam 2007;
39 Wohlfahrt et al. 2019). Therefore, urban plant and pollinator communities can differ from
40 communities in (semi-)natural or rural areas in terms of phenology, abundance, richness and
41 composition (Deguines et al. 2012, 2016; Leong et al. 2016; Harrison et al. 2018).

42
43 A useful approach to studying effects of urbanization on plant and pollinator communities is to
44 study patterns of mutualistic interactions through the use of complex interaction networks. Studies
45 performed along diverse urban gradients have shown mixed results regarding the specialization of
46 interactions, reporting negative (Baldock et al. 2015), positive (Martins et al. 2017) or non-
47 significant (Theodorou et al. 2017) relationships of specialization with the degree of urbanization.
48 However, pollinators always visited a higher diversity of flowering plants, but proportionally fewer
49 of the available species, in more urbanized areas (Baldock et al. 2015; Martins et al. 2017;
50 Theodorou et al. 2017). In a study performed in France (Geslin et al. 2013), the number of
51 interactions decreased with increasing urbanization, while interactions were more evenly distributed
52 in urban than in suburban and agricultural areas. Contrastingly, in a similar study in Germany (Udy
53 et al. 2020), the number of interactions varied along the gradient depending on the taxonomic
54 groups considered, and interaction evenness decreased with increasing urbanization. These results
55 underline a marked regional variability, likely related to a variety of historical, geographical and
56 climatic factors. Moreover, Wenzel et al. (2020) suggested that differential responses to

57 urbanization gradients among studies might be explained by their design. However, while network-
58 level metrics such as these are useful to understand general patterns of species interactions, they
59 may overlook significant differences at lower structural levels (Baker et al. 2015). To date,
60 thorough analyses on species roles and on the distribution and diversity of their interactions within
61 plant-pollinator networks have not yet been performed in urban environments.

62

63 Plant-pollinator interaction networks are also highly dynamic in time (Olesen et al. 2008; Poisot et
64 al. 2015). Temporal changes in floral resource availability and pollinator abundance shape the
65 patterns of interactions and network topology (Bendel et al. 2019; Bramon Mora et al. 2020;
66 CaraDonna and Waser 2020; Guzman et al. 2021). In particular, species phenology is a major driver
67 of interaction networks, as it plays a key role in determining the probability and intensity of
68 interactions (Carter et al. 2018; de Manincor et al. 2020), the structure and properties of interaction
69 networks (Vázquez et al. 2009; Encinas-Viso et al. 2012; Arroyo-Correa et al. 2021), and the role of
70 species within networks (Ponisio et al. 2017). Any modification in the phenology of one or both
71 partners caused by external factors, such as the local climate, has therefore the potential to affect the
72 outcome of their interactions. However, empirical evidence of the effect of phenological changes on
73 the structure of plant-pollinator networks in urban environments has not been reported yet.

74

75 Urban areas can contain diverse floral resources and act as refuges for pollinators, thus offering
76 important opportunities for their conservation (Hülsmann et al. 2015, Hall et al. 2017). The study of
77 interaction networks can be a useful tool to guide and assess conservation and management
78 strategies (Kaiser-Bunbury et al. 2010a; Tylianakis et al. 2010). Describing the distribution and
79 diversity of interactions can help identify vulnerabilities and strengths of networks, and recommend
80 guidelines for the development of targeted conservation measures (Kaiser-Bunbury and Bluthgen
81 2015). Identifying species that interact directly or indirectly through shared partners with numerous
82 other species makes it possible to determine which plants or pollinators play central roles in

83 maintaining network connectivity and cohesion (Martín González et al. 2010). On the other hand,
84 identifying species with only one or a few interaction partners can be important for targeting
85 conservation actions to facilitate rare or specialist species. For example, careful selection of plant
86 species in urban environments (Garbuzov and Ratnieks 2014; Lowenstein et al. 2019; Staab et al.
87 2020) and the maintenance of diverse habitats (Baldock et al. 2019) can enhance the conservation of
88 urban pollinators.

89

90 Here we analyse how the structure of plant-pollinator interaction networks changed between spring
91 and summer along an urbanization gradient in the metropolitan area of Lille, France. Strong
92 phenological mismatches between plants and their pollinators have been previously observed along
93 this gradient, where flowering peaked significantly earlier in the season in more urbanized areas
94 while flight phenology did not differ among pollinator communities (Fisogni et al. 2020). Because
95 phenological mismatches can affect patterns of interactions between mutualistic partners, we expect
96 trends in network structure to change along the urbanization gradient according to the availability of
97 flower resources. Specifically, we ask (i) how does the structure of plant-pollinator interaction
98 networks change along an urbanization gradient? and (ii) how do species roles within networks and
99 patterns of interactions change through time along a gradient where the phenology of plant and
100 pollinators showed different responses? To survey comparable sites in terms of plant communities,
101 while differing in the urban environment, we compared sites that were managed by local
102 practitioners with standardized native plant seed mixes along a gradient of importance of
103 impervious surfaces. This is an emerging method of managing green spaces in cities, which allows
104 higher comparability among studies from different geographical areas.

105

106 To comprehensively understand the changes that have taken place in networks over space and time,
107 we approach these questions on multiple levels. First, we assess how general patterns of interaction
108 density and distribution (i.e., connectance, evenness, specialization) varied among networks. Such

109 an analysis at the macroscopic scale allows a direct comparison with the existing literature on urban
110 pollination networks (Geslin et al. 2013; Baldock et al. 2015; Theodorou et al. 2017; Martins et al.
111 2017; Udy et al. 2020). Second, we detail how species interactions are distributed within networks
112 by looking for species clusters. Such an analysis allows to highlight groups of species that interact
113 in similar ways and therefore potentially undergo similar ecological processes along the space-time
114 gradient. Third, we assess changes in the centrality and position of species within motifs, and in the
115 interaction paths between them within each network. Finally, we tackle how urbanization influences
116 α - and β -diversity of plants, pollinators, and their interactions. Considering different levels of
117 complexity allows us to get a more accurate picture of the spatio-temporal trajectories of interaction
118 networks along the urban gradient. We draw from our results to discuss implications for nature
119 conservation and land-use management in urban areas.

120

121 2. Methods

122 2.1. Study sites

123 This study was performed in the Métropole Européenne de Lille (MEL), in Northern France, an
124 area historically subject to prolonged and strong anthropogenic pressure (Toussaint et al. 2008;
125 Hautekète et al. 2015; Insee 2017). We collaborated with the MEL Parks and Gardens Services to
126 find meadows with public access that have been managed in the same way for at least two years
127 prior to our study conducted in 2017. We thus chose sites that had been sown between 2010 and
128 2015 with the same standardised seed mix including only native and perennial herbaceous plants
129 native to the region (purchased from Ecosem, Corroy-le-Grand, Belgium; list of species in Table
130 A1). Sites had different sizes and irregular shapes, and were sown throughout their surface with the
131 standardized seed mix (Table A2). All sites were left free to develop throughout the sampling
132 period until the beginning of July, when they were all mown for management purposes. Among the
133 available sites, we selected 12 sites about 1 km apart from each other to avoid overlapping flight
134 ranges for most pollinators, and equally divided them into three classes of urbanization (Fig. 1).
135 Classes were based on the percentage of impervious areas within a 500 m buffer around each site: a
136 low urbanization class (< 50 %), a medium urbanization class (between 50 % and 70 %), and a high
137 urbanization class (≥ 70 %). To standardize the measurement of urbanization degree among sites,
138 buffers were drawn around the edges of the sites (i.e., size and shape of sites did not affect the
139 surface considered within the buffers). A buffer of 500 m is sufficient to include the estimated
140 maximum foraging distance of most wild bees and hoverflies species (Wratten et al. 2003;
141 Zurbuchen et al. 2010; Wright et al. 2015), and comprises the maximum distance at which
142 successful pollen transfer may be expected in urban areas (Van Rossum and Triest 2010).
143 Impervious areas (i.e., buildings, roads, parking lots, commercial and industrial areas, railroads)
144 were defined at a 5 m resolution on the basis of GIS analysis (ArcGIS version 10.4, ESRI, 2011) of
145 a pre-existing land-use map for the *Métropole Européenne de Lille* (OCS2D, Agence de

146 développement et d'urbanisme de Lille Métropole (ADULM), 2016) and photo interpretation of
147 aerial photographs taken in 2015 (www.ppige-npdc.fr).

148

149 *2.2. Field sampling*

150 We visited each site every other week from the beginning of April to the end of June 2017, for a
151 total of 69 sampling events (six samplings per site, except three sites that were sampled five times
152 due to bad weather). The temporally limited sampling period was dictated by management measures
153 for urban green areas, where local practitioners usually mowed plants during summer (i.e., July) to
154 avoid an overgrowth of grasses and to favour blooming in the following season. We visited three
155 sites per day on four consecutive days, starting sampling trials around 11 am, 1 pm and 3 pm at
156 each site, respectively, to encompass daily variability of insect activity. The order of visits was
157 swapped among sites each sampling day to account for daily variability of temperatures and insect
158 behaviour. Sampling was carried out on days with low wind, low cloud cover and average air
159 temperatures higher than 15°C (April) or 20°C (May, June). The same two people sampled each site
160 for 45 minutes throughout the season, walking randomly throughout the site and capturing all bees
161 (Hymenoptera: Anthophila) and hoverflies (Diptera: Syrphidae) visiting open flowers, and
162 recording the observed interactions. We focused on these groups because they included the vast
163 majority of floral visitors in the study sites and are the major pollinators at middle European
164 latitudes (Ballantyne et al. 2017; Ollerton 2017), although other taxa might frequently visit plants in
165 urban areas (e.g., Baldock et al. 2019). Sampled insects were individually placed into plastic tubes
166 (Falcon, Dutscher) containing strips of paper soaked in ethyl acetate, and later pinned in the
167 laboratory. Each individual was identified at the genus level by AF and at the species level by
168 expert taxonomists (full list in the Acknowledgements section). Specimens are deposited at the EEP
169 laboratory at the University of Lille. Flowering plants were identified at the species level by AF,
170 NH and YP with the help of a dichotomous key (Lambinon et al. 2004).

171

172 2.3. Data analysis

173 2.3.1. Interaction matrix construction

174 All analyses were performed using R v. 3.4.3 (R Core Team 2019) and the associated script can be
175 found at <https://zenodo.org/record/5570297>. To analyse the spatial and temporal dimensions of
176 plant-pollinator networks, we constructed different weighted interaction matrices for bipartite
177 networks (i.e., networks comprising two levels of species which only interact between levels, not
178 within) in which the value in the cell at row ‘a’ and column ‘p’ represents the number of visits of
179 pollinator species ‘a’ to plant species ‘p’ in a given observation period. Because mean species
180 turnover between sites in the same urbanization class was low for both plants and pollinators (see
181 Table A3 for values and distributions), we aggregated data from the four study sites within each
182 urbanization class to increase the statistical robustness of network analyses. First, we built one
183 overall pollinator-by-plant visit matrix for each urbanization class considering the complete three-
184 month study period. Then, we built three monthly (April, May, June) pollinator-by-plant visit
185 matrices for each urbanization class. This subdivision was made to obtain robust networks
186 sufficiently dense to correctly represent the marked temporal changes of flowering phenology and
187 diversity previously observed along the studied gradient (Fisogni et al. 2020). Moreover, because
188 we only aggregated data collected from two consecutive sampling events within each month,
189 species turnover was low for both plants and pollinators (Table A3). Although some ‘forbidden
190 links’ (i.e., constraints due to the absence of species in urbanization classes at any given moment;
191 Jordano et al. 2003) were potentially created, these should only marginally affect the analyses used
192 here. The urbanization gradient was thus characterized by three overall networks (one per
193 urbanization level), and nine monthly networks (three per urbanization level), that allowed to
194 analyse changes in network structure and species roles over the time \times space dimensions here
195 considered.

196

197 2.3.2. Network-level metrics

198 For each network, we calculated three widely used metrics: (i) network connectance, i.e., the
199 proportion of realised links among all possible ones; (ii) interaction evenness of weighted links,
200 based on Shannon's diversity (Blüthgen et al. 2008); (iii) specialization at the whole network level
201 (H_2'), a Shannon entropy index that varies between 0 (complete generalization) and 1 (complete
202 specialization; Blüthgen et al. 2006). Network specialization was calculated using the R package
203 'bipartite' (Dormann et al. 2008). To evaluate if these metrics varied significantly across space
204 (urban classes) or time (months), we compared differences in observed values with those obtained
205 by permutation-based null models assuming random location or timing of visits: for each network
206 pair to compare, we pooled together the two networks, we kept constant the number of visits in each
207 one, and we re-sampled the visits by randomly shuffling them between the two networks (R script
208 available at <https://zenodo.org/record/5570297>). We then compared the observed absolute
209 difference in the metric of interest to its distribution given by 10,000 permutations of visits between
210 networks to look for significant differences. The P -values of these tests were obtained by
211 computing the permutation-based probability of drawing an absolute difference larger than the
212 observed value. These metrics describe general patterns of interactions within networks, and
213 underline fundamental structural properties of the entire plant-pollinator communities.

214

215 2.3.3. *Clustering of species in the network*

216 To analyse non-random associations of subgroups of species in the three urbanization classes (i.e.,
217 clusters of highly interacting species), we applied latent block models (LBMs) on weighted
218 networks using the R package 'blockmodels' (INRA and Leger 2015). LBMs are probability-based
219 models that allow to simultaneously cluster rows (here pollinator species) and columns (here plant
220 species) based on latent blocks which determine model parameters – in our case, the mean number
221 of visits per insect-plant pair following a Poisson distribution (Govaert and Nadif 2008; Keribin et
222 al. 2015; Thomas et al. 2015). LBMs are the most efficient method to retrieve the number and the
223 composition of subgroups in weighted bipartite networks (Leger et al. 2015). Following the

224 inference of blocks, a rearranged incidence matrix was generated for each time period and
225 urbanization class to highlight homogeneous blocks of plant and pollinator species. This analysis
226 shows how plants and pollinators are divided into subgroups including species that interact in a
227 similar way at any point in time and space.

228

229 *2.3.4. Species centrality within networks*

230 For each plant and pollinator species, we calculated their centrality using the eigenvector centrality
231 score (Bonacich 1972) in order to assess their position with respect to the whole network, using the
232 R package ‘igraph’ (Csardi and Nepusz 2006). This measure is a true node-centrality when
233 normalized using the Euclidean norm (Ruhnau 2000), and is much less correlated with species
234 degree (i.e., the number of links per species) than betweenness centrality (Koschützki and Schreiber
235 2004). Eigenvector centrality depends on the number and quality of links, roughly giving to each
236 species a score proportional to the sum of the scores of its neighbours (Newman 2010).
237 Standardized centrality scores vary between 0 (low centrality) to 1 (high centrality). To evaluate
238 whether species rank based on centrality changes among urbanization classes across all the season,
239 we used Spearman’s rank-order correlation tests for both plant and pollinator species. Centrality
240 quantifies how connected species are with each other. Central species are highly connected to
241 species that are themselves interconnected, and are therefore important for network structure and
242 stability.

243

244 *2.3.5. Direct and indirect interactions*

245 To describe network structure in terms of direct and indirect (species not directly interacting but
246 connected through paths of common interacting species) interactions, we used the motif analysis
247 proposed by Simmons et al. (2019a) for bipartite mutualistic networks implemented in the R
248 package ‘bmotif’ (Simmons et al. 2019b). Motifs are sets of nodes connected by a given pattern of
249 edges, e.g., motif 2 (Fig. A1) comprises one pollinator node and two plant nodes, both of them

250 connected to the pollinator node. The motifs we considered comprise between two and six species
251 (nodes), as this is the most common size used in bipartite networks to achieve a good compromise
252 between motif sophistication, mathematical tractability, and computation time (Simmons et al.
253 2019a), and all possible interaction patterns between them. Within a single motif, species occupy a
254 unique position (in Fig. A1, the 44 possible six-node motifs and the 148 unique species positions
255 are represented). The general idea behind the study of motifs within networks is that comparing
256 motif counts with expectations from random network models will help assess which interaction
257 patterns are associated to each environmental condition (here, urbanization classes), and thence
258 formulate ecological hypotheses as to why, e.g., some more asymmetric motifs can be more
259 prevalent in rural than in urban context (Stouffer et al. 2007; Simmons et al. 2019a; Ouadah et al.
260 2021). Motif counts can also be considered as a “signature” of networks which can help compare
261 them without having to resort to actual species identity (i.e., connection patterns can be compared
262 using motifs even if no species are shared between networks).

263

264 First, we decomposed the seasonal and the monthly networks in all urbanization classes in their
265 constituent motifs and we calculated the frequency with which each motif occurred. We normalised
266 motif frequencies using the number of sets of species that could potentially form a given motif
267 (Simmons et al. 2019b). Second, we calculated the frequency with which each species occurred in
268 each position to describe species roles within motifs. We used sum-normalisation to divide position
269 counts for each node by the total number of times that node appears in any position (Simmons et al.
270 2019b). A species role was thus defined by this normalized vector of position counts. To evaluate if
271 motif frequency and species roles within motifs varied between months and urbanization classes,
272 we performed the non-parametric multivariate analysis of variance advocated by Anderson (2001)
273 using the function ‘adonis2’ in the R package ‘vegan’ (Oksanen et al. 2019) with 1000 permutations
274 and Mahalanobis distance to account for covariance between motif positions in multivariate space
275 (De Maesschalck et al. 2000). To simplify the visual representation of multivariate (i.e., spatial-

276 temporal) patterns of motif positions, we performed a Principal Component Analysis (PCA) in the
277 ‘ade4’ R package (Dray and Dufour 2007).

278

279 *2.3.6. Species and interaction diversity*

280 To measure the diversity of species (i.e., nodes) and interactions (i.e., links) across the spatial and
281 temporal scale, we used the framework proposed by Ohlmann et al. (2019), implemented in the R
282 package ‘econetwork’ (Dray et al. 2019). We calculated Hill numbers with $q = 1$ (corresponding to
283 the exponential of Shannon’s entropy) on species and interaction abundances to measure α -diversity
284 in each of the seasonal and monthly networks. To measure dissimilarities in species and link
285 abundances between urbanization classes in the different months, we computed pairwise Horn
286 dissimilarities, which are built from Hill numbers of order $q = 1$ (Ohlmann et al. 2019). We chose
287 Hill numbers of order 1 because they weight rare and abundant species equally well (i.e., in
288 proportion to their frequency in the community), while Hill numbers of order 0 do not count species
289 abundances (i.e., they are equal to species richness), and Hill numbers of order 2 favour abundant
290 species and discount rare species (Chao et al. 2014). Spatial and temporal variation of species and
291 interaction dissimilarity were visualised using a Principal Coordinate Analysis (PCoA) in the ‘ade4’
292 R package (Dray and Dufour 2007). These analyses show how patterns of α - and β -diversity of the
293 plant and pollinator communities and of their interactions are affected by different levels of
294 urbanization.

295

296 All p -values were adjusted using the Benjamini and Hochberg method to control the false discovery
297 rate (Verhoeven et al. 2005).

298

299 3. Results

300 3.1. Overall plant-pollinator interactions

301 At the end of the sampling season in the 12 study sites, we had sampled a total of 56 plant species
302 and 121 pollinator species (full list of species in Tables A1, A4), accounting for 2,630 plant-
303 pollinator visits overall. The number of interactions was lowest in April and highest in June in all
304 urbanization classes (Fig. 2). The number of interactions increased through the season at low (Fig.
305 2a) and medium (Fig. 2b) urbanization, while they showed a marked increase between April and
306 May at high urbanization level (Fig. 2c). The total number of interactions was similar among the
307 three urbanization classes ($N = 846$, $N = 929$ and $N = 855$ at low, medium and high urbanization,
308 respectively).

309

310 *Centaurea jacea* and *Leucanthemum vulgare* were the most abundant (Table A1) and the most
311 visited species overall, accounting for around 35 – 50% of all visits in each urbanization class. In
312 addition to these, only five other plant species received more than 5% of pollinator visits in at least
313 one urbanization class (Table 1): species that received > 5% of pollinator visits overall accounted
314 for a total of > 60% of all recorded visits in all urbanization levels (Table 1). These plant species
315 hosted more than 77% of the recorded pollinator species at low and medium urbanization levels,
316 and 66% of the recorded pollinator species at high urbanization level (Table 1). The overall highest
317 number of visits was observed for the bee family Apidae ($N = 1494$), followed by the diptera
318 Syrphidae ($N = 457$). Bees of the family Halictidae and Andrenidae had similar number of
319 interactions ($N = 211$ and $N = 199$, respectively), followed by Megachilidae ($N = 141$) and
320 Colletidae ($N = 128$). The contribution of each pollinator family to the observed interactions varied
321 through time (Fig. A2).

322

323 3.2. Network-level metrics

324 3.2.1. Overall spatial variability

325 Overall, connectance was significantly higher at medium (0.091) than at low (0.078) urbanization
326 (from null model comparisons: $P < 0.05$), while no differences were found between low or medium
327 urbanization and high urbanization level (0.086). Interaction evenness was similar among all
328 urbanization classes (0.578, 0.589 and 0.586 at low, medium and high urbanization, respectively),
329 as well as network level specialization ($H2'$: 0.396, 0.392 and 0.369 at low, medium and high
330 urbanization, respectively). Seasonal bipartite networks are shown in Fig. A3. All delta and P -
331 values are reported in Table A5.

332

333 *3.2.2. Spatial variability within months*

334 Connectance was significantly higher at low than at high urbanization level in April, while it was
335 lower at low than at both medium and high urbanization levels in May (Fig. 3). Interaction evenness
336 was comparable among urbanization levels in all months (Fig. 3). Network specialization ($H2'$) was
337 comparable among urbanization levels in April, while it was higher at medium than at both low and
338 high urbanization levels in May, and it was higher at high than at low urbanization level in June
339 (Fig. 3). All delta P -values are reported in Table A5.

340

341 *3.2.3. Temporal variability within urbanization classes*

342 Connectance always decreased through time except at low urbanization where it decreased in May
343 and increased back in June, with significant differences between April and June at all urbanization
344 levels (Fig. 3). Interaction evenness showed the same trend in the three urbanization classes, with
345 lower values in June than in both April and May at all urbanization levels (Fig. 3). Network
346 specialization ($H2'$) was significantly lower in May and June compared to April at low urbanization
347 level (Fig. 3), while no significant differences were found among months at medium urbanization
348 level and $H2'$ was only marginally significantly higher in June than in April and May at high
349 urbanization level (Fig. 3). Monthly bipartite networks are shown in Fig. A4–6. All delta and P -
350 values are reported in Table A6.

351

352 *3.3. Clustering of species in the network*

353 LBMs retrieved several cohesive groups for both plant and pollinator species in all urbanization
354 classes and time periods. Considering the overall season, super-generalist species with long
355 phenology tended to cluster alone or with one or two other species, while more specialist species
356 with overlapping phenology clustered in medium-sized blocks. Infrequent species with different
357 phenology were included in large blocks (Fig. A7).

358

359 The composition of cohesive groups in monthly networks was mainly driven by the level of species
360 generalization and by the number of interactions (Fig. A8–10). A few groups corresponded to
361 oligolectic foraging behaviour in pollinators (e.g., the bees *Anthidium manicatum* and *Megachile*
362 *willughbiella* at medium urbanization and *Colletes daviesanus* at high urbanization in June, Fig.
363 A9–10). The hoverfly species *Eristalis tenax* and *Sphaerophoria scripta* were generally included in
364 large clusters in April and in smaller clusters as the season advanced. In particular, both species
365 were included within the same cluster in June at all urbanization classes, where they mainly visited
366 abundant and long-flowering plant species (e.g., *C. jacea*, *L. vulgare*, *A. millefolium*; Fig. A8–10).
367 A strong reorganisation of blocks between urbanization classes was highlighted in April.
368 *Taraxacum* sect. *ruderalia* formed an individual cohesive block at low and medium urbanization,
369 being visited by most of the observed pollinator species, while it was included in a block with two
370 other plant species at high urbanization level because of a higher number of shared interactions with
371 other plant species (Fig. 4a–b). *Anthophora plumipes* and *Bombus pascuorum* were included in the
372 same cohesive group at low and medium urbanization level, while they were split into two different
373 groups at high urbanization level following changes in their foraging choices (Fig. 4a–b).

374

375 *3.4. Species centrality within networks*

376 Considering the overall season, super-generalist species with long phenology were the most central
377 in all urbanization classes (e.g., *C. jacea* and *L. vulgare* for plants, *Bombus lapidarius*, *B. terrestris*,
378 *B. pascuorum*, *Apis mellifera* and the hoverfly *Sphaerophoria scripta* for pollinators, Fig. A11).

379
380 Monthly networks generally showed the same patterns, with different generalist plant and pollinator
381 species having the highest centrality scores depending on month and urbanization class (Fig. A12–
382 14). Similar to LBMs, clear changes in species centrality scores between urbanization classes were
383 highlighted in April. *Taraxacum* sect. *ruderalia* was the only central species at low and medium
384 urbanization levels, while it shared high centrality scores with other species at high urbanization
385 level (Fig. 4c). *Eristalis tenax* and *S. scripta* had comparably high centrality scores in June
386 throughout the gradient (Fig. A12–14).

387
388 The rank of species eigenvector centrality scores was not significantly correlated between urban
389 classes for plants (low vs. medium: Spearman's $\rho = 0.14$, $P = 0.44$; low vs. high: $\rho = 0.09$, $P = 0.62$;
390 medium vs. high: $\rho = -0.19$, $P = 0.31$) and for pollinators (low vs. medium: $\rho = 0.17$, $P = 0.14$; low
391 vs. high: $\rho = 0.02$, $P = 0.84$; medium vs. high: $\rho = 0.09$, $P = 0.44$). In other words, the centrality of
392 both plant and insect species varied quite substantially between urban classes.

393

394 3.5. Direct and indirect interactions

395 Motif frequency was not significantly different among urbanization classes (Adonis: $F = 1.02$, $P =$
396 0.49) or months (Adonis: $F = 0.75$, $P = 0.99$). Plant species positions (i.e., roles) within motifs
397 changed significantly among urbanization classes (Adonis: $F = 2.20$, $P = 0.001$) and among months
398 (Adonis: $F = 2.39$, $P = 0.001$). Plant roles were more different between high urbanization and both
399 low and medium urbanization classes in April than in the other months (Fig. 5a, A15a). The first
400 PCA axis distinguished motifs including specialist plant species that had indirect interactions with
401 both other plant and pollinator species, from motifs with generalist plant species with few indirect

402 interactions with other plant species only. The second PCA axis distinguished motifs including
403 generalist plant species that shared the same pollinator species, from motifs with super-generalist
404 plant species that had few indirect interactions with other plant species only (details in Fig. A16a).

405

406 Pollinator species positions within motifs also changed significantly among urbanization classes
407 (Adonis: $F = 3.95$, $P = 0.001$) and among months (Adonis: $F = 4.81$, $P = 0.001$). Pollinator roles
408 showed the highest temporal variability in the low urbanization class, while they showed limited
409 temporal variability in the medium and especially high urbanization classes (Fig. 5b, A15b). The
410 first PCA axis opposed specialist pollinators with indirect interactions with both plants and
411 pollinators to super-generalist pollinator species with indirect interactions with other pollinators
412 only. The second PCA axis opposed peripheral specialist pollinators with indirect interactions with
413 both plants and pollinators to specialist pollinators visiting a same super-generalist plant species
414 (details in Fig. A16b).

415

416 *3.6. Species and interaction diversity*

417 Species α -diversity slightly decreased from low to high urbanization class, while the diversity of
418 network interactions was constant among urbanization classes when considering the overall season
419 (Fig. A17). Monthly species α -diversity was quite constant at high and medium urbanization
420 classes, while it was more variable at low urbanization with the lowest diversity found in April and
421 the highest diversity in May (Fig. A18a). Interaction α -diversity showed similar patterns in the three
422 urbanization classes, with lowest diversity in April and highest diversity in May (Fig. A18b).

423

424 PcoA highlighted high species dissimilarity between low urbanization and both medium and high
425 urbanization classes in April and May, while dissimilarity was lower among the three urbanization
426 classes in June (Fig. 6a). A similar pattern was observed for the dissimilarity of interactions, except
427 for a higher diversity between medium and high urbanization classes in April (Fig. 6b). The first

428 principal axis highlighted a similar temporal trajectory of dissimilarities for both species and
429 interactions, with a more gradual dissimilarity observed in sites at low urbanization compared to
430 sites at medium and high urbanization (Fig. 6a–b).

431 **4. Discussion**

432 Here we showed that asymmetric changes in plant phenology affected the temporal dynamics of
433 plant-pollinator interaction networks in different ways along an urbanization gradient. We found
434 limited variability in the macroscopic network structure along the urbanization gradient. Fewer and
435 more specialized interactions occurred at urban than at peri-urban sites in early summer, coinciding
436 with reduced resources available to pollinators driven by advanced flowering phenology. When
437 considering species roles, we found common patterns shared throughout the gradient. Long-
438 flowering generalist plants were visited by different types of pollinators along the season, providing
439 a basic resource for both specialists and generalists with varying flying phenology. Moreover, both
440 plants and pollinators with long phenology were highly central to all networks, even though their
441 identity changed throughout the season and gradient. This suggests that such species are important
442 to guarantee network stability, regardless of resource availability and changes in species phenology.
443 The significant advancement of flowering in urban sites (Fisogni et al. 2020) increased the presence
444 of long-flowering species throughout the study period, which led to similar interaction patterns
445 between spring and summer. Conversely, higher temporal species turnover led to increased
446 interaction diversity and stronger temporal dynamics at low-urbanization sites over the season.
447 These results suggest that favouring diverse flowering communities in urban areas, including early-
448 flowering species, can be an effective strategy to support the local pollinator fauna in artificial
449 environments.

450

451 *4.1. Network-level structure*

452 Considering the whole sampling period, we did not find any significant variation in the level of
453 network specialization along the urbanization gradient. These results are in accordance with
454 Theodorou et al. (2017) but in contrast with both Baldock et al. (2015), who found higher
455 specialization in farmlands than in urban areas, and Martins et al. (2017) who found higher
456 specialization in suburban than semi-natural areas. Moreover, we found comparable interaction

457 evenness across the gradient, in contrast with both Geslin et al. (2013) and Udy et al. (2020) who
458 found increasing and decreasing evenness with increasing urbanization, respectively. These
459 discrepancies among studies suggest the presence of regional variability of plant-pollinator
460 networks in response to different gradients of urbanization. However, because such studies use
461 different experimental designs and plant communities (e.g., comparing urban *vs* either agricultural
462 areas or suburban gardens), comparison of results and extrapolation of urbanization effects may be
463 limited (Wenzel et al. 2020). Here, we surveyed similar plant communities in order to highlight the
464 effect of phenological shifts on mutualistic partners along the urbanization gradient. When
465 comparing whole-season networks, we agree with Baldock et al. (2015) and Wenzel et al. (2020)
466 that the ecological quality of the sites, including non-native plant species richness, might drive the
467 observed patterns. However, differences might be expected along the season, due to the asymmetry
468 in phenological shifts of the mutualistic partners alone.

469

470 Monthly networks showed moderate temporal variation, with two general patterns that can be
471 recognised. First, connectance has decreased over time, consistent with the fact that the number of
472 visits has not increased as fast as the number of species, and interactions were less evenly
473 distributed among species later in the season. Less connected networks can be less functionally
474 robust (Kaiser-Bunbury and Blüthgen 2015), potentially increasing their fragility as the season
475 advances. Second, specialization showed two opposite patterns: networks became more generalised
476 at low urbanization and more specialised at high urbanization later in the season, following changes
477 in floral resource availability. A smaller proportion of resources used by pollinators in urban areas
478 could reduce pollination efficiency by reducing pollen flow, while at the same time increasing
479 pollination efficiency through reduced heterospecific pollen deposition (Briggs et al. 2016).
480 Although we could not relate changes in network metrics to plant reproductive success, to date no
481 clear relationship between increased network specialization in urban areas and pollination success
482 has been found (Theodorou et al. 2017).

483

484 *4.2. Interaction homogeneity*

485 Super-generalist plant species with long phenology acted as temporal connectors within cohesive
486 blocks of highly interacting species (Fig. A7). Pollinators with short flight periods may have time
487 constraints and rely heavily on these plants because of overlapping phenology; at the same time,
488 pollinators with longer flight periods can use these plants as a constant resource for pollen or nectar
489 within a context of rapid turnover of other floral resources (Ogilvie and Forrest 2017). Similarly,
490 long-flowering generalist plants can be critical in providing pollen to some oligolectic pollinators,
491 as well as in supplying a basal amount of nectar and pollen to polylectic bees and hoverflies that
492 rely on different resources for their sustenance (Pellissier et al. 2012; Larson et al. 2014; Lundgren
493 et al. 2015).. Therefore, long-flowering plant species can mitigate potential negative impacts due to
494 asymmetric changes in the phenology of plants and pollinators, as observed along the studied
495 gradient (Fisogni et al. 2020), by providing flower resources more consistently throughout the
496 season (Salisbury et al. 2015; Deguines et al. 2016). These species can therefore act as a lifeline in
497 fast changing “food landscapes” and should be included in management plans of urban green areas.

498

499 *4.3. Species centrality within networks*

500 Long-flowering generalist plants and generalist pollinators with long flight periods were the most
501 central throughout the gradient, highlighting their key roles in seasonal and monthly networks.
502 However, in both cases the same species could rank differently depending on the level of
503 urbanization. Generalist species are usually central in mutualistic networks and are therefore
504 important for maintaining their structure and cohesiveness, being at close distance to several species
505 in the network and connecting different sub-groups of interacting species (Martín González et al.
506 2010; Sazima et al. 2010). Our results suggest that the presence of several generalist species that
507 “replace one another” throughout the season is a potential asset to guarantee network stability, as
508 different species can play the same central role in different periods. Moreover, the marked temporal

509 dynamics observed in a relatively limited time period emphasize the importance of considering
510 different temporal scales to identify changes in the centrality of species.

511

512 Some pollinator species became more central throughout the urbanization gradient as the season
513 advanced. This pattern was driven by the widespread availability of long-flowering generalist
514 species, which buffered phenological shifts (i.e., advanced flowering) in more urbanized areas and
515 the consequent reduction in the availability of short-flowering species (Fisogni et al. 2020).

516 However, strong rearrangements in network structure and species centrality related to plant
517 phenological shifts were observed throughout the urbanization gradient early in the season. For
518 example, the large generalist bees *B. pascuorum* and *A. plumipes* stopped visiting *Taraxacum*
519 flowers in the presence of a wider array of plants in urban sites (Fig. 4), likely to reduce
520 interspecific foraging competition (Fründ et al. 2013; Carvalho et al. 2014) and to find more
521 suitable pollen resources (Génissel et al. 2002; Rasmont and Dehon 2015).

522

523 4.4. Direct and indirect interactions

524 Motif analysis indicated that plant and pollinator species positions changed significantly through
525 time and space along the urbanization gradient, highlighting changes in the frequency of direct and
526 indirect interactions. Low-urbanization sites showed higher temporal variability than medium- and
527 especially high-urbanization sites, likely due to the asymmetric shifts in plant phenology occurred
528 along the gradient (Fisogni et al. 2020). The advanced flowering in urban areas reduced the
529 presence of short-flowering species early in the season while increasing long-flowering species
530 throughout the study period, leading to more homogeneous interaction dynamics between plants
531 and pollinators over the season (Olesen et al. 2008). By contrast, the higher temporal species
532 turnover in sites at low urbanization led to greater differences in species roles within motifs
533 between spring and summer.

534

535 Plants mostly acted as generalists hosting specialist pollinators and were mainly involved in direct
536 interactions in April at medium and low urbanization. The limited floral resources available to
537 pollinators have likely increased specialist interactions, even though none of the pollinators were
538 true oligolectic species (Table A1). However, plants acted as both generalists and specialists and
539 were connected to other plant species through several indirect interactions at high-urbanization sites
540 in April, as well as throughout the gradient in May and June. Differences in species positions along
541 the gradient early in the season imply potentially different vulnerabilities among sites under
542 different urban pressures. The loss of super-generalist plants hosting specialist pollinators can
543 potentially disrupt entire networks in less urbanized areas (Memmott et al. 2004; Martín González
544 et al. 2010). Conversely, an increase in complex interactions in more urbanized areas can partially
545 buffer the loss of some species and increase robustness of networks, especially if species are able to
546 switch interaction partners (Kaiser-Bunbury et al. 2010b; Burkle et al. 2013).

547

548 *4.5. Species and interaction diversity*

549 We did not observe marked variations in species or interaction α -diversity among urban classes
550 throughout the whole sampling period. However, we detected variations in both species and
551 interaction α -diversity when considering temporal variability. At low urbanization, both species and
552 interaction α -diversity were lowest in April and highest in May. A similar trend was observed for
553 interaction α -diversity in medium and high urbanization sites, while species α -diversity was
554 constant throughout the study period. This pattern was mainly driven by the advanced flowering in
555 urban areas (Fisogni et al. 2020), that increased the availability of floral resources early in the
556 season. The temporal variation of interacting partners highlighted by bipartite networks and species
557 clustering indicates that rewiring of species interactions played a major role in defining temporal
558 interaction diversity.

559

560 Both species and interaction dissimilarity showed similar temporal trajectories. Low-urbanization
561 sites were more dissimilar to medium- and high-urbanization sites in April and May, and more
562 similar in June. These results are in accordance with changes in species positions within network
563 motifs. As for motifs, asymmetric shifts of plant flowering phenology have likely influenced the
564 temporal dynamics of species and interaction dissimilarity throughout the gradient. The marked
565 differences in the availability of interacting partners and the consequent rewiring of interactions in
566 April increased the spatial dissimilarity early in the season, while the presence of more
567 homogeneous communities increased species and interaction similarity later in the season.

568

569 *4.6. Conservation perspectives*

570 We found only two oligolectic bee species. *Hoplitis adunca* (Family Megachilidae) collects pollen
571 only from species in the genus *Echium* (Family Boraginaceae), while *Hylaeus signatus* (Family
572 Colletidae) collects pollen from the two related species *Reseda lutea* and *R. luteola* (Family
573 Resedaceae). Not surprisingly, these bee species were found at the only sites where the host plants
574 were present. This simple result shows how managing green areas by planting target species can be
575 a key factor in facilitating the presence of specialist bees. Moreover, both *H. adunca* and *E. vulgare*
576 are thermophilic species that could be favoured by higher temperatures in urban environments
577 (Hofmann et al. 2018), further ensuring their persistence and potentially their dispersal.

578

579 Our results add to the growing evidence underscoring the importance of *Taraxacum* as a foraging
580 resource for pollinators (e.g., Lázaro and Totland 2010; Larson et al. 2014). *Taraxacum* is a good
581 nectar and pollen resource (Hicks et al. 2016). In our study *Taraxacum* was a key host plant for
582 early flying pollinators in low and medium urbanization sites, when other flowering species were
583 scarce, while its scarcity together with increased plant diversity caused major interaction rewiring in
584 high urbanization sites. Maintaining and promoting the presence of *Taraxacum*, for example by
585 avoiding mowing at the beginning of the flowering season, can be important to support pollinator

586 communities throughout the urban gradient, and to increase the robustness of plant-pollinator
587 interaction networks (Baldock et al. 2019).

588

589 Typically, gardens composed by standard seed mixes are dominated by a few species and lack
590 early-flowering plants, even if species composition can vary regionally (Hicks et al. 2016). These
591 few species usually contribute the most to nectar and pollen production, and are the most important
592 to attract pollinators (Hicks et al. 2016; Warzecha et al. 2018). We found that the abundant and
593 resource-rich plants *L. vulgare* and *C. jacea* (Rusterholz and Erhardt 1998; Hicks et al. 2016) were
594 the most visited across the whole urbanization gradient by bees and hoverflies. However, both
595 species flowered later in the season, leaving a gap in floral resource availability in April, especially
596 at low urbanization. While plants in the surrounding areas likely play an important role in providing
597 nectar and pollen, there is certainly room for improvement in the design of seed mixes by including
598 more early-flowering native species to support the early-flying pollinators.

599

600 *4.7. Limitations of the study*

601 This study only includes data for one habitat type in April, May and June, therefore missing other
602 urban habitats potentially available to pollinators and part of the summer and fall seasons. The
603 temporal limitation was due to management practices aimed at promoting further flowering of
604 native plants while reducing weeds. Consequently, we lack the overall picture of plant-pollinator
605 interactions throughout the season. We expect pollinators to use floral resources present in the areas
606 surrounding the study sites throughout their activity period, especially after sites are mown in July
607 and native flowers are scarce or no longer available. Residential and community gardens in
608 particular (Baldock et al. 2019), in addition to other green areas, can play key roles in supporting
609 insect communities throughout the season, with a large contribution given by exotic and ornamental
610 species beyond the study period (Lowenstein et al. 2019; Staab et al. 2020). Exotic ornamental
611 plants, if resource-rich and with accessible flowers (Comba et al. 1999; Corbet et al. 2001), might

612 be useful next to patches displaying native plant species (Salisbury et al. 2015; Rollings and
613 Goulson 2019). However, given the already large use of exotic species in gardens (Garbuzov and
614 Ratnieks 2014; Erickson et al. 2020), we encourage sowing native plant mixes to increase plant
615 diversity and support pollinators in urban environments throughout their activity period.

616

617 Our study is focused only on one urban area. This may limit the generalization of our results to
618 other contexts, especially in the presence of marked historical and socio-cultural differences.

619 However, given the historical background of the metropolitan area of Lille, characterized by a large
620 industrial sector surrounded by intensive agriculture, our results could be compared to many urban
621 contexts under similar conditions, especially in Western Europe. Indeed, regional differences in
622 land management and in the composition of plant and pollinator communities may lead to changes
623 in the responses of species interactions along different urban gradients.

624

625 Changes in species interactions among habitats can be simply driven by changes in species
626 abundance (i.e., random encounters), or can result from interaction preferences related to specific
627 behaviour (Staniczenko et al. 2017). Species preferences can be important to define how
628 interactions are partitioned within networks (Staniczenko et al. 2013). In this article we have not
629 explicitly tested models that take into account random encounters vs interaction preferences.

630 Because we have aggregated sites within urbanization levels, local differences driven by changes in
631 species abundance may have occurred, although these were likely limited by the low species
632 turnover detected between sites. The spatial and temporal changes observed among urbanization
633 levels and months may be partially related to changes in species abundance. However, our results
634 indicate that some interaction rewiring observed along the gradient was related to species
635 behaviour. For example, the bees *B. pascuorum* and *A. plumipes* switched to diverse and more
636 suitable floral resources (Fig. 4) when available in urban sites.

637

638 **5. Conclusion**

639 Our results highlight the importance of considering the temporal variability in plant-pollinator
640 networks in addition to the spatial scale. Although limited to one season, we observed significant
641 changes in network structure in time and space along an urbanization gradient. Including the
642 temporal dimension allowed us to detect fine-scale variations that were otherwise hidden when
643 considering the whole season together. Moreover, combining classic network-level metrics with
644 more detailed methodologies to investigate modifications in species roles and interaction patterns
645 proved quite useful. For example, the use of latent block models and network motifs allowed to
646 better understand the environmental effects on the structure of interactions between species.
647 Although difficult to apply, especially at the community level, it would be important to link changes
648 in the network structure with measures of pollination efficiency. Finally, our results can be useful
649 for the future management of urban green areas, aimed at preserving the diversity and functionality
650 of interaction networks in potentially hostile environments. The use of local plants with different
651 flowering phenology and the preservation of wild species can be an efficient solution to support a
652 substantial part of the bee and hoverfly pollinator diversity in cities as well as in peri-urban
653 environments.

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Tables

Table 1 Overall proportion (%) of pollinator visits received by the most visited (> 5% of the visits) plant species in the three urbanization classes throughout the study period. The number of pollinator species (followed by the percentage of total pollinator species) hosted by these plant species in each urbanization class is also reported.

Urbanization class	<i>Centaurea jacea</i>	<i>Leucanthemum vulgare</i>	<i>Lotus corniculatus</i>	<i>Trifolium repens</i>	<i>Taraxacum</i> section <i>ruderalia</i>	<i>Geranium pyrenaicum</i>	<i>Achillea millefolium</i>	Total visits	N of pollinator species (%)
Low	22.2	12.2	15.3	7.2	7.8	< 5	< 5	> 64.7	65 (77.4)
Medium	33.9	15.4	< 5	< 5	5.3	8.9	< 5	> 63.5	64 (79.0)
High	25.5	18.4	< 5	< 5	< 5	7.5	9.1	> 60.5	45 (66.2)

Figure legends

Fig. 1. Map of the 12 study sites along an urbanization gradient in the metropolitan area of Lille, France.

Fig. 2. Number of plant-pollinator interactions recorded along the urbanization gradient and the sampling season.

Fig. 3. Network-level metrics calculated along the urbanization gradient and the sampling season. For each metric, different capital letters (A, B) indicate significant differences between urban classes within each month, while lowercase coloured letters (x, y, z) indicate significant differences between months within a same urban class. Lack of letters indicates no significant differences. $H2'$ indicates network level specialization (0: complete generalization, 1: complete specialization). All values are given in Tables A5-6.

Fig. 4. Representation of bipartite plant-pollinator interaction networks (lower bars = plants, upper bars = pollinators), latent block models (rows = pollinators, columns = plants) and eigenvector centrality scores (x-axes: species ordered by decreasing score) obtained in the three urbanization classes during the month of April. Exemplifying species (*Taraxacum* sect. *ruderalia*, *Anthophora plumipes*, *Bombus pascuorum*) and their interactions are highlighted by specific colours. Black indicates all other plant and pollinator species. Red lines separate homogeneous clusters of interactions. See Fig. A4–14 for complete figures with species labels.

Fig. 5. Principal Component Analysis (PCA) plot of (a) plant and (b) pollinator positions within motifs in the three urbanization classes and in the three time periods considered. Labels indicate the centroid for each time \times urbanization level category. Full point distributions and ellipses are shown in Fig. A15.

Fig. 6. Principal Coordinate Analysis (PCoA) plot of pairwise dissimilarities for (a) species and (b) interactions in the three urbanization classes and in the three time periods considered.

Figures

Fig. 1.

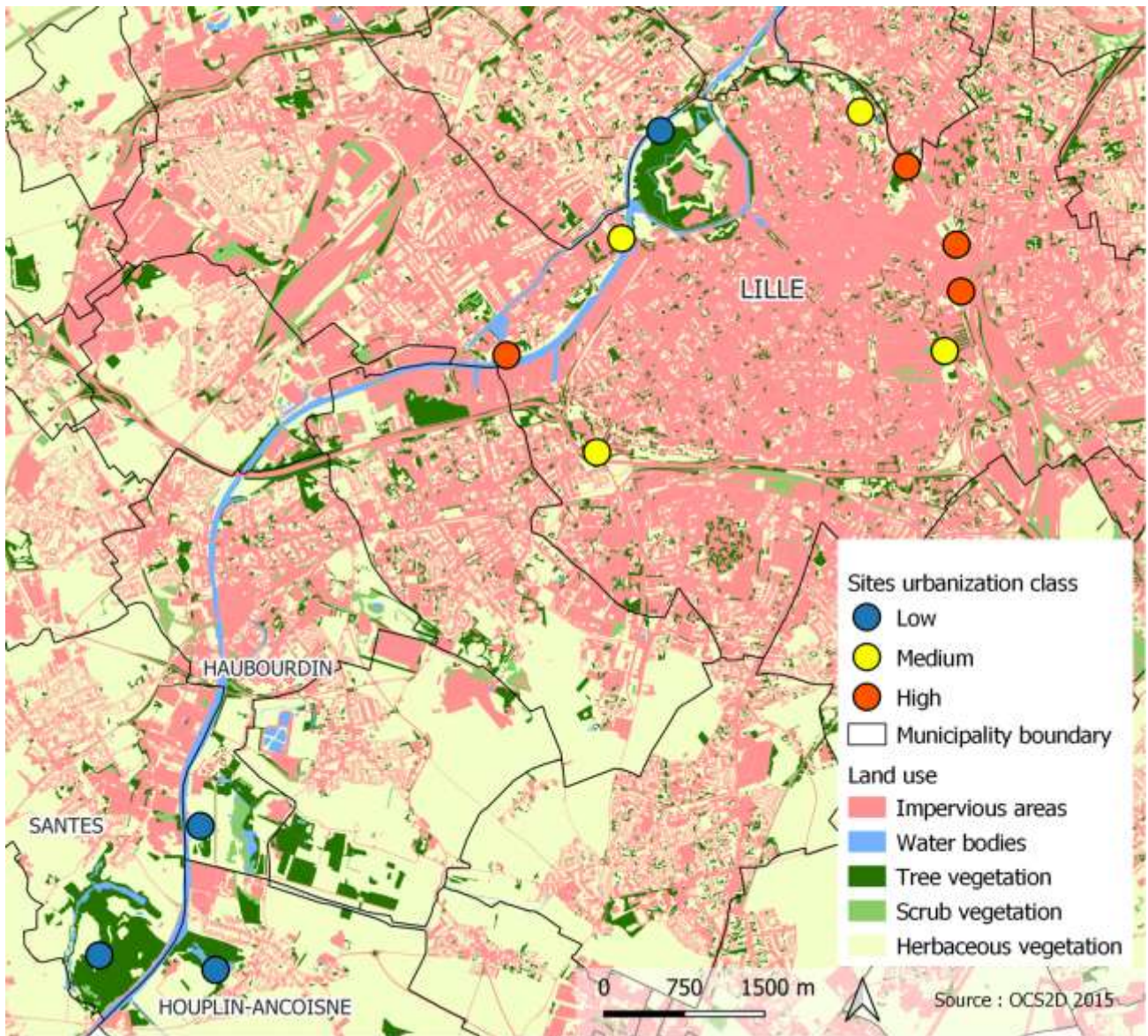


Fig. 2.

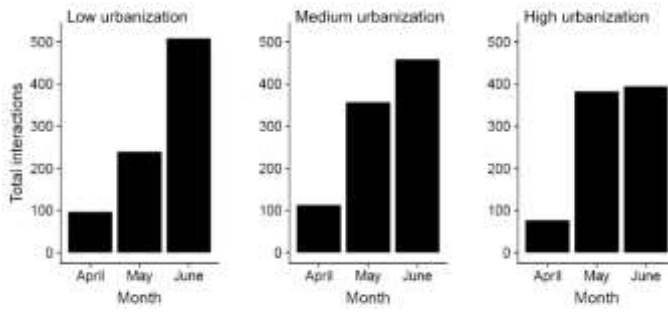


Fig. 3.

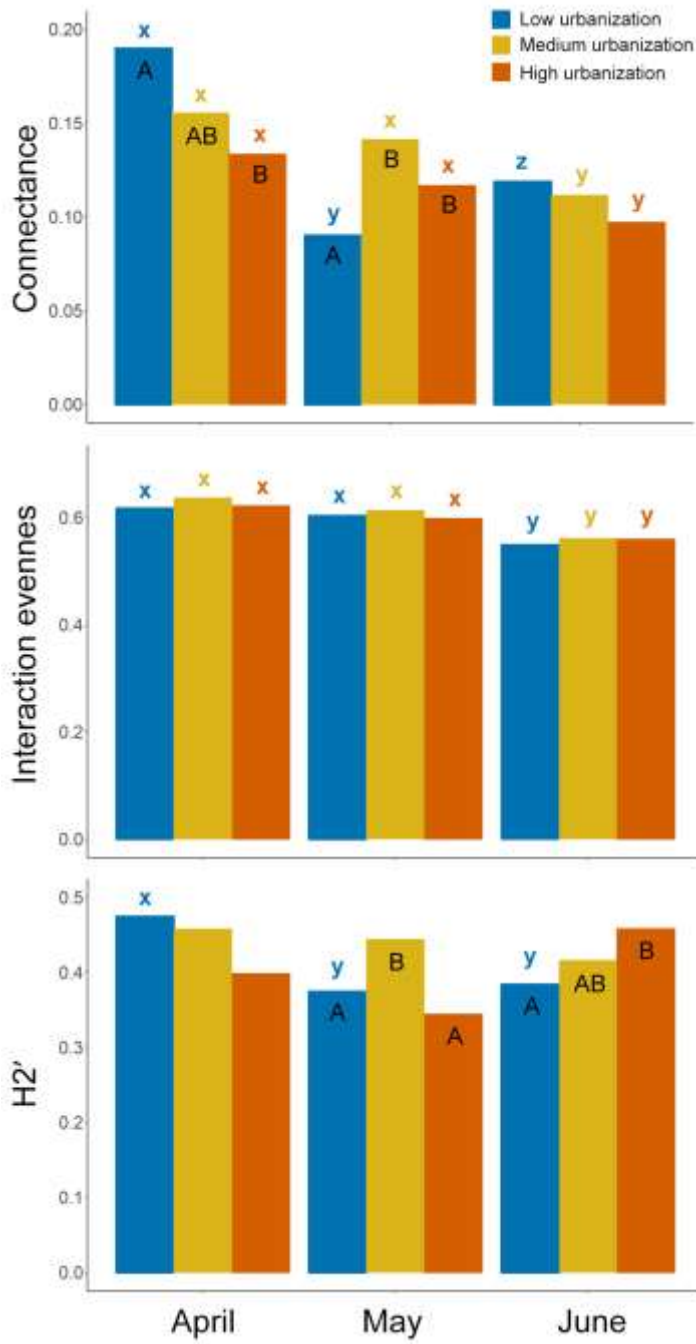


Fig. 4.

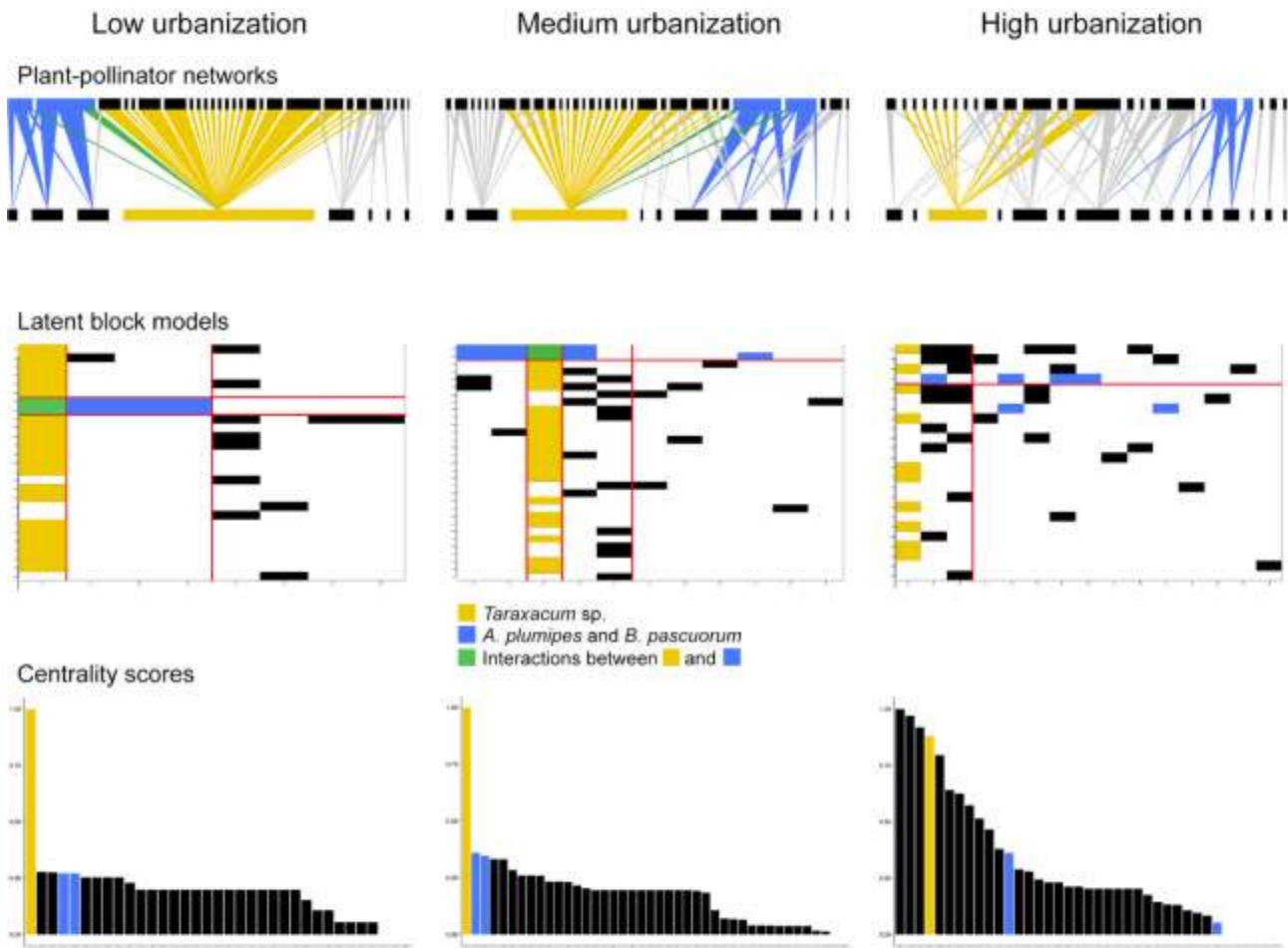


Fig. 5.

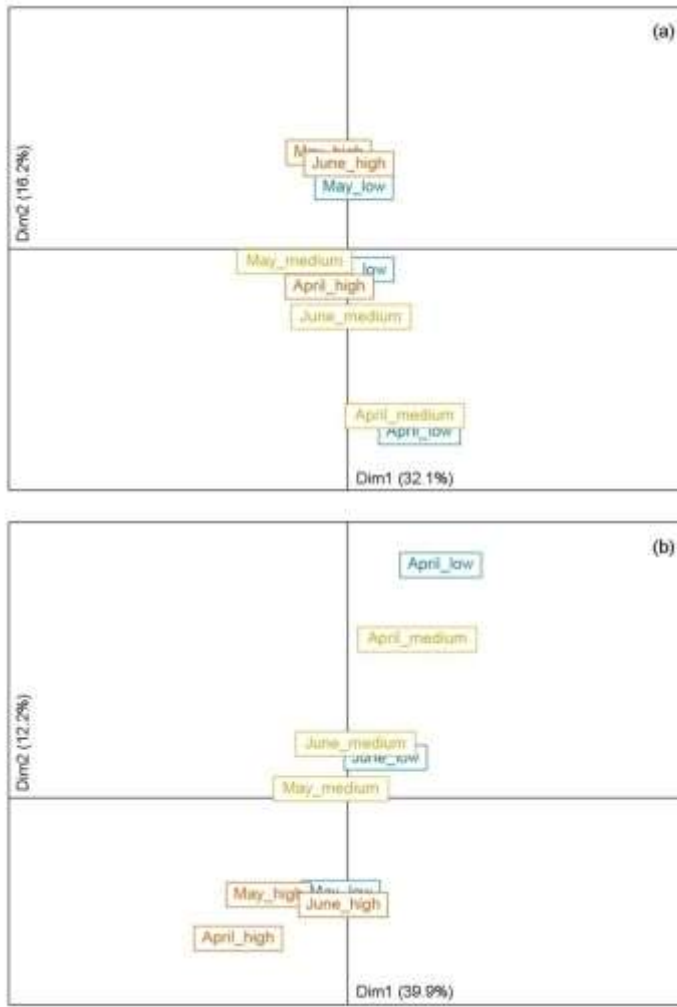


Fig. 6.

