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**Contribution of private gardens to habitat availability, connectivity and conservation
of the common pipistrelle in Paris**

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Abstract

Urban sprawl is one of the greatest global changes with major negative impacts on biodiversity and human well-being. Recent policies have acknowledged the value of urban green areas in counterbalancing such impacts. However, these policies are largely focused on public green areas, ignoring the role and potential of private green areas for urban ecological value. This paper aims at evaluating the importance of private gardens for habitat availability and connectivity in Paris, France, using the common pipistrelle as model. We hypothesize that public green areas contribute more to habitat availability than private gardens because of their large area, and that private gardens contribute more to connectivity than public green areas because of their scattered locations in the city. Using data on common pipistrelle activity and information on vegetation and building height, we quantify the respective contribution of public green areas and private gardens in the bat habitat availability and connectivity. Our results show that despite the low proportion of private green areas in Paris (36% of the total green areas), they still contributed up to 47.9% of bat habitat availability and decrease the resistance of the city matrix by 57%. The distribution in the city matrix and vegetation composition of those areas appeared especially beneficial for bat habitat availability and connectivity. The study demonstrates the importance of private gardens in the ecological value of cities in complementing public green areas. Our results confirm the need to develop more inclusive urban conservation strategies that include both public and private stakeholders.

Highlights

- The urban ecological value of private gardens outweighs that of public gardens

- This is true for both habitat availability and connectivity
- Biodiversity policies in cities should also focus on private green areas
- Inclusive conservation strategies are also needed in cities

Keywords

Greenveining; bats; urban policies; land use complementation; ecological network;

Circuitscape

Word count (body of manuscript + references): 8144

2 **1. Introduction**

3 Urbanization is one of the main drivers of the biodiversity crisis, leading to the erosion of
4 species diversity (McDonald, Kareiva, & Forman, 2008; Olden, Poff, & McKinney, 2006), a
5 decrease in both total abundance in communities (Newbold et al., 2015; Pellissier, Mimet,
6 Fontaine, Svenning, & Couvet, 2017) and in the number of individuals of most species (C. G.
7 Threlfall, Law, & Banks, 2012), and biotic homogenization (McKinney, 2006). The
8 underlying mechanisms include direct loss of natural habitat (Devictor et al., 2008; Devictor,
9 Julliard, Couvet, Lee, & Jiguet, 2007), as well as disconnection of the habitat patches of
10 populations, thus impeding movement (Clauzel, Jeliaskov, & Mimet, 2018; Tannier,
11 Bourgeois, Houot, & Foltête, 2016). Depending on their size, composition, configuration and
12 management, urban green areas have the potential to support wildlife populations by
13 providing habitat and by contributing to the connectivity of natural populations (Alberti,
14 2005; Muratet & Fontaine, 2015; Muratet, Machon, Jiguet, Moret, & Porcher, 2007; Pellissier,
15 Cohen, Boulay, & Clergeau, 2012; Politi Bertoncini, Machon, Pavoine, & Muratet, 2012;
16 Shwartz, Turbé, Julliard, Simon, & Prévot, 2014). There is increasing recognition that urban
17 green areas have ecological value (Breuste, Niemelä, & Snep, 2008; Goddard, Dougill, &
18 Benton, 2010), a recognition going along with a call to develop a better understanding of the
19 roles of urban green areas in biodiversity in order to guide conservation actions within urban
20 areas (Dearborn & Kark, 2010; Shwartz et al., 2014).

21 The benefits of urban green areas are tracked by urban authorities and policies, which
22 favor different types of actions to promote urban biodiversity such as ecological management
23 (e.g., delay mowing the grass in the parks to live time to insects and plans for reproduction),
24 reduction of pesticides and maintaining and developing ecological corridors, as in London,
25 Dublin, Berlin or Paris (City of Berlin, 2012; City of Dublin, 2016; City of London, 2016;
26 Conseil de Paris, 2018; Ville de Paris, 2017). These policies aim to make cities crossable and

27 livable to natural populations, usually by targeting the larger public green areas but
28 overlooking private ones, such as gardens (Evans et al., 2012; Goddard et al., 2010). Yet
29 gardens provide significant amounts of green areas and resources for wildlife in urban areas
30 (Cameron et al., 2012; Davies et al., 2009), complementing large public green areas such as
31 parks by increasing habitat availability and connectivity (Colding, 2007; Loram et al., 2008;
32 Melles, Glenn, & Martin, 2003; Rudd, Vala, & Schaefer, 2002). However, our understanding
33 of this complementation process remains incomplete. We do not have estimates or a general
34 understanding of the relative contributions of gardens and public green areas to habitat
35 availability and connectivity in cities, especially considering that said contributions are
36 expected to be species-dependent (Lepczyk et al., 2017) and configuration-dependent
37 (Goddard et al., 2010). Urban ecology literature has stressed the importance of different
38 scales (i.e. local to the landscape scale) and of vegetation structure and heterogeneity in
39 explaining the distribution of species and diversity in an urban context (Goddard et al., 2010;
40 Goddard, Dougill, & Benton, 2013; Lepczyk et al., 2017; Melles et al., 2003). Getting
41 accurate estimates of the relative contributions of gardens and public areas to habitat
42 availability and connectivity therefore requires multiscale analyses including vegetation
43 structure and heterogeneity.

44 Bats are one of the few strictly protected mammals living within urban environments (they
45 are included in Annex IV Council Directive 92/43/EEC, 1992). Previous researches have
46 shown the detrimental effects of urbanization on bat populations (Azam, Le Viol, Julien, Bas,
47 & Kerbiriou, 2016; Walsh & Harris, 1996) but certain bat species occur in cities, using trees
48 planted along streets and parks as urban substitutes for their natural foraging habitat Some
49 species use man-made structures for breeding roosts and can live in cities if other basic
50 requirements, like access to water, are also met (Marnell & Presetnik, 2010; Simon,
51 Huttenbugel, & Smit- Viergutz, 2004). (Oprea, Mendes, Vieira, & Ditchfield, 2009; C.

52 Threlfall, Law, Penman, & Banks, 2011). As long-lived insectivorous species with a slow
53 reproductive rate, bats are considered good indicators of the response of biodiversity to
54 anthropogenic pressure (Jones, Jacobs, Kunz, Wilig, & Racey, 2009). The strength of the
55 impacts of urbanization on bats appears to be context-dependent, i.e., the degree of
56 urbanization, the amount of vegetation remaining and patch connectivity have been shown to
57 largely explain observed distribution patterns (Oprea et al., 2009; C. Threlfall et al., 2011).
58 Among common bat species, *Pipistrellus pipistrellus* (common pipistrelle) is one of the most
59 abundant in North European urban areas (Gaisler, Zukal, Rehak, & Homolka, 1998; Hale,
60 Fairbrass, Matthews, & Sadler, 2012; Lintott et al., 2015).

61 With the goal of evaluating the benefits of including private green areas (i.e. gardens) in
62 urban conservation initiatives, this study aims to quantify the respective contributions of
63 public and private green areas to habitat availability and connectivity for the common
64 pipistrelle, focusing the analysis on the city of Paris.

65
66 The study focuses on testing three hypotheses. First, we hypothesize that **the bat pass**
67 **abundance depends on the vegetation spatial heterogeneity and on the area and height**
68 **of vegetation and buildings, at different spatial scales.** Because of their large size, we
69 **secondly hypothesize that public green areas are the most important contributors to the**
70 **availability of habitat area for the common pipistrelle,** only marginally complemented by
71 private green areas. Because of their scattered spatial configuration, **we thirdly hypothesize**
72 **private green areas to be the main providers of habitat connectivity in the city,** providing
73 the bats with stepping-stone connectivity across the urban matrix between larger habitat
74 patches centred on public green areas.

75

76 ▪ 14m² of public green area / inhabitant (21m² for Berlin, 68m² for Madrid, 31m² in
77 average for the large french cities)

78 ▪ 450 public green areas (parcs, gardens, promenades ...)

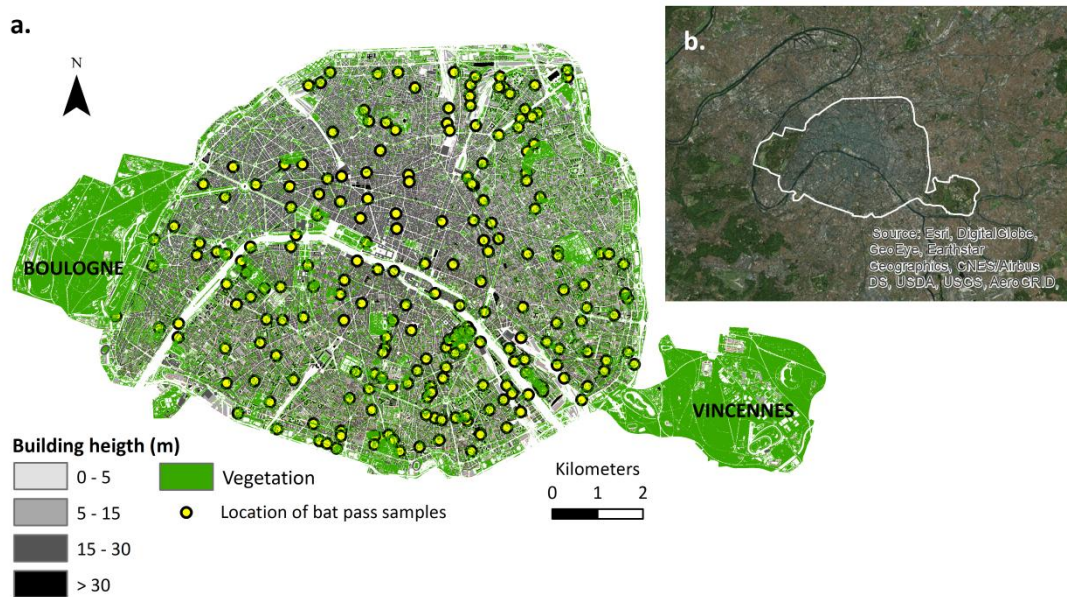
79

80

81 **2. Methods**

82 **2.1. Study area**

83 The study was conducted in intramural Paris, a densely populated city of 105 km² (21,067
84 inhab/km² in 2014) in the heart of the Greater Paris region. Intramural Paris refers to the
85 central part of this agglomeration, bounded by the *Périphérique* ring-road, and administered
86 by the *Mairie de Paris* (city council). Built areas are dominated by low-rise buildings of six
87 to seven floors (i.e., 18 to 30 meters high) (Pellissier et al., 2012). The number and size of
88 green areas is low compared to most other European big cities. The percentage of public
89 green space is about 9.5% of the Paris area, while it is around 18.8% in Brussel and 38.9% in
90 Rome (<http://www.worldcitiescultureforum.com>). Two woods – Vincennes (9.95 km², east of
91 Paris), and Boulogne (8.5 km², west of Paris) – are the largest green areas in the city, bringing
92 some nature right into the heart of Paris (Figure 2). These two woods are known to house
93 roosts of large viable populations of the common pipistrelle, while very little is known about
94 roosts location in intramural Paris. This study therefore considers these two woods as viable
95 source habitat patches of the common pipistrelle, that can be connected by foraging
96 movement or dispersal. We model the foraging-commuting habitat availability and
97 connectivity between these woods through the rest of Paris, acoun.



98

Figure 1: Map of the study area, i.e. intramural Paris. a. shows the location of the bat pass acoustic samplings used in the study and the two large parks (Boulognes and Vincennes) identified as the two habitat patches for the focal species *P. pipistrellus*; b. shows intramural Paris in its densified urban context, at the centre of the Paris megalopolis.

99

100 2.2. Methods overview

101 The general method applied in the paper is to quantify the respective contributions of
 102 public and private green areas to habitat availability and connectivity for the common
 103 pipistrelle by comparing its habitat availability and connectivity in a scenario that includes all
 104 of the green areas in Paris (the All green areas scenario) one that includes only public green
 105 areas (the Only public green areas scenario). To do so, we organized the workflow of the
 106 methods in three steps, following the three hypotheses detailed in the introduction. In a **first**
 107 **step**, we fit a model explaining the abundance of common pipistrelle echolocation calls using
 108 environmental variables. In a **second step**, we estimate foraging-commuting habitat
 109 availability for the common pipistrelle by using the fitted model to predict the pass
 110 abundance for the All green areas and Only public green areas scenarios. We isolate the

111 contribution of private green area to foraging-commuting habitat availability for the common
112 pipistrelle by comparing the foraging-commuting habitat availability values obtained under
113 the two scenarios. In a **third step**, we directly derive conductance from predicted foraging-
114 commuting habitat availability and estimate habitat connectivity under the two scenarios
115 using a circuit modeling approach. We isolate the contribution of private green area to habitat
116 connectivity of the common pipistrelle by comparing the connectivity values obtained under
117 the two scenarios.

118

119 **2.3. Step 1: Modeling and predicting bat pass abundance in Paris**

120 *2.3.1 Bat sampling*

121 We produced foraging-commuting habitat availability and connectivity maps for *P.*
122 *pipistrellus* using data from the French Bat Monitoring Programme (FBMP) for 2008 to 2013.
123 The FBMP is coordinated by the French National Museum of Natural History and follows a
124 standardized data recording methodology (Kerbiriou et al., 2018) (Appendix S1). The
125 sampling scheme consists of randomly chosen 2x2 km squares from a 2x2 km grid. Within
126 each square, observers selected and visited 10 points: at least five of these points were
127 representative of the habitats of the square and the others were located in ‘favorable’ places
128 for bats such as along the edge of woods. Each point was sampled using a continuous
129 recording of 6 minutes and the ten points of a site were sampled on the same night and
130 always in the same order at each visit. Observers recorded bats only when weather conditions
131 were favorable (i.e., no rain, temperature higher than 12°C and wind speed of less than 5
132 m/sec; Appendix S1). Observers conducted the sampling during peak daily activity, i.e.
133 beginning thirty minutes after dusk (FBMP recommendations). It generally took less than 3
134 hours to sample the 10 recording points of the square (Vandeveld, Bouhours, Julien, Couvet,
135 & Kerbiriou, 2014). Data was recorded from 2008 to 2013, between the 16th June and the 5th

136 August, during the reproduction period. We extracted the 224 intramural Parisian points from
137 the FBMP database for 2008 to 2013 (Figure 1). Depending on observers' availability over
138 the years, the sampling effort at each point varied from one to five years. The dataset
139 included 552 recordings at 224 points (139 points in 2008, 158 points in 2009, 72 points in
140 2010, 30 points in 2011, 68 points in 2012, 77 points in 2013).

141 We cannot distinguish individual bats from their echolocation calls, making it impossible
142 to calculate absolute bat density, so we used the number of bat passes recorded every 6
143 minutes as a measure of bat activity (for more detail see Appendix S1). A bat pass is defined
144 as one or more bat echolocation calls during a sound recording of 1.2 s at $\times 10$ time
145 expansion (see Appendix S1 for the methodology used to detect the number of bat passes).
146 The identification of the common pipistrelle does not raise issue in Paris, where species
147 overlapping on acoustic repertoires (such as *Pipistrellu. pygmaeus* or *Miniopterus*
148 *schreibersii*) do not occur. The duration of the recording (1.2 s) is predefined by the ultra-
149 sound detector (Tranquility Transect; David Bale, Courtpan. Design Ltd, Cheltenham, UK)
150 (Roche et al., 2011). We used bat activity as a proxy of habitat suitability in terms of food
151 resources and accessibility, hereafter called foraging-commuting habitat (Frey-Ehrenbold,
152 Bontadina, Arlettaz, & Obrist, 2013; Pinaud, Claireau, Leuchtman, & Kerbiriou, 2018;
153 Raino, 2007; Russo & Jones, 2003). Our data showed zero-inflation and were highly
154 overdispersed, with a lot of sites with zero pass and very few over 4 passes, the maximum
155 being 60 passes in a site. In order to account for over-dispersion in the statistical analyses, we
156 applied an adapted method (Hurdle model, see dedicated section) and thresholded the
157 maximum pass abundance at 4, meaning that recordings with more than 4 bat passes were
158 attributed a number of 4. For all analyses, we averaged the abundance of bats passes observed
159 per sample point over the different years.

160

161 2.3.2. *Creating variables for built areas and vegetation*

162 We described the vegetation and built environment of Paris on a raster grid of 2m
163 resolution. We used a set of 18 built areas and vegetation variables to around each pixel or
164 the raster (see below for description and in Appendix S2). We chose variables known to
165 influence the probability of observing the common pipistrelle because of their power to
166 indicate resource availability, roosting opportunities, movement facilitation, or avoidance
167 behaviour. Each variable was computed for three radii around the pixel, i.e., 20 m, 200 m and
168 500 m, to account for very local (street and garden scale, choice of the local flying route) to
169 foraging home-range-scale processes. 20 m corresponds to the minimum detection distance
170 for the echolocation signal of search flight (i.e. echolocation calls before prey detection)
171 (Barataud, 2015; Kalko & Schnitzler, 1993). 200 m and 500 m are in the order of magnitude
172 of the common pipistrelle home range during the reproduction period, as 75% of the foraging
173 activity occurs in a radius of 100 m and 100% in a radius of 750 m (Davidson-Watts, Walls,
174 & Jones, 2006; Nicholls & Racey, 2006). Because Paris is a small geographic area (about
175 12*9 km) with a high density of sampling points (224), 500 m was also a good compromise
176 to capture larger home-range scale processes while limiting extreme overlap between the
177 larger buffers around the sampling points.

178

179 Built areas and vegetation data

180 *APUR (Agence Parisienne d'URbanisme: Parisian Urban Planning Agency)* provided the
181 data on building and vegetation location and height for the year 2012. The data were prepared
182 by *APUR* based on several orthophoto images with a resolution of 0.5 m that we aggregated
183 to a resolution of 2m. The data and their metadata containing more detailed information about
184 data preparation are freely downloadable from the *APUR's* website (*Atelier Parisien*
185 *d'Urbanisme, 2014; Atelier Parisien D'urbanisme, 2016*). We also obtained the location of

186 the public green areas from the *APUR* website (Atelier Parisien d'Urbanisme, 2016). The
187 location of the private green areas was estimated by subtracting the vegetation of public green
188 areas from overall vegetation. In order to provide a broad overview of the respective spatial
189 organization of public and private green areas in Paris, we computed three simple landscape
190 metrics from the raw data: total area, total number of patches and average area of patches, a
191 patch being defined as a unit composed of adjacent pixels of vegetation. For this simple
192 descriptive analysis, a patch of green area was defined as continuous cells covered by
193 vegetation.

194

195 Variables describing the vegetation

196 We computed four different variables based on vegetation height to describe the
197 vegetation environment of the pixel. *P. pipistrellus* is known to respond to vegetation: it
198 typically commutes at a height of ~3–10 m (Berthinussen & Altringham, 2012; Verboom &
199 Spoelstra, 1999); it tends to avoid open habitats and vegetation higher than 3m mitigates the
200 negative effects of urbanization (Hale et al., 2012). We therefore classified vegetation height
201 into three classes: (i) < 1m, (ii) 1 to 3m and (iii) > 3m. We computed the total area covered
202 by these three classes of vegetation and estimated a fourth variable, i.e., the spatial
203 heterogeneity of the height of the vegetation around each pixel, using the standard deviation
204 of vegetation height. We computed these four variables for the three radii (20 m, 200 m and
205 500 m radius), resulting in 12 vegetation variables in total. We calculated these 12 variables
206 accounting for all green areas in the All green areas scenario, and repeated this process for
207 the Only public green areas scenario, only accounting for vegetation located in the public
208 green areas (i.e. excluding the vegetation located outside of the public green areas).

209

210 Variables describing built areas

211 Buildings can be a barrier to movement (Hale et al. 2015) but may also be used for
212 roosting (Simon et al., 2004). Furthermore, intermediate building height has been shown to
213 be linked to higher abundance of insectivorous bird species in Paris (Pellissier et al., 2012).
214 Beyond their direct effects on movement and habitat availability, buildings' height and
215 density can also be considered as a more general indicator of anthropogenic pressure,
216 correlating with light and noise disturbance on an urbanization gradient (Grimm et al., 2008).
217 We classified buildings within two height classes. Buildings under 15 m mainly consisted of
218 low-rise buildings and individual houses. This class of building was dominant in the external
219 districts of Paris (Figure 1). Buildings over 15 m were mainly located in the old center of
220 Paris and in the north-west. For each of the three scales detailed earlier (i.e., 20 m, 200 m and
221 500 m radius), we computed the area covered by the two building classes and attributed the
222 value to the central pixel.

223

224 *2.3.3. Modeling bat pass abundance using vegetation and built areas*

225 We modeled the relative pass abundance of *P. pipistrellus* with the previously described
226 vegetation (12 variables) and built areas (six variables), using a boosted regression tree
227 modeling approach (gbm) (gbm package; Greg Ridgeway with contributions from others,
228 2017) using R 3.4.0 (R Core Development Team, 2018). The gbm approach was relevant in
229 this study because it can handle a large number of predictors – even collinear ones – and deal
230 with spatial autocorrelation effectively, and it also has a strong predictive performance (J.
231 Elith, Leathwick, & Hastie, 2008). Because the data contained a lot of zeros (130 points out
232 of a total of 224 points), we employed a Hurdle modeling approach to account for zero-
233 inflation (Potts & Elith, 2006; Povak et al., 2013). This approach is consistent with previous
234 studies modeling bat passes (Aurelie Lacoëuilhe, Machon, Julien, Le Bocq, & Kerbiriou,
235 2014; Vandeveldé et al., 2014). The Hurdle model is a two-step modeling approach. The first

236 model, run on data transformed into Presence/Absence pass data, calculates the probability of
237 pass occurrence. The second model is fitted on the pass abundance data (excluding absence
238 data), and aims to predict pass abundance only where bat passes are predicted to potentially
239 occur in the first model. When used for prediction purpose on a new set of environmental
240 data, the Presence/ Absence model is run first. If the predicted value is below a fixed pass
241 occurrence probability (assimilated to predicted absence), the predicted value is maintained.
242 If the predicted value is above the fixed threshold, then it is the value predicted by the
243 abundance model that is retained. Based on the results of Presence/ Absence modeling, we
244 fixed the threshold between absence and presence at 0.45. Because the number of years of
245 observation varied between the different points, we weighted the points by the number of
246 years of observation. We calibrated the models with a learning rate of 0.0005, an interaction
247 depth of 4 (meaning that we consider interactions), a minimal number of individuals per leaf
248 of 10, and a fraction of 0.6 for training the algorithm (J. Elith et al., 2008). We checked for
249 and did not find any significant residual spatial autocorrelation. As output, the boosted
250 regression tree provides the scaled contribution summing up at 100 (or importance, or
251 influence) of the environmental variables included in the model (Jane Elith, Leathwick, &
252 Hastie, 2008).

253

254 **2.4. Step 2: Evaluating the contribution of private green areas to foraging-** 255 **commuting habitat availability**

256 *2.4.1. Estimating foraging-commuting habitat availability*

257 We used the fitted Hurdle model to predict the bat pass abundances over the entire study
258 area for the Only public green areas and the All green areas scenarios. We then used the
259 resulting bat pass abundance as foraging-commuting habitat availability maps. For the All
260 green areas scenario, predictions were based on the vegetation variables encompassing all

261 green areas, whereas for the Only public green areas scenario, vegetation variables were
262 restricted to the green public areas. We measured total foraging-commuting habitat
263 availability (hereafter referred to simply as habitat availability) for each scenario as the sum
264 of all predicted pass abundance in intramural Paris.

265

266 *2.4.2. Contribution of private green areas to foraging-commuting habitat availability*

267 We estimated the contribution of private green areas to habitat availability by subtracting
268 the total predicted pass abundance of *P. pipistrellus* over the entire study area of the Only
269 public green areas scenario from the predicted pass abundance for the All green areas
270 scenario.

271

272 **2.5. Step 3: Evaluating the contribution of private green areas to foraging-** 273 **commuting habitat connectivity**

274 *2.5.1. Conductance maps*

275 Conductance maps depict the ease of movement across the mapped area that varies, for
276 example, with land cover, habitat quality or slope. Conductance maps are used as input data
277 to model connectivity under the Circuit approach. We used the habitat availability maps as
278 conductance maps. This data-based approach is expected to produce more realistic
279 conductance values than would be obtained using expert opinion. We changed the resolution
280 of the two habitat availability maps from 2 m to 20 m by averaging the values of the cells.
281 This change in resolution was needed to be coherent with the bat's perceptual grain, defined
282 as the grain at which an organism responds to the heterogeneity of the landscape (Wade,
283 Mckelvey, & Schwartz, 2015; Wiens & Milne, 1989) (see Appendix S3 for details). As *P.*
284 *pipistrellus* can only detect its prey within a maximum radius of 3.5 m for small prey and of
285 15m for large prey (Holderied & Helversen, 2003), we consider a resolution of 20 m would

286 adequate fit its perceptual range. We then summed predicted bat passes within all pixels for
287 intramural Paris (excluding the Vincennes and Boulogne parks) to obtain a simple indicator
288 of habitat availability. We obtained the conductance maps by rescaling the predicted pass
289 abundances to values between 0 and 10,000.

290

291 *2.5.2. Building connectivity maps*

292 We modelled connectivity using Circuitscape, a program that uses circuit theory to model
293 connectivity in heterogeneous landscapes (McRae & Beier, 2007). The Circuit theory
294 approach provides a continuous estimate of connectivity within the area studied, i.e., for each
295 pixel, integrating all possible pathways. We identified two areas, i.e., Boulogne and
296 Vincennes woods, as habitat patches known to house roosts of viable populations of the
297 common pipistrelle and able to act as source for smaller populations within intramural Paris.
298 Furthermore, we know that intramural Paris houses roosts of the common pipistrelle, but their
299 location is unknown. We therefore created and randomly placed a fishnet of points distant of
300 2 km, each point simulating a possible location of an intramural roost and a potential foraging
301 area. A distance of 2 km corresponds to the higher estimate of the mean distance flight by the
302 common pipistrelle between the roost and the core of the foraging area (Nicholls & Racey,
303 2006). We added the two woods to these points for a total of roosts / foraging areas. We then
304 simulate the connectivity between pairs of points distant of maximum 2 km (for a total of 38
305 pairwise connectivity measures), representing that way the connectivity between each roost
306 and foraging areas located at flying distances. Each roost was therefore connected to one to
307 four other points depending on its location in intramural Paris. We used a pairwise modelling
308 mode, meaning that connectivity was assessed accounting for flows coming from and going
309 to each point, meaning that each point was considered acting as roost and as foraging area.
310 Each node (raster cell) was connected to eight neighbours. For each of the 38 pairwise

311 connectivity measure, Circuitscape provides a connectivity map based on conductance, and a
312 measure of the total conductance between the two points. We obtained a map of connectivity
313 for the entire intramural Paris summing up the 38 connectivity maps to, and estimated the
314 total conductance of intramural Paris summing up the total conductance of the 38 pairwise
315 connectivity measures.

316

317 *2.5.2. Contribution of private green areas to foraging-commuting habitat connectivity*

318 We estimated the contribution of private green areas to habitat connectivity by subtracting
319 the total conductance value for the Only public green areas scenario from the total
320 conductance value for the All green areas scenario for the entire study area.

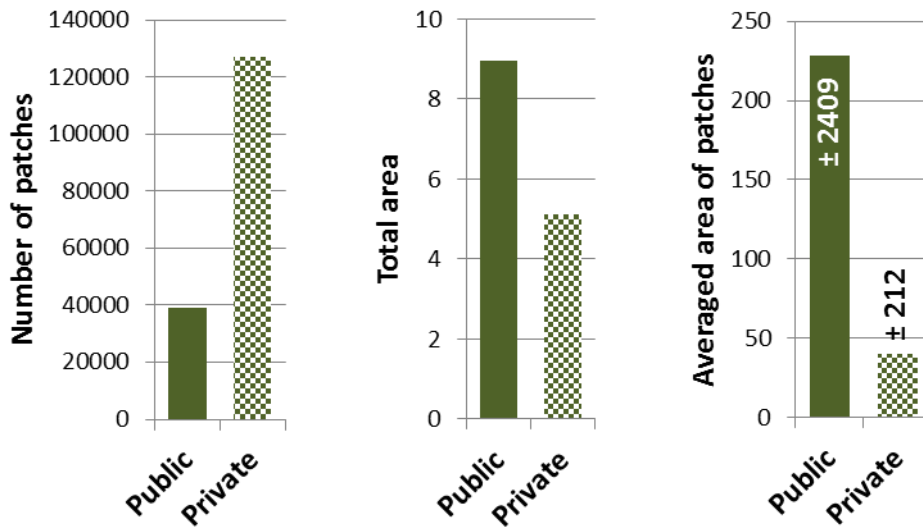
321

322 **3. Results**

323 **3.1. Spatial characteristics of public and private green areas in Paris**

324 The total green area belonging to private owners was smaller than the total public green
325 area (36.4% and 63.6 %, respectively; Figure 2a). The private green areas were much more
326 fragmented, as illustrated by a number of patches that was three times higher than for public
327 areas and an average patch size five times smaller (Figure 2b and 2c).

328



329

Figure 2: Comparison of public and private green areas in the Paris area using three basic landscape metrics: a. total area, b. total number of patches and c. average area of patches with the standard deviation. The metrics have been computed for intramural Paris, excluding the Parks of Vincennes and Boulogne which were excluded from the modeling of the bat pass abundance.

330

331

3.2. Step 1: Modeling and predicting bat pass abundance in Paris

332

The gbm analyses produced contrasting results for Presence/Absence and abundance of passes data for the built areas and vegetation variables and their scale of impact, suggesting different processes underpinning pass occurrence and abundance (Figure 3, Appendix S4).

335

The Presence/ Absence of bat passes was dependent on home-range scale (200 m to 500 m radius). The passes were more likely to occur in areas with a high proportion of vegetation

337

and less likely to occur in areas with large concentrations of buildings under 15 m high. The

338

occurrence of bat passes revealed a higher abundance of bat passes when buildings are

339

smaller (under 15 m high), at these scales. The abundance of passes was mainly driven by

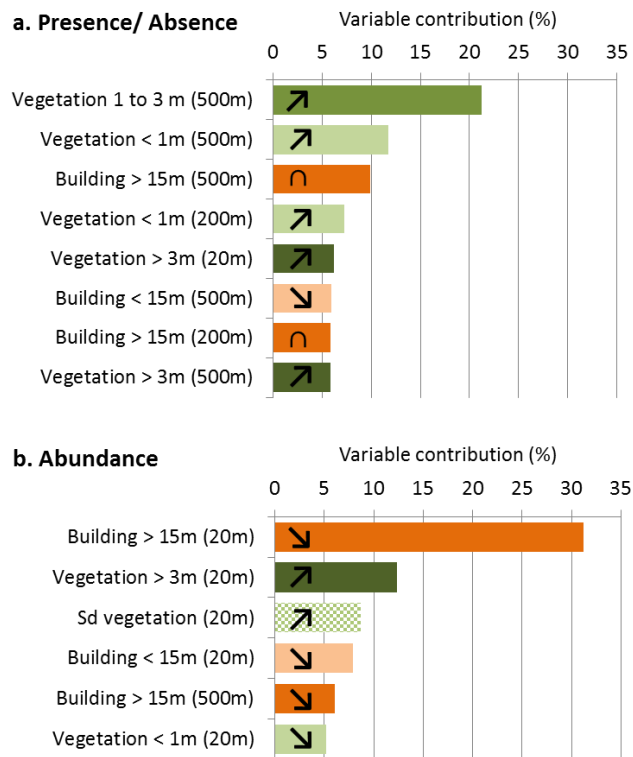
340

very local conditions (20 m) and to a lesser extent by home-range scale conditions (200 m

341

and 500 m). Locally, the high proportion of tall buildings was the strongest driver, negatively

342 impacting the bat pass abundance. Overall, the proportion of buildings tended to decrease the
 343 abundance of passes at all scales. Conversely, a large proportion of tall vegetation as well as
 344 the variation in vegetation height at 20 m and 200 m tended to be beneficial (Figure 3,
 345 Appendix S4).
 346



347

Figure 3: Variables ordered by their contribution to the occurrence and bat pass abundance as estimated by the two gbm analyses (in percent). a. the Presence/ Absence data, and b. the abundance of passes data. The contribution is the relative influence of each variable on the response variable. The signs (increasing and decreasing arrows and unimodal shape) indicate the general form of the response of the bat pass abundance to each variable, i.e., increasing, decreasing or unimodal. Only the variables with higher contributions are shown.

348

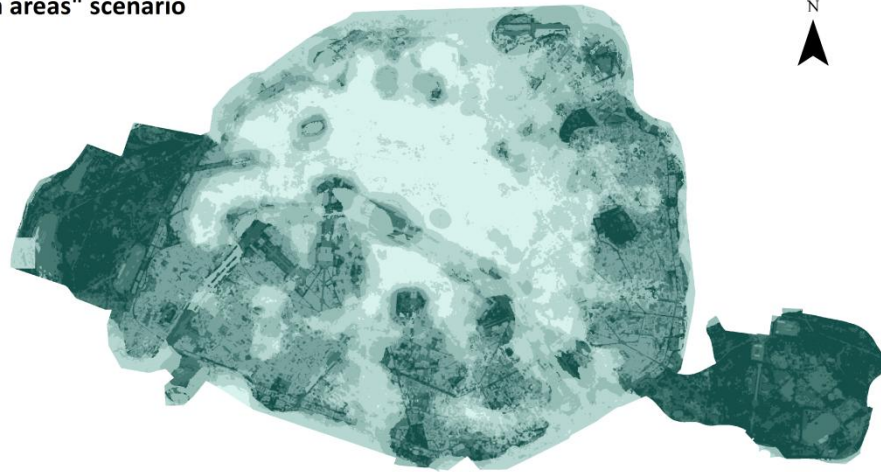
349 **3.3. Step 3: Evaluating the contribution of private green areas to foraging-**
350 **commuting habitat availability**

351 The interpolated predictions of bat pass abundance for the All green areas scenario,
352 showed that larger predicted pass abundances were mainly concentrated in the two large
353 parks of Boulogne and Vincennes (Figure 4) and to a lesser extent within Paris' larger parks.
354 In intramural Paris, the highest predicted pass abundances were found mostly in the southern
355 and eastern peripheral areas. The map of predicted pass abundances under the Only public
356 green areas scenario also identified the two large parks as main areas of habitat (Figure 4).
357 The areas with higher predicted habitat availability were the same in the two scenarios, but
358 the predicted abundances were much lower in the No private areas scenario. The predicted
359 pass abundances were extremely low in the dense city center, north of the Seine River.

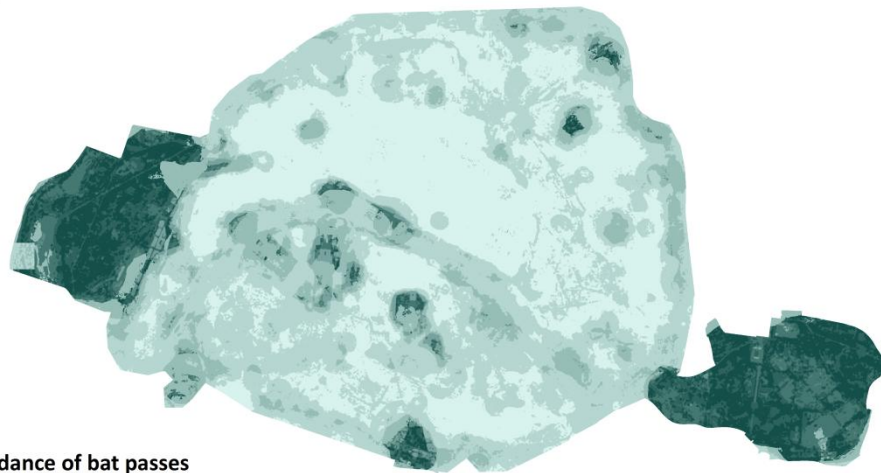
360 The total number of predicted bat passes (summed over Paris excluding the woods) was
361 12,874,960 in the All green areas scenario, and 6,709,623 in the Only public green areas
362 scenario. The difference, i.e., 6,165,337 bat passes, corresponded to the contribution of
363 private green areas to available habitat, and therefore represents 47.9% of the contribution of
364 total green areas to available habitat while private green areas represent just 36.4% of the
365 total green area.

366

a. "All green areas" scenario



b. "No private green areas" scenario



Predicted abundance of bat passes



Kilometers
0 1 2

367

Figure 4: Habitat availability maps of *P. pipistrellus* in Paris showing the bat pass abundance as predicted by the gbm for a. the all green areas scenario and b. the Only public green areas scenario. The bat pass abundance values showed in these maps were rescaled between 0 and 10,000 to give the conductance maps used as input maps for Circuitscape.

368

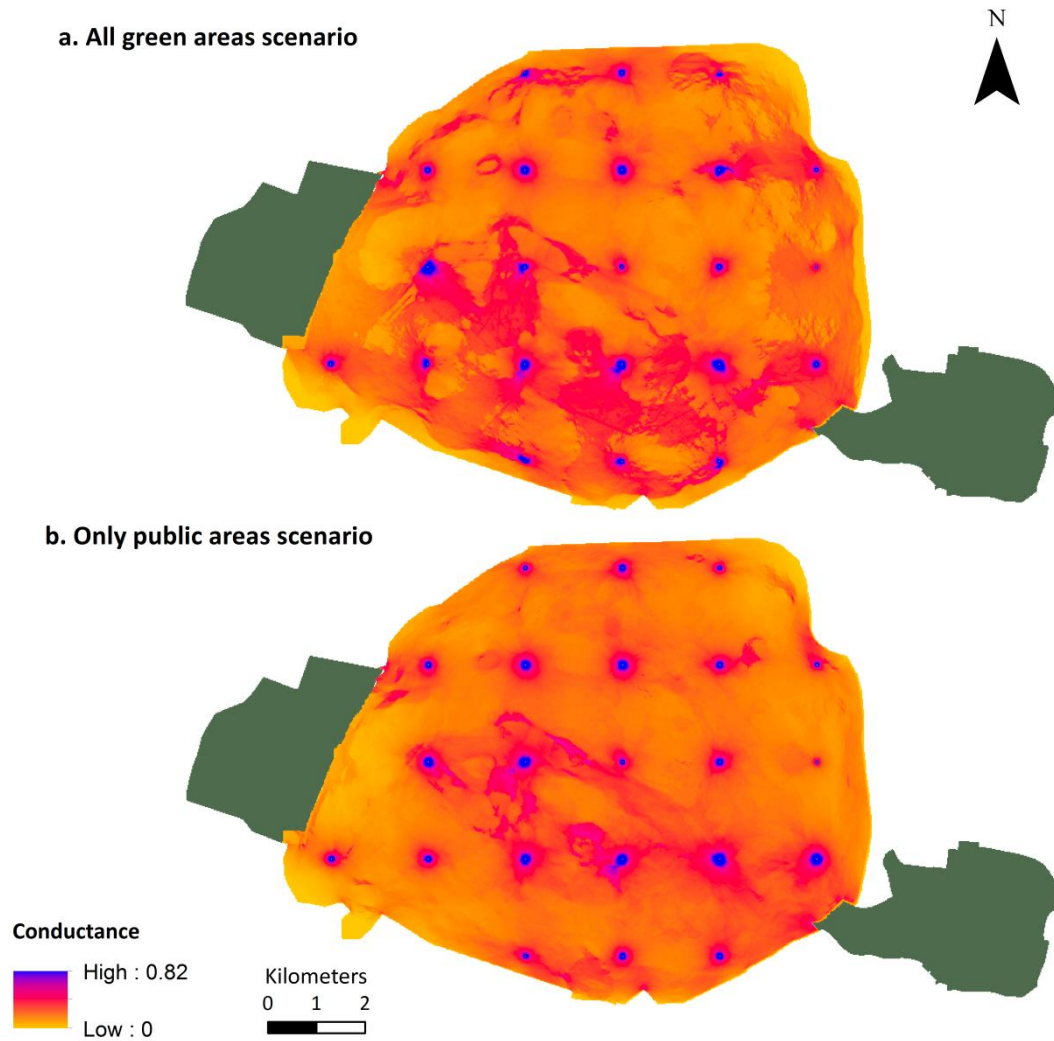
369

370

3.4. Step 3: Evaluating the contribution of private green areas to foraging-commuting habitat connectivity

371 The spatial structuring of the conductance maps under the two scenarios revealed close
372 spatial structures with connectivity paths mainly located in the south of Paris (Figure 5).
373 However, the total resistance in intramural Paris was estimated to be 3.55 in the All green
374 areas scenario, compared to 5.59 for the Only public green areas scenario, meaning that
375 private green areas decreased the city's total resistance by 57.6% when compared to the
376 resistance of the Only public green areas scenario.

377 The connectivity map for the All green areas scenario shows stronger connectivity paths
378 passing through the peripheral areas of the city with the southern area showing higher
379 connectivity levels. In the Only public green areas scenario, the Seine River appeared as the
380 preferred path across Paris, concentrating a large proportion of the flow. The contribution of
381 private green areas to connectivity did not follow clear spatial patterns, either creating new
382 paths or strengthening exiting paths between public green areas, especially in the south
383 (Figure 5).



384

385

Figure 5: Conductance maps for *P. pipistrellus* in Paris representing potential fluxes between simulated colonies (including the Boulogne and Vincennes woods, dark green patches) and foraging areas located at a maximum distance of 2 km, for a. the All green areas scenario and b. the Only public green areas scenario.

386

4. Discussion

387

P. Pipistrellus is among the more habitat generalist of bat species (Regnery, Couvet,

388

Kubarek, Julien, & Kerbirou, 2013) and is regularly found in urban areas (Bartonicka &

389

Zukal, 2003; Hale et al., 2012; Vandeveldel et al., 2014). In line with previous findings, we

390 observed a positive impact on bat occurrence of the total area covered by vegetation at home-
391 range scales (200 m and 500 m) (Azam et al., 2015; Aurélie Lacoeylthe, Machon, Julien, &
392 Kerbirou, 2016). However, while occurrence was more effectively predicted by home-range
393 scale environmental conditions (200m to 500m), bat pass abundance was largely driven by
394 very local conditions (20 m). In other words, while the probability of bat presence was linked
395 to conditions in 200 to 500 m radii, conditions in 20 m to 200 m radii were predominant in
396 explaining the location of the paths. At such very local scales and in line with previous
397 findings, our results showed that higher bat pass abundance is linked to a selection of woody
398 habitats and the avoidance of open habitats (Bartonicka & Zupal, 2003; Hale et al., 2012; C.
399 G. Threlfall, Williams, Hahs, & Livesley, 2016) and to variation in vegetation height (Suarez-
400 Rubio, Ille, & Bruckner, 2018). The proportion of built areas had a negative overall impact
401 on the presence and abundance of passes although an intermediate proportion of higher
402 buildings appeared to be beneficial for the species (Hale et al., 2012). A similar high building
403 effect has previously been observed in Paris for insectivorous birds, so we may hypothesize
404 that this building structure benefits insectivorous species' foraging activity possibly by
405 concentrating the insects in certain areas (Pellissier et al., 2012).

406

407 Regarding habitat availability, higher bat activity was recorded and predicted in the
408 peripheral areas of Paris where the higher density of private green areas both enhanced the
409 attractiveness of large public green areas and greatly extended their benefits for the species to
410 the surrounding areas of the city via a net buffering effect. These results highlight the
411 complementary contribution of private and public green areas to habitat availability and
412 quality, a process known as Ecological land-use complementation in research literature
413 (Colding, 2007). Here, we observed that large public green areas constitute the main patches
414 of available habitat in the city (core areas) while private green areas increase their capacity to

415 support individuals and enlarge their effective area. Comparable complementation effects of
416 gardens for public areas have been documented elsewhere. While the importance of private
417 green areas for the common pipistrelle has already been demonstrated in previous studies
418 (Hale et al., 2012), here we have shown that in Paris private green areas have a
419 disproportionately positive impact on habitat availability *vis-à-vis* their total coverage. Thus,
420 while private green areas only represented 36.4% of the total green area, we found that they
421 actually supported 47.9% of total habitat availability (i.e. foraging-commuting activity) for
422 the common pipistrelle. This importance could be attributable to the differential types of
423 vegetation favored in private green areas when compared with public green areas. Thus, the
424 areas with high density of private green areas also appear to have higher availability of taller
425 vegetation, which is an important driver of bat activity in our study.

426

427 The complementation effect between private and public green areas for the common
428 pipistrelle was even stronger in the case of connectivity, as private green areas decreased the
429 total resistance of the city by 88.7% even though they only represented 36.5% of the total
430 green area. Thus, the spatial configuration of private green areas in the city appeared to be
431 very important for the common pipistrelle, providing the stepping stones between the public
432 green areas that serve as the nodes of the urban network (Rudd et al., 2002). If private green
433 areas consist of small patches uniformly distributed across the city, they appear fragmented
434 but not isolated, with the notable exception of the city center which appears highly resistant
435 for the species. A study focusing on the role of green areas at business sites in the Parisian
436 ecological network drew comparable conclusions, enhancing the functional connectivity role
437 of green areas at business sites as stepping stones (Serret et al., 2014).

438

439 Despite reducing potential connectivity modeling biases using outputs of a model instead
440 of costs for land covers defined by expert opinion, the overall approach we used still has
441 certain limitations. First, as we did not have information about the location of private green
442 areas, we bypassed this problem by only considering public green areas and inferring the
443 importance of private green areas by subtracting the values obtained for the Only public
444 green areas scenario from the All green areas scenario. This method can induce small biases
445 if the delineation of public areas is not perfect, i.e. if the vegetation of the public areas
446 slightly exceeds the shape of the polygons delineating the public green areas. This problem
447 leads at not recognizing those exceeding pixels as being part of the public green areas, while
448 they should be. This translates into an underestimation of the area of public green spaces,
449 while the impact on the location is very little as those pixels are adjacent to the public green
450 areas. It is not possible to quantify the amount or proportion of area concerned by this bias,
451 but it concerns maximum few pixels per public green area. As a consequence, such error is
452 likely to induce a small underestimation of the abundance predicted for the “Only public
453 areas” scenario compared to what would be obtain without this error. Such small variation is
454 expected to have only very small impact on the estimations of the relative importance of
455 public versus private areas for habitat availability and connectivity that could not change the
456 general conclusions of the study. Second, we limited our study area to intramural Paris,
457 excluding the surrounding urban areas where the density of built areas is sometimes lower
458 than in intramural Paris. In other words, we excluded potential connectivity paths linking the
459 two parks but bypassing Paris. The existence of such paths would reduce the flux of
460 individuals flying in/through Paris but would not change the observations concerning habitat
461 availability and connectivity patterns.

462

463 **5. Conclusions**

464 This study has two outcomes important for management and conservation strategies in city.
465 First, it shows the disproportionately high contribution of private green areas to the common
466 pipistrelle habitat availability and connectivity as compared with their total area. Second, it
467 gives support to previous finding on public and private green areas complementary effects.

468 These findings tend to confirm the benefits of moving towards more inclusive
469 conservation strategies that include both public and private stakeholders in cities (Rands et al.,
470 2010). Private areas have been found to contain more plant diversity and rarer species than
471 public areas (Politi Bertoncini et al., 2012). Wildlife-friendly gardening, as time investment
472 in the garden and reducing pesticide, has been shown to positively impact wildlife (Goddard
473 et al., 2013; Muratet & Fontaine, 2015). Thus, it is the way in which private green areas are
474 managed that could be targeted by new conservation initiatives in cities, following the ones
475 applied to public green areas over the past few years (City of Dublin, 2016; City of London,
476 2016; Conseil de Paris, 2018; Ville de Paris, 2017). The challenge for conservation is
477 therefore to organize and manage these human-occupied areas to increase their ecological
478 value (Dearborn & Kark 2010). This objective for conservation comes with important
479 difficulties linked to the lack of space in cities and changes in owners' needs (Warhurst et al.
480 2014). Such changes have for instance led in the past decades to a trend toward gardens'
481 conversion to impervious surfaces, as car parks, clearly antagonistic to conservation
482 objectives (Perry & Nawaz 2008; Warhurst et al. 2014).

483

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738

Appendices

Appendix S1: Detailed information on recording settings and conditions

1. Protocol

1.1. General description

739 **Table S1-1:** Characteristics of the protocol and sampling design used for the monitoring of
740 the temporal trends of bat populations on a national scale by the French Bat Monitoring
741 Programme (Vigie-Chiro, 2018), supervised by the French Museum of Natural History. In
742 brackets and bold are indicated the small adaptations of the protocol made for the data used in
743 the present study.

| | |
|------------------------------------|---|
| Count point survey sampling | |
| <i>Scope</i> | 2x2 km square randomly selected by the Museum. |
| <i>Number of point per circuit</i> | 10 |
| <i>Recording duration</i> | 6 minutes |
| <i>Period of sampling</i> | from the 15th June to 31th July (to 5th August) |
| <i>Weather conditions</i> | no rain, low wind speed (< 7m/s i.e 25km/h), temperature > 12°C |
| <i>Survey start</i> | if possible 30 minutes after sunset |

| | |
|--|--|
| Bat recording | |
| <i>Acoustic detectors</i> | Tranquility Transect Bat detector (Courtpan Design Ltd., Cheltenham, UK) |
| <i>Intercalibration of detectors</i> | Sensitivity levels were set to enable the detection of echolocation calls while minimizing background noise due to wind or insects, intercalibration of detectors were operate at the MNHN |
| Acoustic settings | |
| <i>Time expansion factor</i> | 10 |
| <i>The duration of the record predefined by the ultra-sound detector</i> | 1.2 sec |
| <i>High pass filter</i> | 5 kHz |
| <i>Frequency</i> | 96 000 sample/sec |
| <i>Recording device</i> | Zoom H2 digital recorder (Samson technologies, USA) |
| <i>File storage format</i> | WAV |

| | |
|---------------------------|---|
| Bat identification | |
| <i>Software</i> | Syrinx 2.6 |
| <i>Procedure</i> | - Training: The majority of volunteers involved in bat monitoring had participated in 2-day training courses organized since 2007, providing homogeneity in the identification criteria. - Bat first identification: by volunteers - Bat identification validation: by MNHN (all calls were checked) |

| | |
|----------------------------|---|
| Meteorological data | - Temperature (°C) and cloud cover (% in four classes: 0-25%, 25-50%, 50-75%, 75-100%) were recorded by volunteers during the survey. - Wind speed (km/h) was provided by the closest meteorological station, (i.e. Paris Monsouris) using public archives available at Infoclimat [http://www.infoclimat.fr/] |
|----------------------------|---|

1.2. Bat activity records

We used Syrinx software version 2.6 (Burt, 2006) for spectrogram and Adobe Audition for spectral analysis together with Scan'R (Binary Acoustic Technology, 2010) to isolate each bat vocalization and automate measurement of relevant parameters (Gannon et al., 2004, Obrist et al., 2004, Barataud 2012). Sound species identification was verified by coordinators of the French Bat Monitoring Program (Jean-François Julien & Christian Kerbiriou). *P. pipistrellus* is a bat which identification does not raise noticeable identification uncertainty,

and even less in continuous urban fabric context such as Paris where species overlapping on acoustic repertoires (such as *P. pygmaeus* or *Miniopterus scherbersii*) do not occur.

1.3. Measurement of bat activity

Bat activity at the point scale is calculated as the sum of the number of bat passes recorded per 6 minutes (Fig S1-2a). We identified a bat pass as a call sequence containing one or more pulses and when the time between calls exceeded four times the inter-pulse interval (Parsons & Jones, 2000, Kerbiriou et al. 2019). In the protocol followed in this study, the duration of the record is fixed at 1.2 seconds. Within each 1.2 s recording, the minimum number of bat recorded simultaneously were estimated using inter-pulse interval and frequency (Fig S1-2b).

Figure S1-2a: example of a 6 minutes recording period (expressed in ms) including 10 records of sound event at a $\times 10$ time expansion. A sound event is triggered by a bat echolocation call or any other ultrasonic emission.

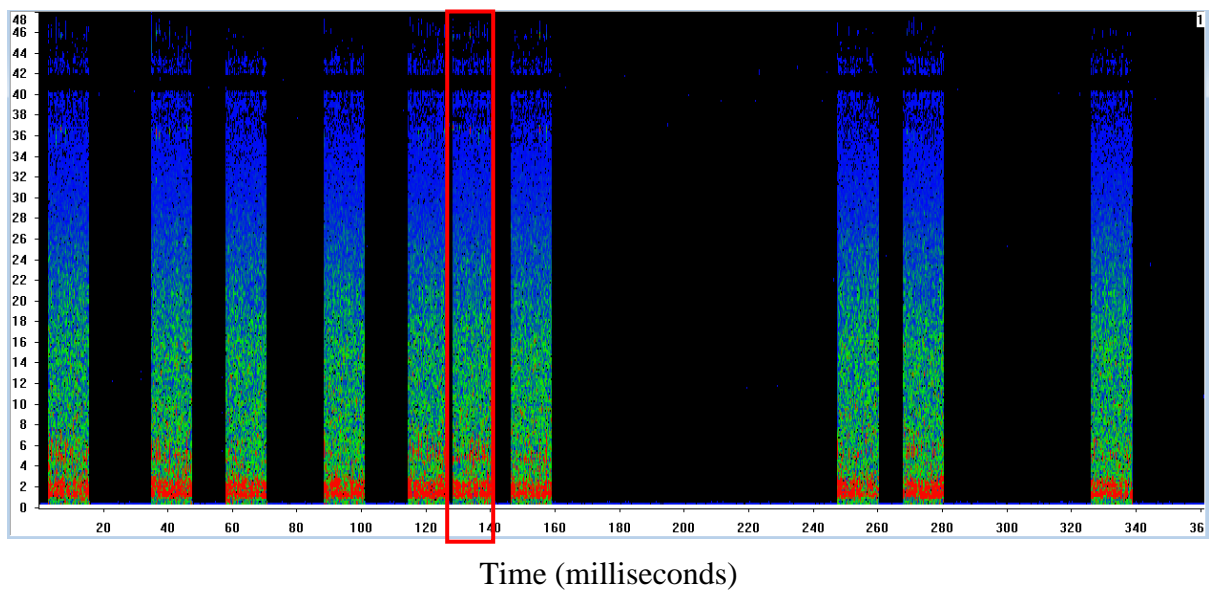
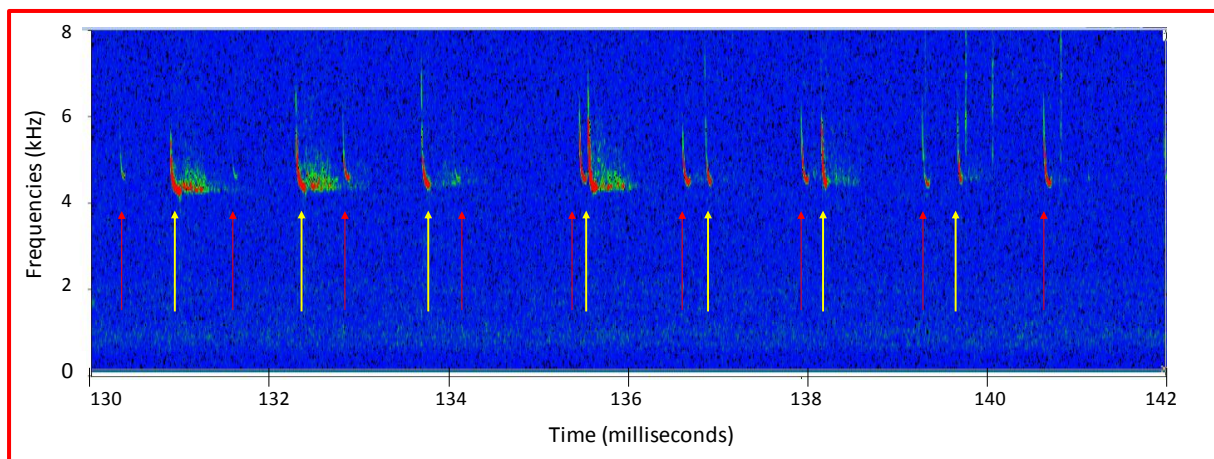
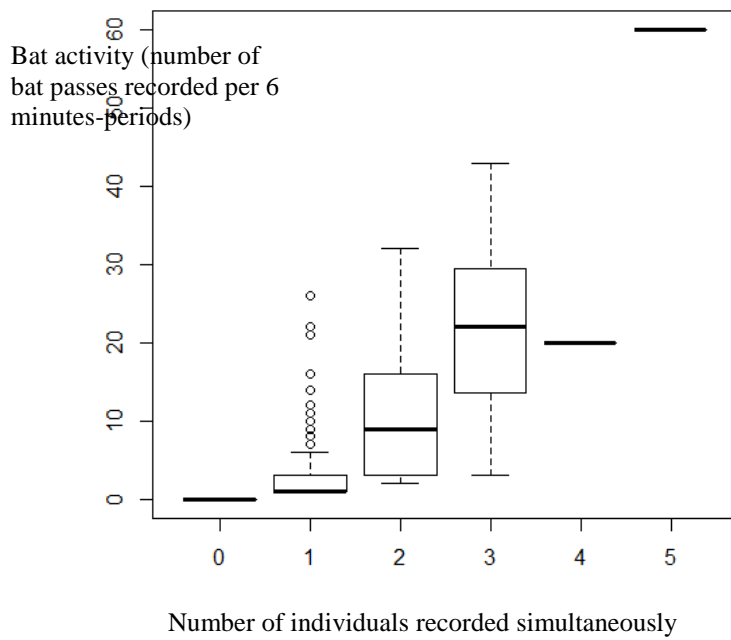


Figure S1-2b: focus on a 1.2s sound sample (time expansion, expressed in ms) recorded at the time 130ms of the previous recording period example (see red inset in Fig. S1-2a). This sound event includes 2 individuals of *P. pipistrellus* (highlighted by red and yellow arrows).



1.4. Relationship between bat activity and the number of recorded individuals

Figure S1-3: Relationship between bat activity and the number of individuals recorded simultaneously



Model structure:

bat activity ~ number of individuals recorded simultaneously + site | recording session

where *recording session* identify a point *i* sample at a date *k*

GLMM Negative Binomial (theta= 0.979)

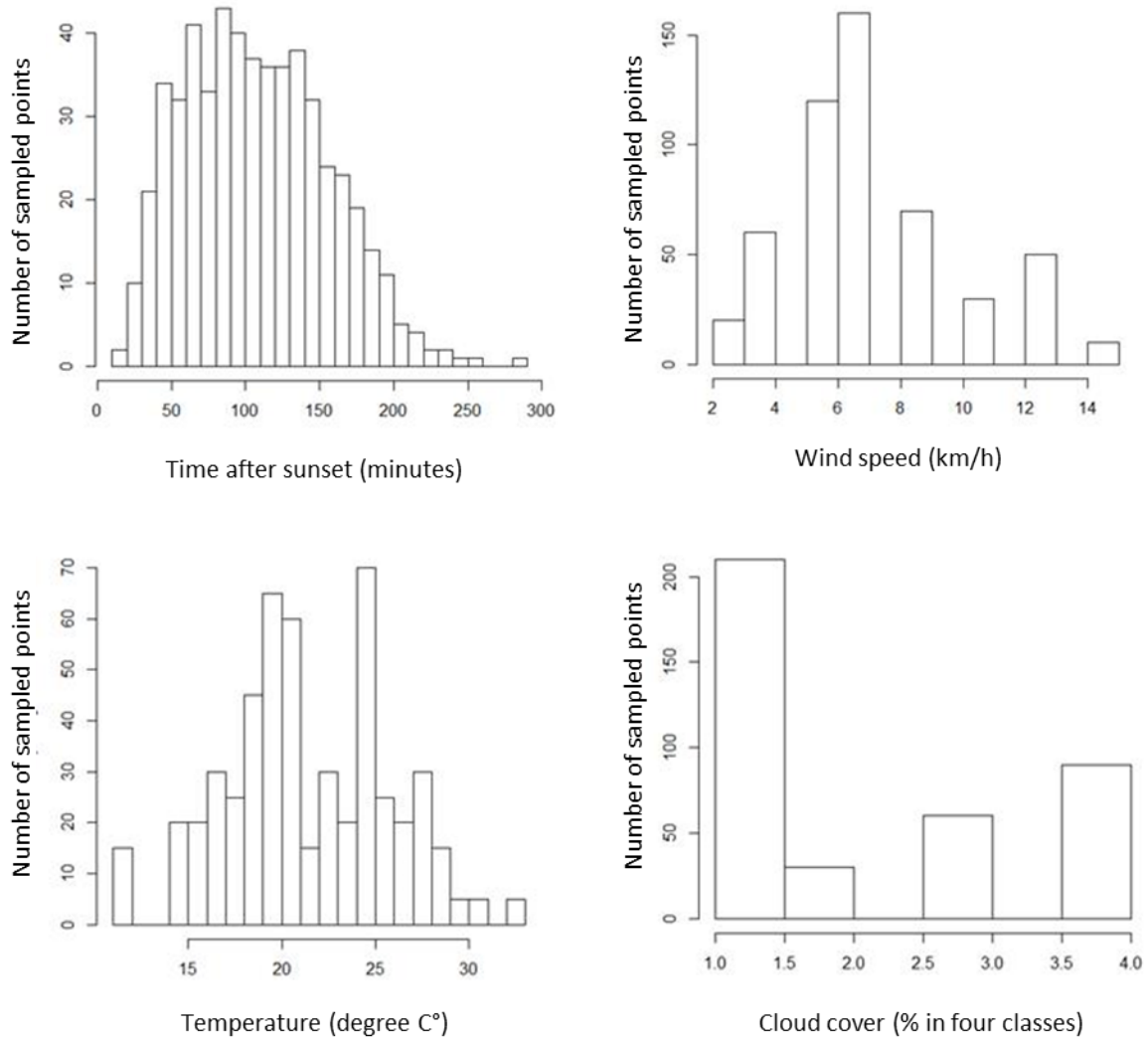
P<0.0001,

Deviance explained : 71%,

R² = 0.49

2. Data sampling conditions

Figure S1-1: Time and weather sampling conditions

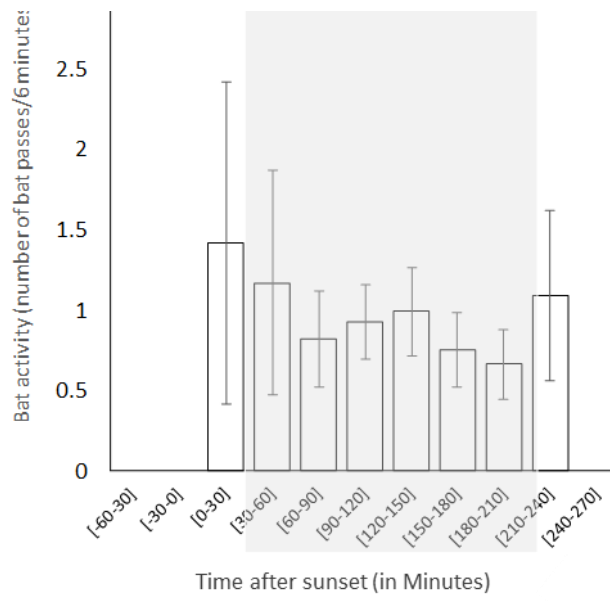


3. Exploring potential biases

3.1. *Patterns of nightly activity of P. pipistrellus*

Volunteers are strongly encouraged to conduct their sampling during daily peak activity (Roche et al., 2005), i.e. beginning thirty minutes after dusk (FBMP recommendations). It usually takes less than 3 hours to sample the 10 recording points of each square: 97% of data collected in Paris occurred between 30 minutes and 3h30 after sunset. During this period the pattern of nightly activity in urban context for *P. pipistrellus* is relatively flat (Fig. S1-4)

Figure S1-4: Pattern of nightly activity of *P. pipistrellus* in Paris, with the data of the present study ($n = 552$ 6-minutes recordings, 224 points, averaged over the years 2008 to 2013). The time section highlighted in light grey represent the daily sampling time (between 30 minutes and 3 hours and 30 minutes after sunset, as recommend by the FBMP).



3.2. Correlation between time of recording and the set of explanatory variables

744 **Table S1-2:** Correlation (Spearman's ρ) between time of recording and the explanatory
 745 variables (all explanatory variables are in m²).

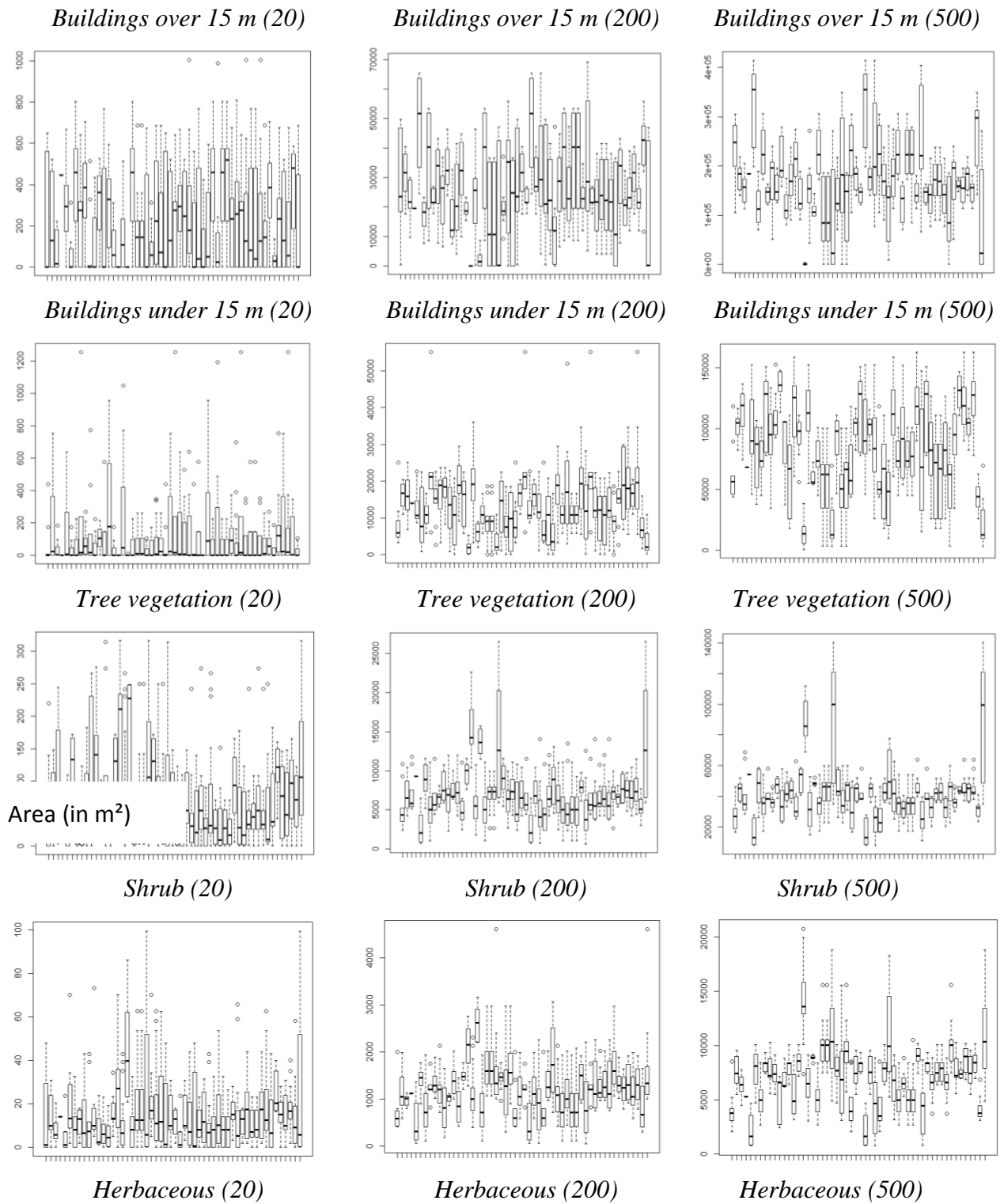
| Landscape-scale | 20 | 200 | 500 |
|-----------------------------|-------------------------------|-------------------------------|-------------------------------|
| <i>Buildings over 15 m</i> | $\rho=0.048$; $P=0.265$ | $\rho=0.054$; $P=0.209$ | $\rho=0.027$; $P=0.522$ |
| <i>Buildings under 15 m</i> | $\rho=0.055$; $P=0.200$ | $\rho=-0.070$; $P=0.1039$ | $\rho=-0.109$; $P=$ 0.011 |
| <i>Tree vegetation</i> | $\rho=0.029$; $P=0.503$ | $\rho=-0.017$; $P=0.690$ | $\rho=-0.023$; $P=0.593$ |
| <i>Shrub</i> | $\rho=-0.013$; $P=0.758$ | $\rho=-0.004$; $P=0.931$ | $\rho=-0.040$; $P=0.352$ |
| <i>Herbaceous</i> | $\rho=-0.014$; $P=0.743$ | $\rho=0.010$; $P=0.823$ | $\rho=-0.039$; $P=0.362$ |
| <i>Sd vegetation height</i> | $\rho=-0.042$; $P=$ 0.325 | $\rho= 0.100$; $P=$ 0.020 | $\rho= 0.082$; $P=$ 0.056 |

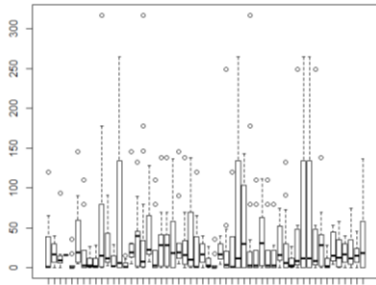
746

747 To protect from Type I error, a Bonferroni correction should be considered: for an alpha-
 748 value ($\alpha_{original}=0.05$) the Bonferroni correction ($\alpha_{adjusted} = \alpha_{original}/k$; $\alpha_{adjusted}=0.0028$), thus to
 749 determine if any of the 18 correlations is statistically significant, the P -value must be
 750 $P<0.0028$

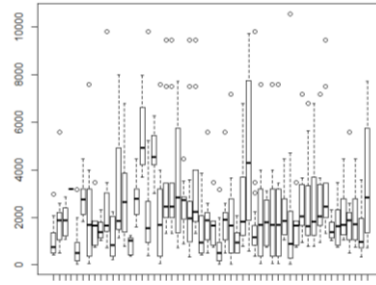
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753 **Figure S1-5:** Boxplots of the explanatory variables of the samples ordered along recording
 754 nights. The figure shows that there is no relationship between the type of urban space
 755 sampled and the sampling period within the year.

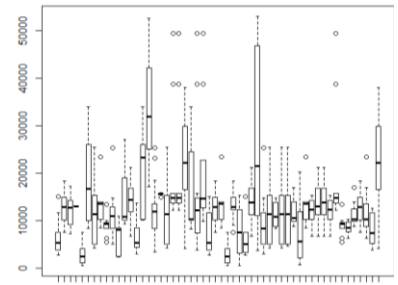




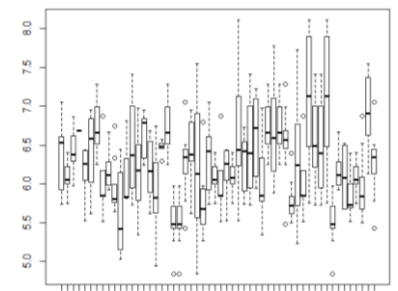
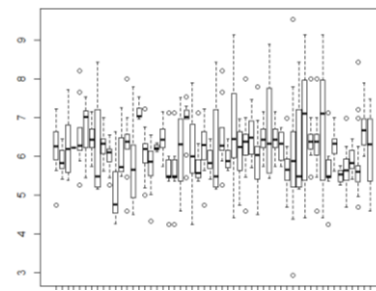
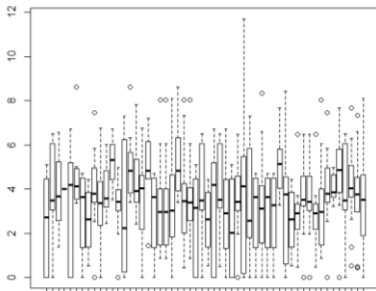
Sd vegetation height (20)



Sd vegetation height (200)



Sd vegetation height (500)



Nights of recording (in chronological order)

756

757

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766 **Appendix S2: List of environmental variables used to model the abundance of the**
767 **common pipistrelle in Paris (step 1)**

768

769 20 m radius:

- 770 - Area of building over 15 m height
- 771 - Area of building under 15 m height
- 772 - Area of vegetation under 1 m
- 773 - Area of vegetation between 1 m and 3 m
- 774 - Area of vegetation over 3 m
- 775 - Standard deviation of vegetation height

776 200 m radius:

- 777 - Area of building over 15 m height
- 778 - Area of building under 15 m height
- 779 - Area of vegetation under 1 m
- 780 - Area of vegetation between 1 m and 3 m
- 781 - Area of vegetation over 3 m
- 782 - Standard deviation of vegetation height

783 500 m radius:

- 784 - Area of building over 15 m height
- 785 - Area of building under 15 m height
- 786 - Area of vegetation under 1 m
- 787 - Area of vegetation between 1 m and 3 m
- 788 - Area of vegetation over 3 m
- 789 - Standard deviation of vegetation height

790

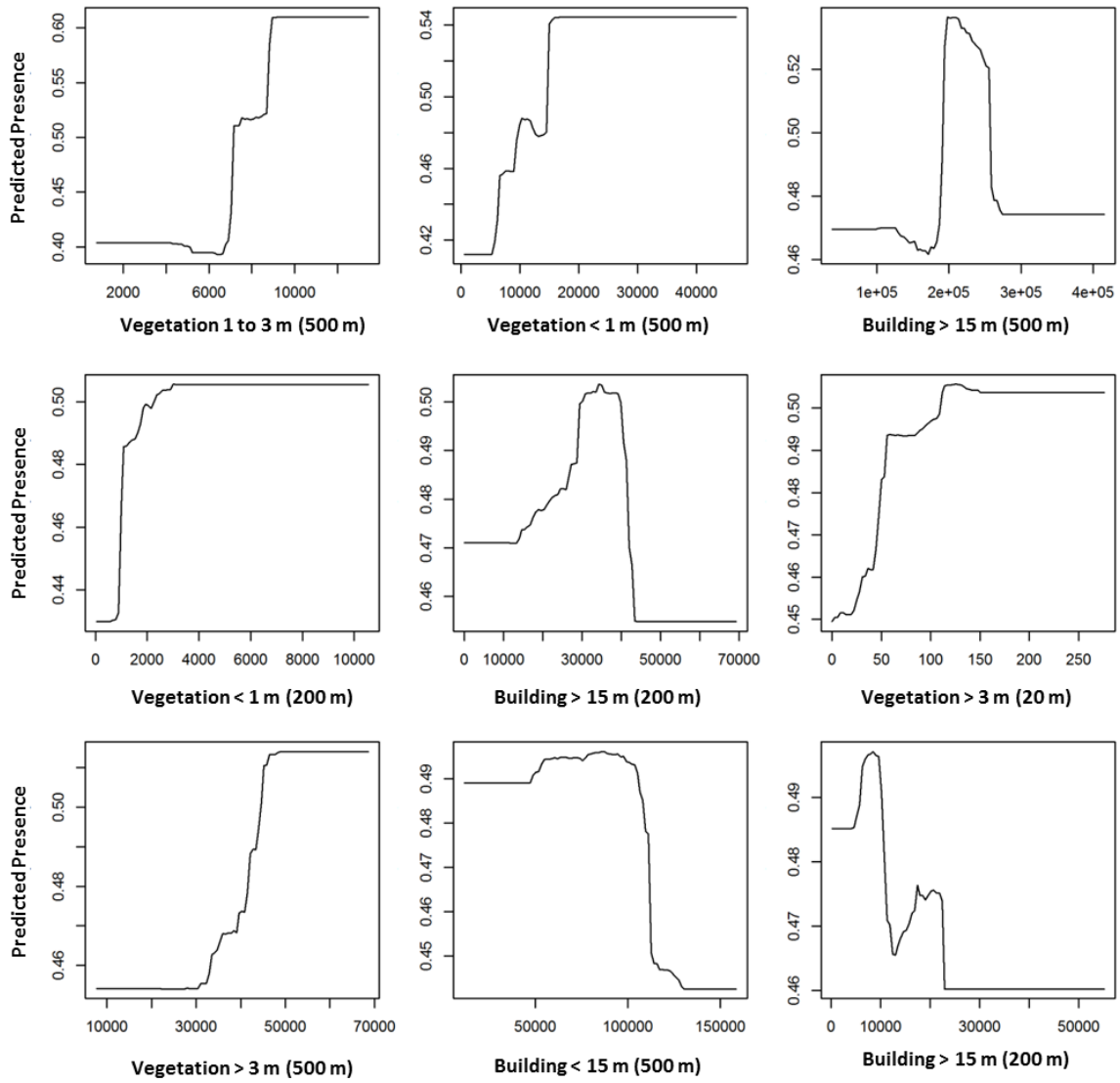
Appendix S3

Too small a resolution would result in increasing the resistance of the matrix by allowing very small elements (in this case 2m) to counter the movement, while the individual could in reality bypass the element.

We chose to aggregate data at this step, and not earlier in the analyses, mainly because the private green areas are usually small areas and would have disappeared with the degradation of the vegetation raster, resulting in an extensive loss of primary information for the object being studied. When tackled at this stage, the problem is much less important because we are dealing with continuous data that are simply averaged at the coarser resolution.

Appendix S4: Response of the common pipistrelle Presence/ Absence and abundance to the vegetation and building drivers, as produced by the gbms: a. for Presence/ Absence, and b. for abundance. Only the drivers with an importance over 5% are shown (see Figure 4).

a. Presence/ Absence



b. Abundances

