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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

1. Introduction

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

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

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

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

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

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

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

- 14m² of public green area / inhabitant (21m² for Berlin, 68m² for Madrid, 31m² in average for the large french cities)
- 450 public green areas (parcs, gardens, promenades …)

2. Methods

2.1. Study area

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

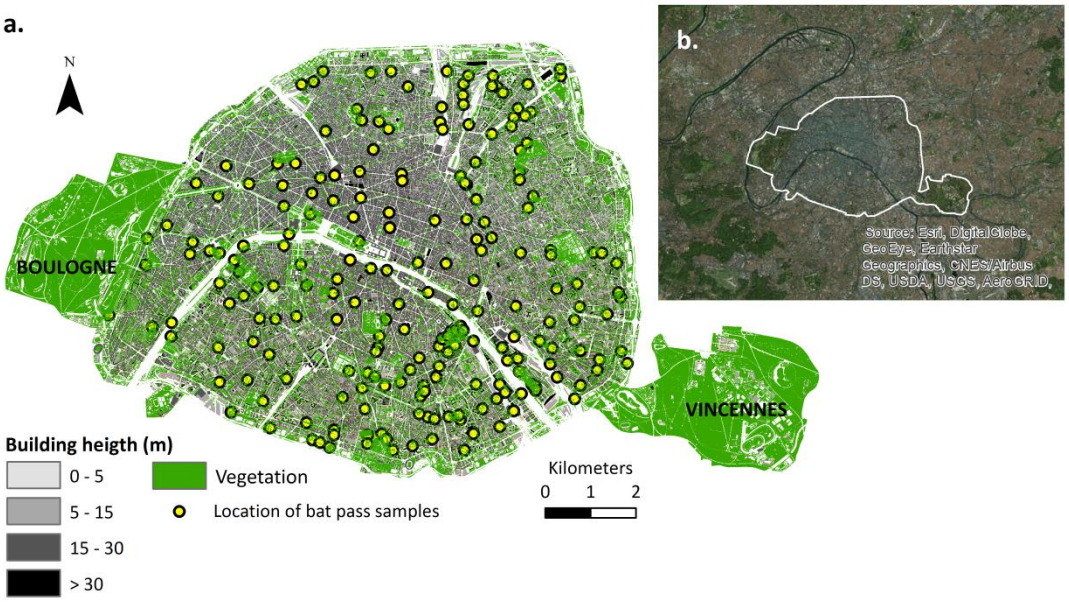

Figure 1: Map of the study area, i.e. intramural Paris. a. shows the location of the bat pass acoustic samplings used in the study and the two large parks (Boulognes and Vincennes) identified as the two habitat patches for the focal species *P. pipistrellus*; b. shows intramural Paris in its densified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

2.2. Methods overview

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

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

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

2.3.1 Bat sampling

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

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

We cannot distinguish individual bats from their echolocation calls, making it impossible to calculate absolute bat density, so we used the number of bat passes recorded every 6 minutes as a measure of bat activity (for more detail see Appendix S1). A bat pass is defined as one or more bat echolocation calls during a sound recording of 1.2 s at × 10 time expansion (see Appendix S1 for the methodology used to detect the number of bat passes). The identification of the common pipistrelle does not raise issue in Paris, where species overlapping on acoustic repertoires (such as *Pipistrellu. pygmaeus* or *Miniopterus scherbersii*) do no occur. The duration of the recording (1.2 s) is predefined by the ultra-sound detector (Tranquility Transect; David Bale, Courtpan. Design Ltd, Cheltenham,UK) (Roche et al., 2011). We used bat activity as a proxy of habitat suitability in terms of food resources and accessibility, hereafter called foraging-commuting habitat (Frey-Ehrenbold, Bontadina, Arlettaz, & Obrist, 2013; Pinaud, Claireau, Leuchtmann, & Kerbiriou, 2018; Raino, 2007; Russo & Jones, 2003). Our data showed zero-inflation and were highly overdispersed, with a lot of sites with zero pass and very few over 4 passes, the maximum being 60 passes in a site. In order to account for over-dispersion in the statistical analyses, we applied an adapted method (Hurdle model, see dedicated section) and thresholded the maximum pass abundance at 4, meaning that recordings with more than 4 bat passes were attributed a number of 4. For all analyses, we averaged the abundance of bats passes observed per sample point over the different years.

2.3.2. Creating variables for built areas and vegetation

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

Built areas and vegetation data

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

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

Variables describing the vegetation

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

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 Lacoeuilhe, Machon, Julien, Le Bocq, & Kerbiriou,
235 2014; Vandevelde et al., 2014). The Hurdle model is a two-step modeling approach. The first

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

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

2.4.1. Estimating foraging-commuting habitat availability

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

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

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

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

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

2.5.1. Conductance maps

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

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

2.5.2. Building connectivity maps

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

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

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

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

3. Results

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

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

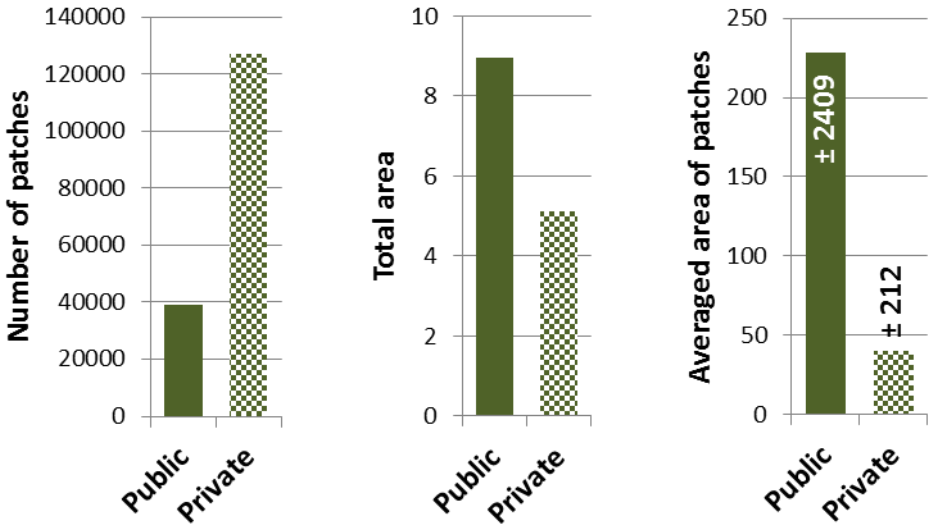

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Figure 2: Comparison of public and private green areas in the Paris area using three basic landscape metrics: a. total area, b. total number of patches and c. average area of patches with the standard deviation. The metrics have been computed for intramural 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
333 passes data for the built areas and vegetation variables and their scale of impact, suggesting
334 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
336 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

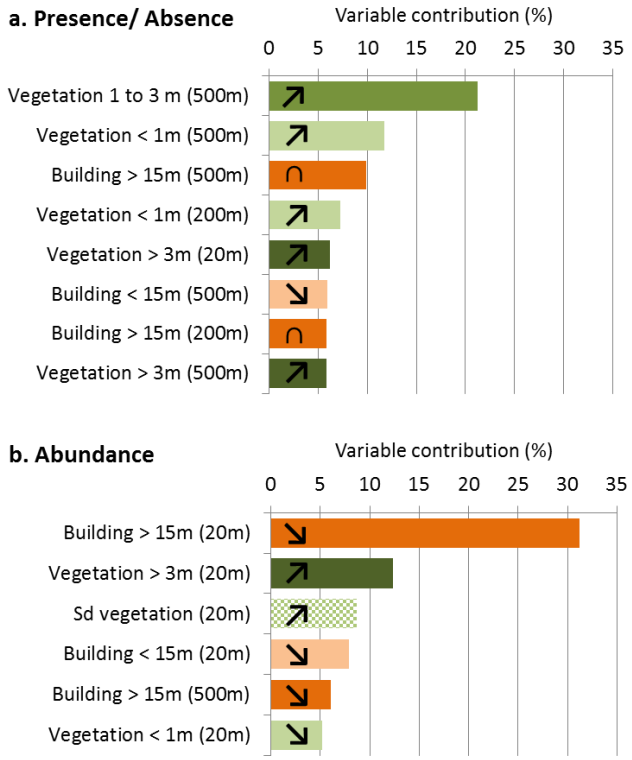

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Figure 3: Variables ordered by their contribution to the occurrence and bat pass abundance as estimated by the two gbm analyses (in percent). a. the Presence/ Absence data, and b. the abundance of passes data. The contribution is the relative influence 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

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

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

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

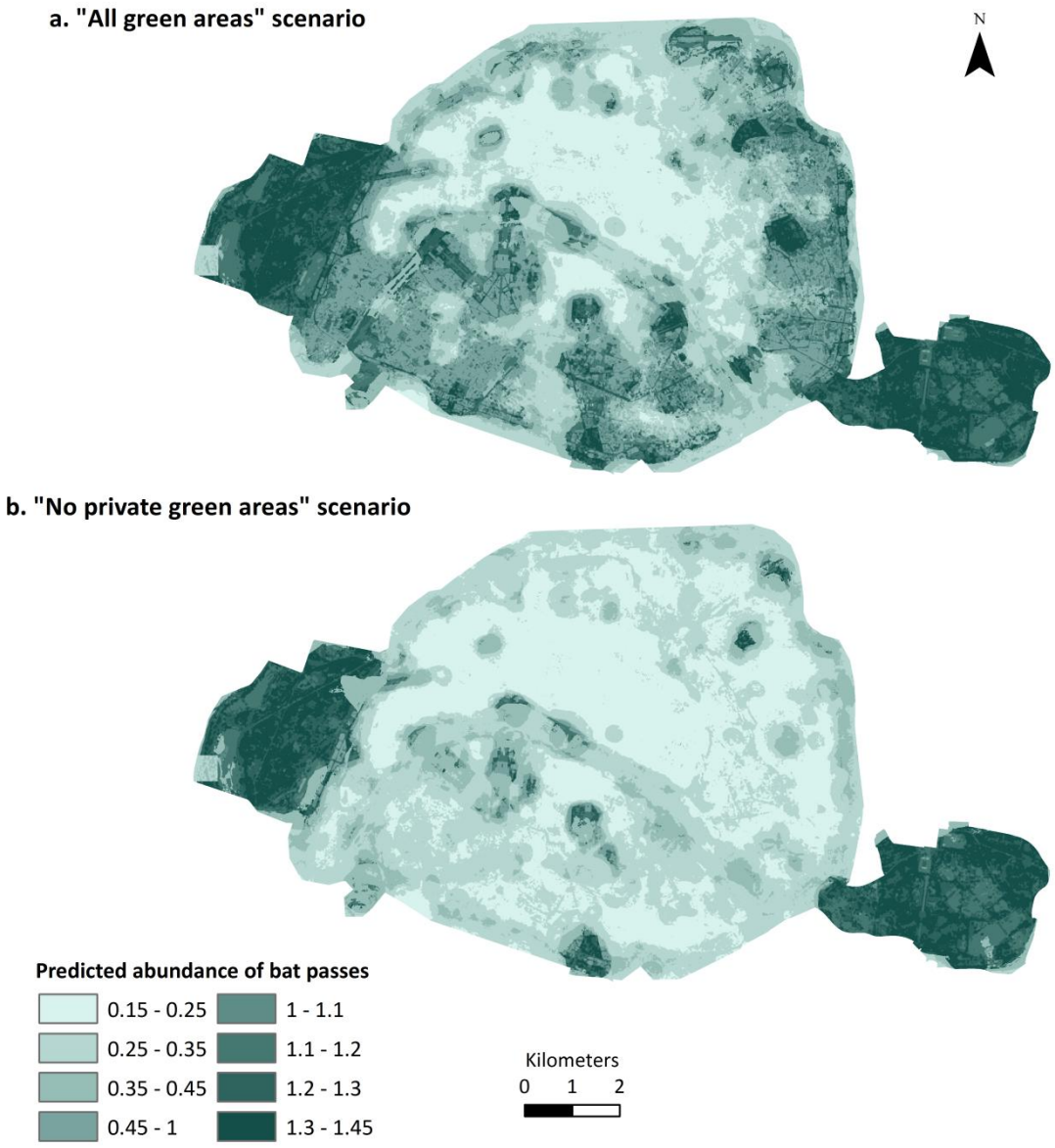

Figure 4: Habitat availability maps of *P. pipistrellus* in Paris showing the bat pass abundance as predicted by the gbm for a. the all green areas scenario and b. the Only public green areas scenario. The bat pass abundance values showed in these maps were rescaled between 0 and 10,000 to give the conductance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

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).

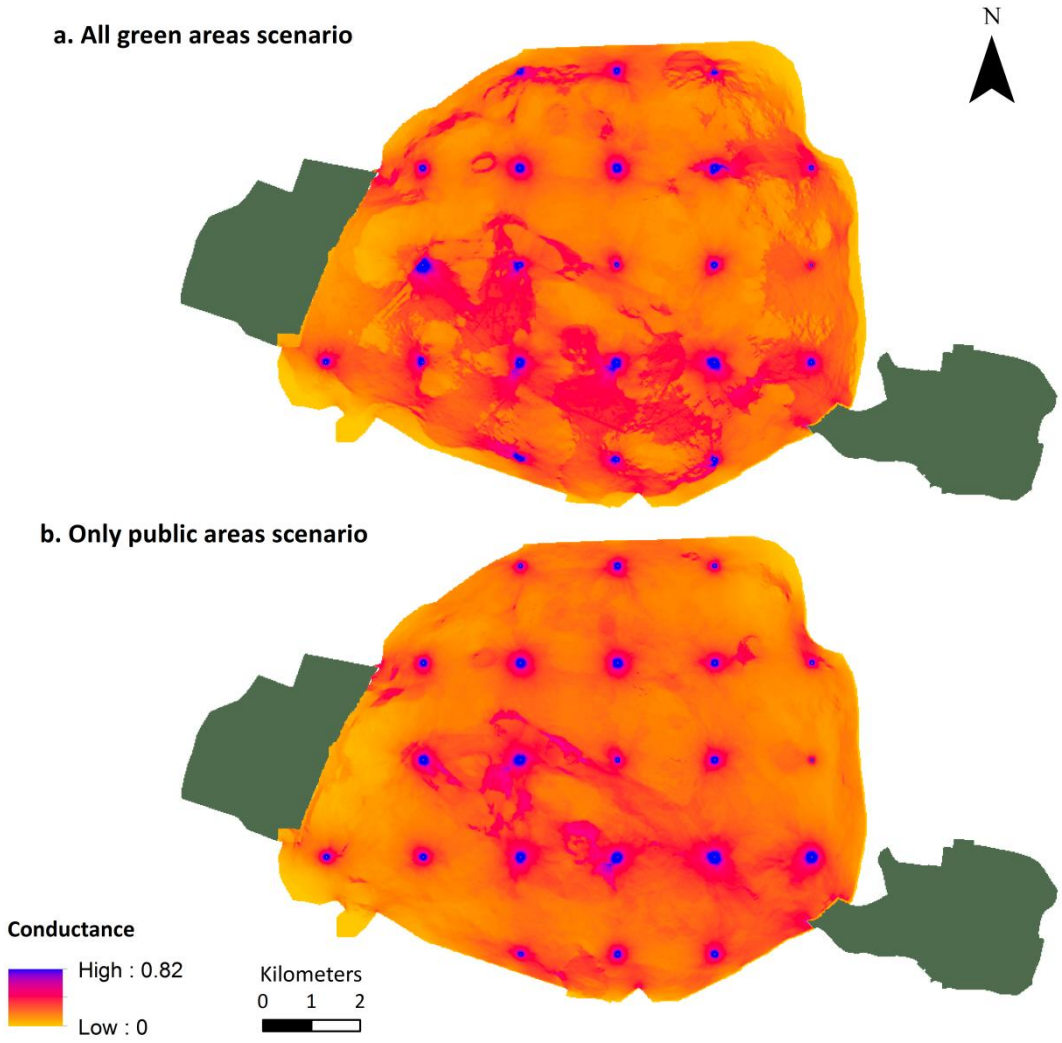

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Figure 5: Conductance maps for *P. pipistrellus* in Paris representing potential fluxes between simulated colonies (including the Boulogne and Vincennes woods, dark green patches) and foraging areas located at a maximum distance of 2 km, for a. the 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, & Kerbiriou, 2013) and is regularly found in urban areas (Bartonicka &
389 Zukal, 2003; Hale et al., 2012; Vandevelde et al., 2014). In line with previous findings, we

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

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

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

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

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

5. Conclusions

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

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

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Appendices

Appendix S1: Detailed information on recording settings and conditions

1. Protocol

1.1. General description

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

Count point survey sampling	
Scope	2x2 km square randomly selected by the Museum.
Number of point per circuit	10
Recording duration	6 minutes
Period of sampling	from the 15th June to 31the July **(to 5th August)**
Weather conditions	no rain, low wind speed (< 7m/s i.e 25km/h), temperature > 12°C
Survey start	if possible 30 minutes after sunset
Bat recording	
Acoustic detectors	Tranquility Transect Bat detector (Courtpan Design Ltd., Cheltenham, UK)
Intercalibration of detectors	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	
Time expansion factor	10
The duration of the record predefined by the ultra-sound detector	1.2 sec
High pass filter	5 kHz
Frequency	96 000 sample/sec
Recording device	Zoom H2 digital recorder (Samson technologies, USA)
File storage format	WAV
Bat identification	
Software	Syrinx 2.6
Procedure	- **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

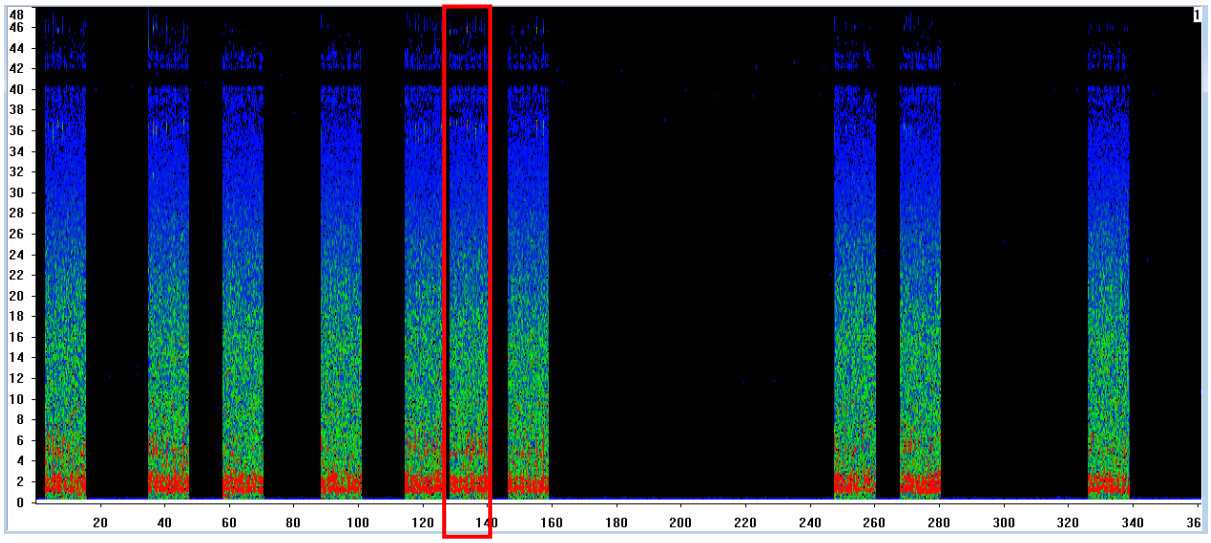
We used Syrinx software version 2.6 (Burt, 2006) for spectrogram and Adobe Audition for spectral analysis together with Scan'R (Binary Acoustic Technology, 2010) to isolate each bat vocalization and automate measurement of relevant parameters (Gannon et al., 2004, Obrist et al., 2004, Barataud 2012). 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 no occur.

1.3. Measurement of bat activity

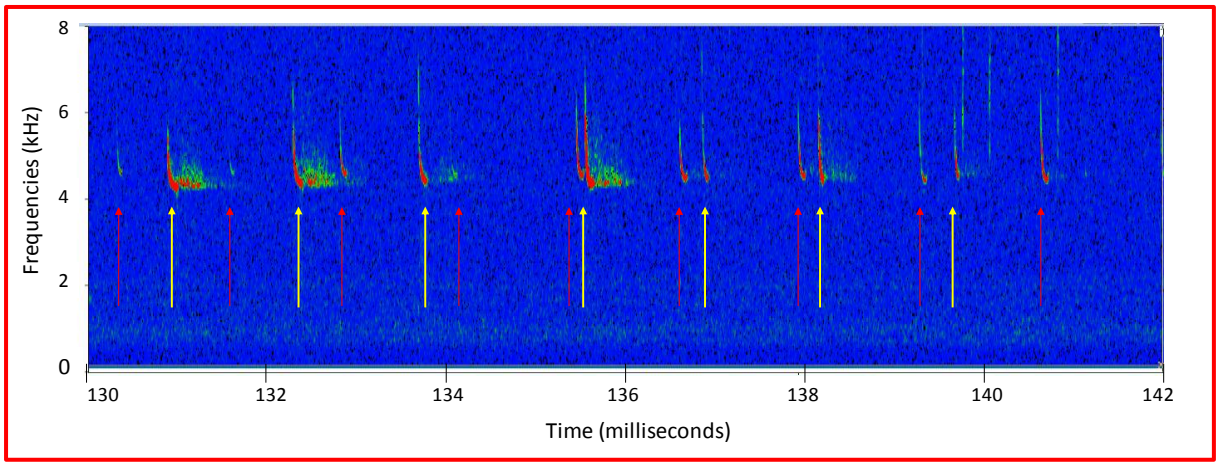
Bat activity at the point scale is calculated as the sum of the number of bat passes recorded per 6 minutes (Fig S1-2a). We identified a bat pass as a call sequence containing one or more pulses and when the time between calls exceeded four times the inter-pulse interval (Parsons & Jones, 2000, Kerbiriou et al. 2019). In the protocol followed in this study, the duration of the record is fixed at 1.2 seconde. Within each 1.2 s recording, the minimum number of bat recorded simultaneously were estimate 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 × 10 time expansion. A sound event is triggered by a bat echolocation call or any other ultrasonic emission.



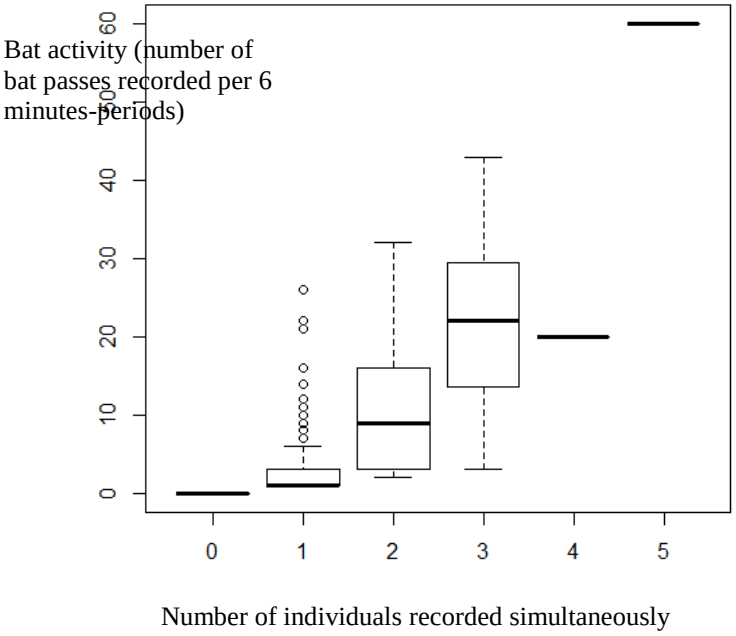
Time (milliseconds)

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)

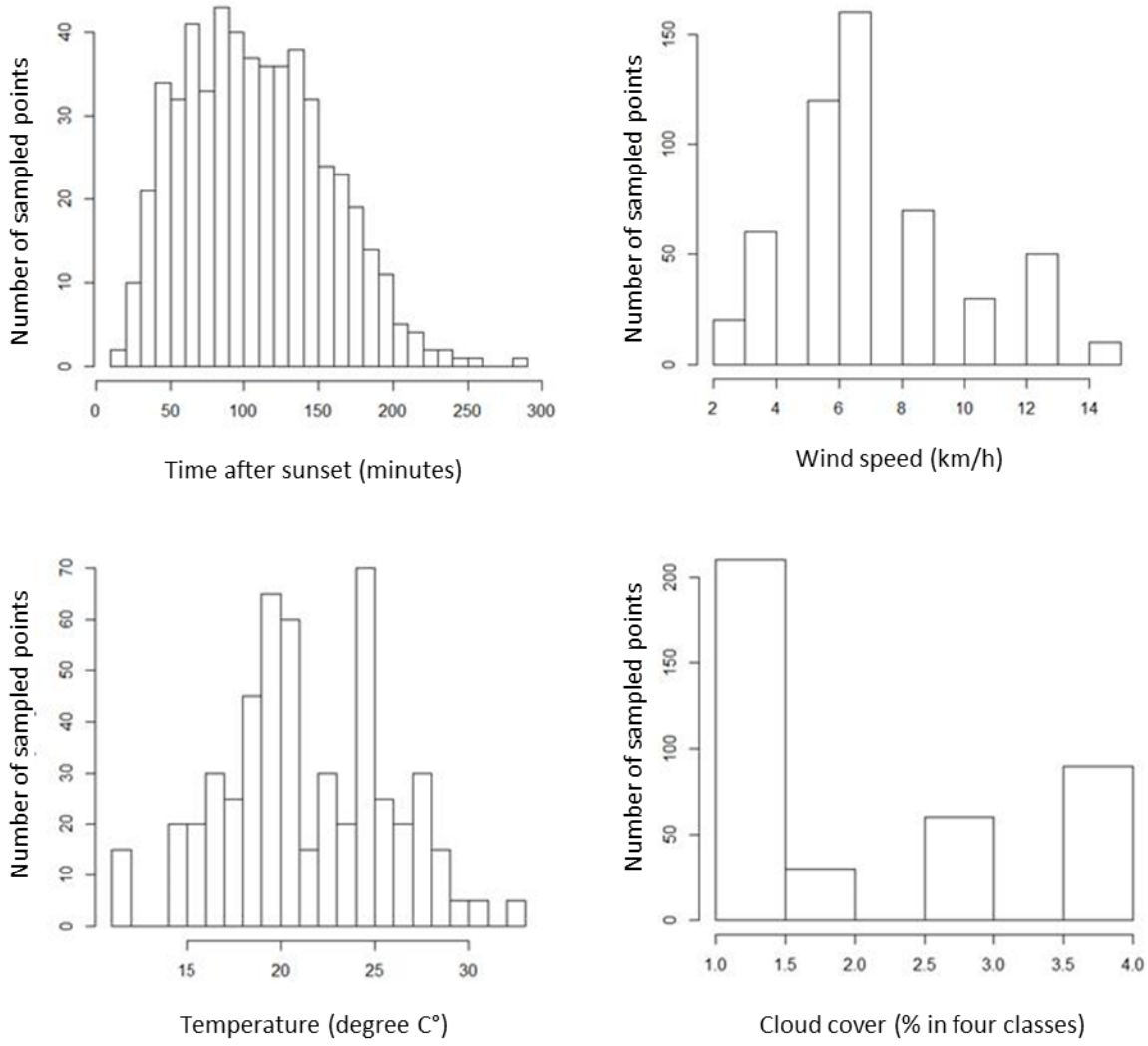
P<0.0001,

Deviance explained : 71%,

$R^2 = 0.49$

2. Data sampling conditions

Figure S1-1: Time and weather sampling conditions

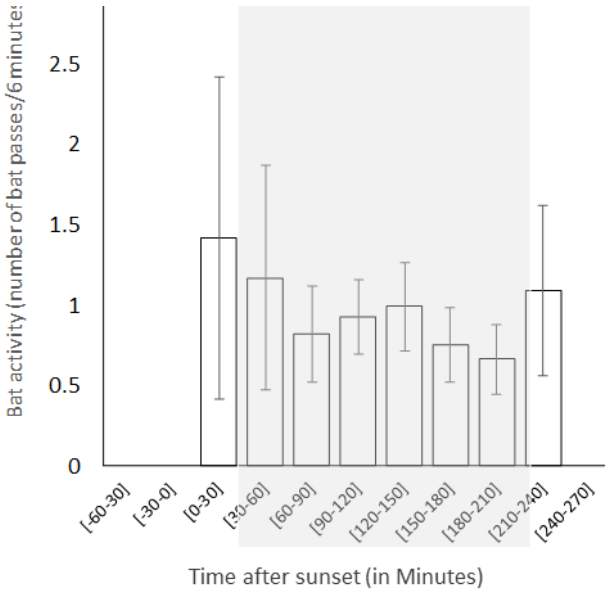


3. Exploring potential biases

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).


Bat activity (number of bat passes/6 minutes
2.5
2
1.5
1
0.5
0
[-60-30]
[-30-0]
[0-30]
[30-60]
[60-90]
[90-120]
[120-150]
[150-180]
[180-210]
[210-240]
[240-270]
Time after sunset (in Minutes)

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

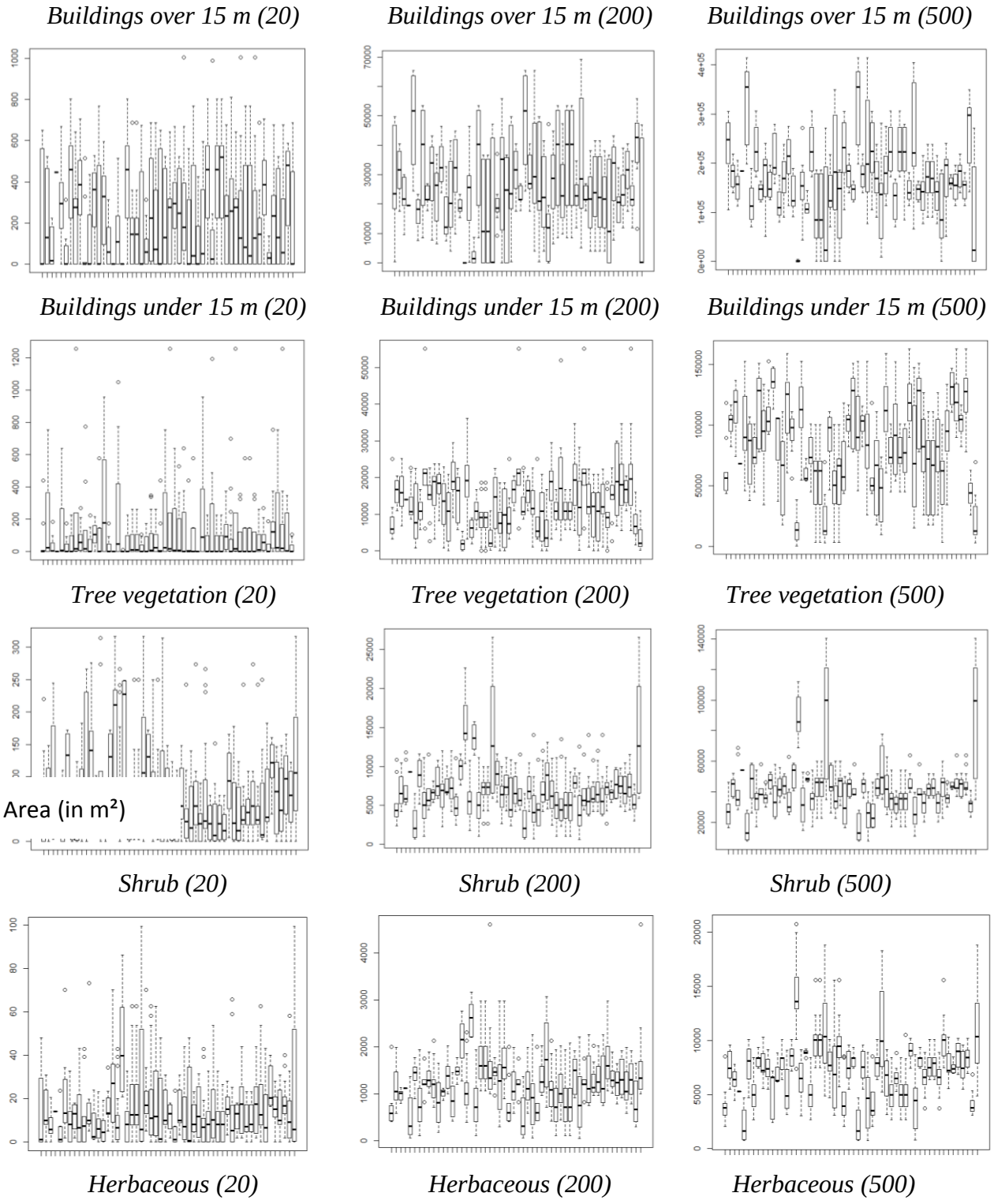
Table S1-2: Correlation (Spearman's *rho)* between time of recording and the explanatory variables (all explanatory variables are in m²).

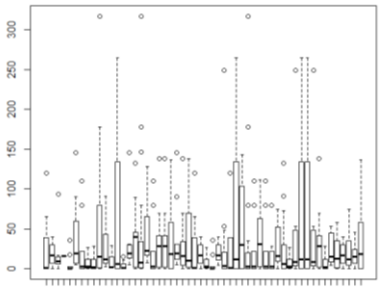
Landscape-scale	20	200	500
Buildings over 15 m	rho=0.048 ; *P*=0.265	rho=0.054 ; *P*=0.209	rho=0.027 ; *P*=0.522
Buildings under 15 m	rho=0.055 ; *P*=0.200	rho=-0.070 : *P*=0.1039	rho=-0.109 ; *P*= 0.011
Tree vegetation	rho=0.029 ; *P*=0.503	rho=-0.017 ; *P*=0.690	rho=-0.023 ; *P*=0.593
Shrub	rho=-0.013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

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

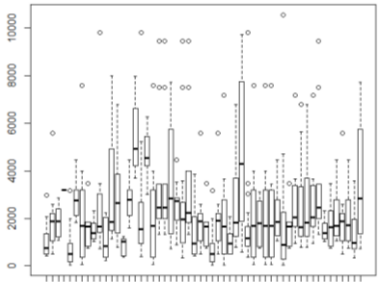
3.3.Variation of explanatory variables among recording's nights

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

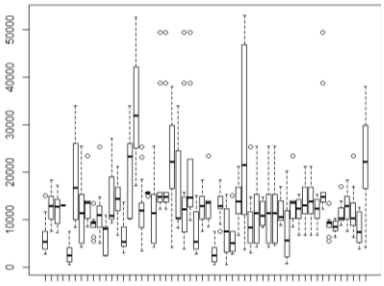




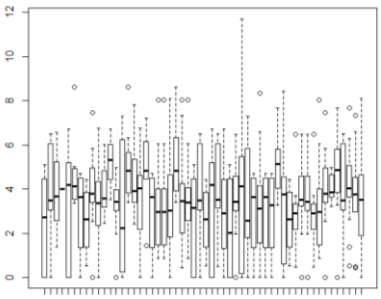
Sd vegetation height (20)

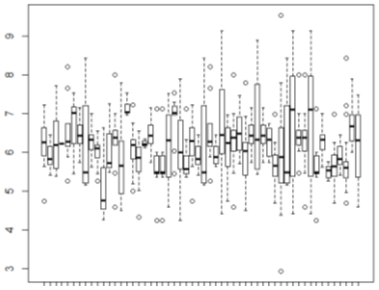


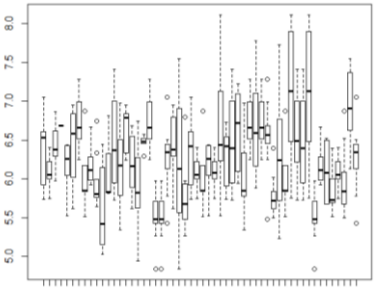
Sd vegetation height (200)



Sd vegetation height (500)







Nights of recording (in chronological order)

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

20 m radius:

- Area of building over 15 m height
- Area of building under 15 m height
- Area of vegetation under 1 m
- Area of vegetation between 1 m and 3 m
- Area of vegetation over 3 m
- Standard deviation of vegetation height

200 m radius:

- Area of building over 15 m height
- Area of building under 15 m height
- Area of vegetation under 1 m
- Area of vegetation between 1 m and 3 m
- Area of vegetation over 3 m
- Standard deviation of vegetation height

500 m radius:

- Area of building over 15 m height
- Area of building under 15 m height
- Area of vegetation under 1 m
- Area of vegetation between 1 m and 3 m
- Area of vegetation over 3 m
- Standard deviation of vegetation height

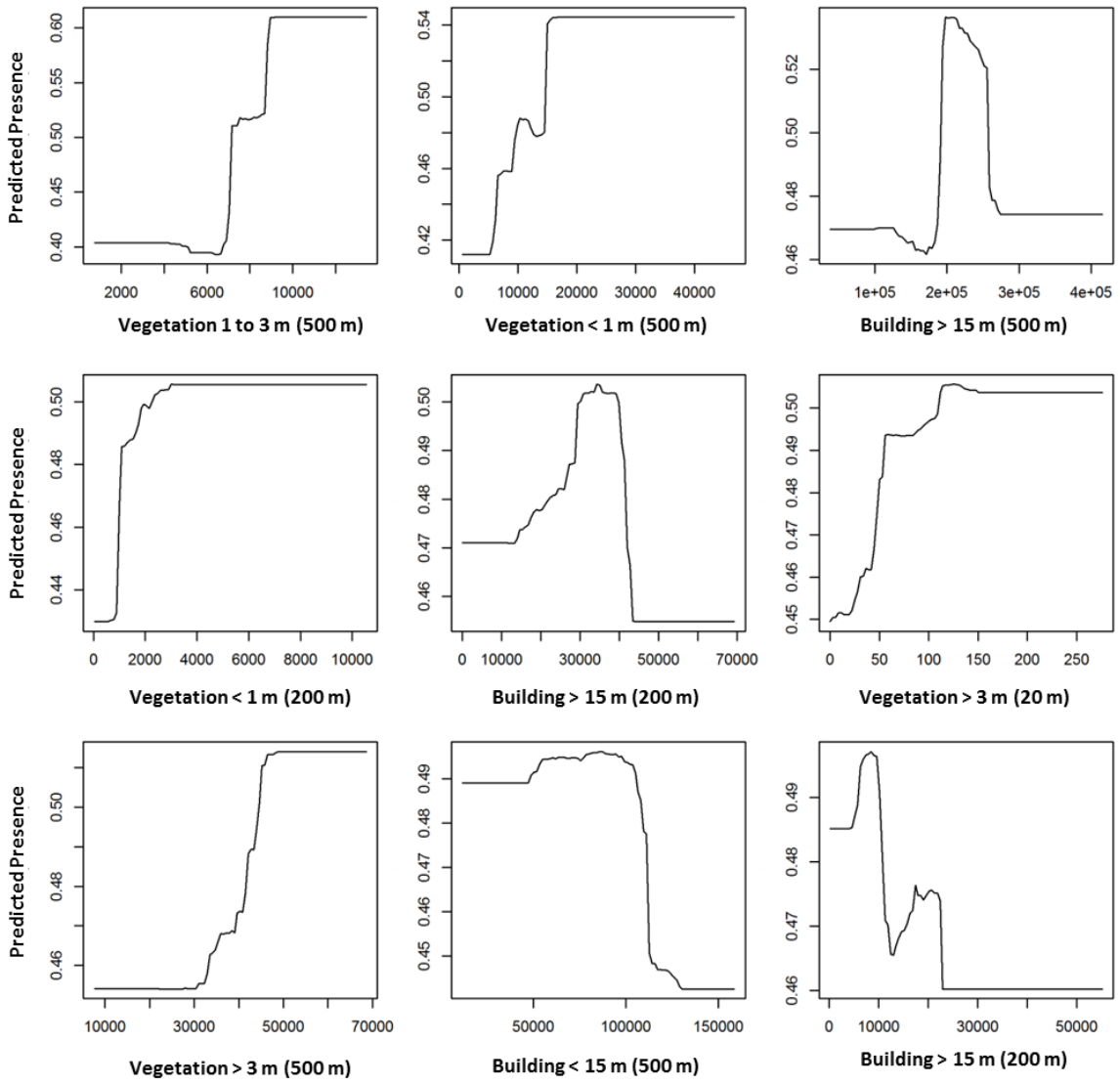
Appendix S3

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



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b. Abundances