Birds are also sensitive to landscape composition and configuration within the city centre

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\textbf{A B S T R A C T}

Maintaining biodiversity in urbanised landscapes has become a conservation issue. Although numerous studies have shown that avifauna decreases according to urbanisation level, little is known about the influence of urban characteristics on avifauna in densely urbanised areas. This study took place in the centre of a highly urbanised area, Paris, France, where we defined a grid of 94 cells of 1 km\textsuperscript{2} each. Using Bayesian model averaging, we examined the variation of diversity and abundance of breeding birds (41 species) through their feeding and nesting behaviours. We then analysed the responses of these guilds to composition (proportion of different types of buildings and green spaces) and configuration (heterogeneity, spatial arrangement of green spaces). The abundance of omnivorous and tree nester species was influenced by urban characteristics such as building heterogeneity. The positive influence of shrub cover on insectivorous species abundance was greater in areas with a high density of medium-height buildings. Omnivorous species abundance increased with the juxtaposition of vegetation when the bare soil cover was low, and decreased otherwise. Globally, the abundance of omnivorous, ground and tree nester species was sensitive to building characteristics, whereas insectivorous and granivorous species as well as roof nesters may benefit from green space management. We concluded that urban planning can also promote avifauna abundance in the city centre by varying the heights of buildings in urban renewal projects rather than clustering buildings of similar height, or by focusing on the spatial configuration of green spaces (especially their proximity) rather than their area.

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1. Introduction

The permanent and irreversible landscape changes caused by urbanisation are detrimental to rural or natural landscapes and ecosystems. This conversion of land use is globally increasing as greater numbers of people settle in or near urban areas (UN Population Division, 2010). Because of this growing demand for urban space, it is important to focus on maintaining ecosystem services in cities (McDonald, 2008) and also within downtown areas. Urban biodiversity and especially avifauna may be considered as a cultural ecosystem service, sensitising citizens to biodiversity conservation issues (Niemela, 1999) and increasing the well-being of city dwellers (Fuller, Irvine, Devine-Wright, Warren, & Gaston, 2007).

Avifauna is an important component of biodiversity in cities. Indeed, birds are one of the biological groups best known to the non-scientific public (Chace & Walsh, 2006). The effect of urbanisation on bird communities is quite well known. Urbanisation tends to homogenise the avifauna because the environmental conditions within cities lead to a decrease in specialist species that are subsequently replaced by generalist species (Blair, 2001; Clergeau, Croci, Jokimaki, Kaisanlahti-Jokimaki, & Dinetti, 2006; McKinney, 2006). Even though cities are expected to harbour more bird individuals than the surrounding countryside, the species richness is generally lower (Beissinger & Osborne, 1982). Urbanisation thus favours only a limited number of bird species, acting on biological traits as an environmental filter (Croci, Butet, & Clergeau, 2008). Bird species are separated into two groups according to their response to urbanisation – urban adapters and urban avoiders (Blair, 1996) – whose biological traits such as feeding or nesting habits differ. Thus, when compared to the surrounding countryside, urban avian communities include less ground and shrub nesters (Clergeau et al., 2006), whereas they tend to favour granivorous, insectivorous and resident species over migrant species (Allen & O’Connor, 2000).

However, most of the literature concerning relationships between avifauna and urbanisation has used a gradient approach, comparing the specific or functional composition of communities in plots located within and outside the city. Urbanisation intensity has...
generally been neglected, considering urbanisation only as a global phenomenon opposing the suburban and urban core. Even Sorace and Gustin (2010) used the gradient approach in a meta-analysis of an urban bird atlas of Europe, comparing sparsely built-up areas to the urban core of cities.

To our knowledge, town planning design has never been taken into account in assessing the distribution and abundance patterns of bird species, especially in densely urbanised areas. The characteristics of city structure, such as the relative proportion of surface area covered and the distribution within the city of each type of building (characterised by different heights and building periods, corresponding to architectural trends and urban conceptions) (Jordan, 2004; Panerai, Castex, Depaule, & Samuels, 2004) or the spatial arrangement of the different types of vegetation (Stefulesco, 1993), are generally disregarded in the literature, focusing only on the importance of natural areas within the urban landscape. Nevertheless, some authors have focused on non-biotic elements of the city by linking avifauna patterns and socio-economic patterns (Melles, Glenn, & Martin, 2003; Kinzig, Warren, Martin, Hope, & Katti, 2005; Strohbach, Haase, & Kabisch, 2009) or building age patterns (Loss, Ruiz, & Brawn, 2009).

In this paper, we focused on the possible effects of some elements of city composition and configuration (buildings and green spaces) in a dense urban area on avifauna traits (nesting habitats and feeding).

2. Materials and methods

2.1. Observation site

The area studied is the city of Paris, the administrative capital of France. The city proper has an area of 105.40 km² and a mean density of 20,980 inhabitants per km². It is surrounded by heavily urbanised suburbs, and is home to 12,000,000 inhabitants (including the city proper and its suburbs). The area studied is thus extremely urbanised and the observations were made at the very extreme end of an urbanisation gradient. The study area was limited to the area within the city limits of Paris, i.e., within the ring road (Fig. 1).

The study area was divided into 1-km² cells, in accordance with the bird observation method. A total of 94 cells were obtained (Fig. 1). Because of the sub-circular shape of the city, some cells were not square. We therefore merged cells with an area of less than 0.5 km² with an incomplete neighbour cell to form a new cell with a surface area greater than 0.5 km².

2.2. Bird data

We focused on breeding birds that were well studied within Paris from 2005 to 2008 (Malher, Lesaffre, Zucca, & Coateur, 2010). The database was provided by the CORIF (Centre Ornithologique Ile de France). The data were gathered by volunteer citizen-scientist but each cell was under the supervision of a professional ornithologist. The observations were made every two to three weeks, for 2 h per cell, from March to July, thus leading to at least 15 person-hours per year. Each cell was surveyed from two to four years. The breeding structure of each bird species was evaluated in each cell according to the European Bird Census Council Atlas of European Breeding Birds (Hagemeijer & Blair, 1997) and we assessed the number of breeding pairs for each species in each cell only for the certified breeding species. Birds were assessed as a certified breeding species if at least one of the following evidence was found in the cell: adults exhibited a dissuasion manoeuvre, nest in use (containing egg, egg shell or fledglings), juveniles flying off the nest, adults carrying food to the nest, adults on a nest. Observers were asked to make efforts to avoid double count of individuals or family, for instance by counting juveniles only if they were on the nest or flying off the nest (i.e., not counting juveniles flying over the cell). To ensure that our data did not overestimate the number of breeding pairs, we used the smallest number of pairs per species per cell among all the survey years.

Out of the 45 breeding species observed, two were carnivorous, nine were granivorous, ten were omnivorous and 24 were insectivorous (some of them were occasional frugivorous species (Table S1)). The two carnivorous species were removed prior to subsequent analysis because of very low abundance. Concerning the nesting habits of these species, out of the 43 remaining species, four were ground nesters, two were water nesters, ten were shrub nesters, 24 were nesting in trees or high in buildings and three were roof nesters (Yeatman-Berthelot & Jarry, 1994). The water nesters were clustered in only a few cells and therefore removed, leaving 41 species in the end for analysis in the dataset.

2.3. Urban data

City structure data were provided by the APUR (Paris Urban Planning Agency) and were gathered by InterAtlas (aerial photography corporation) as orthophotos from a 2005 campaign. The orthophotoplans were transformed into 0.5 m pixel raster using a remote sensing approach.

Three land use types were identified: bare soil, vegetation and built-up areas. The vegetation height was determined by subtracting the digital elevation model from the digital surface model on the vegetation pixels. APUR provided the visible vegetation height according to three classes: herbs (less than 1 m), shrubs (from 1 m to 10 m) or trees (more than 10 m). The building height was determined in the same way on the built pixels in order to determine the height of each building. The buildings were subsequently classified into three classes: H1 < 18 m, 18 m < H2 < 30 m and H3 > 30 m. These thresholds were inferred from our knowledge about architectural trends (Jordan, 2004; Panerai et al., 2004). The vegetation and building layers were intersected with the grid containing the bird count data using ArcGis 9.3 (Esri) to determine the proportion of the cell covered by each class of vegetation and of building height (Table 1). The proportion of the cell rather than the surface areas was used to avoid issues in the boundary cells of less than 1 km². The heterogeneity of the buildings was computed as the standard deviation of the height of the buildings present in each cell (Table 1).

As a measure of spatial arrangement of the three vegetation layers (herbs, shrubs and trees), we computed the Interspersion and Juxtaposition Index (JI), using Fragstat 3.3. This index explicitly takes the spatial configuration of patch types into account by considering the neighbourhood relationship between patches, with low values to characterise landscapes where patch types are clumped together and high values to characterise landscapes where patch types are equally adjacent to the other (McGarigal, Cushman, Neel, & Ene, 2002).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean [min–max]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Building classes</td>
<td></td>
</tr>
<tr>
<td>H1 (&lt;18 m)</td>
<td>0.15 [0.05–0.30]</td>
</tr>
<tr>
<td>H2 (18–30 m)</td>
<td>0.18 [0.00–0.44]</td>
</tr>
<tr>
<td>H3 (&gt;30 m)</td>
<td>0.02 [0.00–0.06]</td>
</tr>
<tr>
<td>Vegetation classes</td>
<td></td>
</tr>
<tr>
<td>Herb</td>
<td>0.07 [0.01–0.17]</td>
</tr>
<tr>
<td>Shrub</td>
<td>0.10 [0.02–0.18]</td>
</tr>
<tr>
<td>Tree</td>
<td>0.07 [0.01–0.16]</td>
</tr>
<tr>
<td>Bare soil cover</td>
<td></td>
</tr>
<tr>
<td>Urban design and green spaces variables</td>
<td></td>
</tr>
<tr>
<td>Building heterogeneity</td>
<td>8.35 [3.49–22.04]</td>
</tr>
</tbody>
</table>

Table 1 Variables used to describe the urban design and urban green space structure of Paris.
The proportion of built-up area ranged from 9.0% to 59.3% (Fig. 2). The cells in the centre and the western part of the city had the highest proportions of built-up area, whereas the cells near the boundaries and along the waterways had a lower proportion of built-up area. The north-western part of the city was planned by Haussmann during the second half of the 19th century and contained a large cover of buildings from 21 to 30 m (six to seven floors, H2), with very similar buildings made of stone with zinc roofs. The centre of the city is similarly built-up and homogeneous with some older buildings (wood, tile or zinc roofs, five storeys, 18–21 m, H2). The belt of inner suburbs is very heterogeneous around this densely built core. The buildings were constructed during the late 19th century and throughout the 20th century. This area combines tile-roofed private housing estates with tiny gardens and
little buildings (H1 class, buildings < 18 m), medium-height buildings, with some Haussmanian boulevards (H2 class, height ranging from 18 to 30 m), and low-density modern dwellings, some of them reaching considerable heights (H3 class, buildings > 30 m) (Jordan, 2004; Panerai et al., 2004).

Conversely, the proportion of vegetation ranged from 4.5% to 46.9%, with the lowest values being found in the centre of the city. The highest values were found near the western banks of the Seine, near the Bois de Boulogne on the western boundary, along the eastern boundary, and over a large southern portion. The highest proportion of tree strata was observed in the city centre where most of the monuments are located and in the Haussmanian districts, along the southwestern and northwestern boundaries, and in the cells containing wooded parks or cemeteries (Fig. 3). The highest values of the JII index were also found in cells containing wooded green spaces (cemeteries, parks) and in the Haussmanian and central densely built-up districts, where trees are associated with lawns along boulevards, around monuments and in inner gardens (Fig. S1). Those with the lowest JII index values were located along railroad lines and where lawns are dominant (esplanades, sports grounds, etc.).

2.4. Data analyses

We examined the species richness and abundance patterns of nesting and feeding guilds using Bayesian model averaging (BMA). BMA methods allowed us to avoid selecting a single model among all possible models, given our explanatory variable sets. Indeed, using a single model assumes that the probability that this model generated the data is 1, which is a strong and mistaken assumption (Montgomery & Nyhan, 2010). Thus, the uncertainty involved in choosing only one model over other plausible models is often neglected in classical inferences. Bayesian inferences make it possible to compute the posterior probability of an individual model conditional on the data. In the averaged model obtained using the BMA procedure, the individual models are weighted according to their degree of plausibility (in this case, their posterior probability). Only models that meet a defined selection criterion are included in the averaged model (in this case, Occam’s window was used, i.e., only models with a ratio of the posterior probabilities of the candidate model to the best model of less than 0.05 are included) (Ellison, 2004). Furthermore, once the average estimates and standard deviation for each individual variable are computed, it is then possible to compute posterior probabilities for these variables (PP for a variable i is defined as the sum of the posterior of each model including the variable i). A rule of thumb for using these posterior probabilities is to consider that for PP > 0.5, 0.95–0.75, 0.5–0.75 and < 0.5, there is strong, weak and no evidence, respectively, that these variables are useful predictors. These threshold are roughly corresponding to the classical p-values < 0.01, 0.01–0.05, > 0.05 of classical inference (Viallefond, Raftery, & Richardson, 2001; Azevia, Bouchard, Pothier, Fortin, & Hebert, 2011).

We computed average models to explain the species richness and abundance of each feeding and nesting guild using GLM with either (1) the urban metrics as single terms, (2) their interaction with the building heterogeneity as well as the vegetation height variable as single terms, or (3) their interaction with the JII. We did not use the full interaction design (single terms and interaction together) to avoid co-linearity issues. We assumed a log-link and Poisson distribution for species richness data and a negative binomial distribution for abundance data. The negative binomial distribution was used because of over-dispersion issues using the Poisson distribution in this particular case.

After the models were fitted, the abundance of each guild was predicted using the most useful predictors. When an interaction occurred, two predictions were plotted on the same curve for two different levels of one of the terms of the interaction. When interactions occurred between one variable and several cover variables of the same group (e.g., the interactions between building heterogeneity and H1 and H2 cover), the sum of the cover variables remained constant (e.g., in the above-mentioned case, as the sum of H1 and H2 was 40%, we considered H1 = 0 and H2 = 40% in the first case, and H1 = 40% and H2 = 0%, in the second case.). When several interactions occurred with several variables, only the most useful predictor (defined as the predictor with the highest PP) was used.

3. Results

The correlation between the data and fitted values after Bayesian model averaging ranged from r = 0.32 to r = 0.66. The correlation coefficient was generally higher for the species richness data than for the abundance data (Table 2).

Considering the species richness of each feeding and nesting guild, only five variables were useful predictors (i.e., posterior probability > 50%) of the species richness patterns of birds. However, none of these variables were strong useful predictors since the maximum PP was 64.7% (Table 3). None of the species richness patterns for granivorous or omnivorous species or for shrub nesters had a useful predictor in our model.

The insectivorous richness was positively associated with the interaction between the juxtaposition index and the proportion of trees. Ground nester richness was negatively influenced by the proportion of buildings between 18 and 30 m high (H2). The tree nester richness was positively influenced by the proportion of trees in the cell. Finally, the species richness of roof nesters was negatively influenced by both the bare soil proportion and the proportion of buildings less than 18 m high (H1).

When considering the abundance of bird guilds, 18 variables were useful predictors, of which seven had a posterior probability of over 75%, thus being strong predictors (Table 4). Insectivorous abundance was positively influenced by the proportion of shrubs in the cell. This influence was greater when the proportion of buildings between 18 and 30 m was high (Fig. 4a). Granivorous abundance was positively influenced by both the proportion of medium-height buildings (H2) and the interaction between the juxtaposition index and the proportion of shrubs. However, when the shrub cover was high, the juxtaposition index barely influenced the abundance (a steady curve could fit within the standard deviations around the prediction curves, Fig. 4b). Omnivorous species abundance was influenced in a positive way by the proportion of trees in the cell and by the interaction between the JII and the proportion of bare soil. Abundance was also strongly influenced by the interaction between building heterogeneity and the proportion of low and medium-height buildings (H1 and H2). As shown by the prediction curves, when the medium-height building cover increased (along with a decrease in low building cover), the heterogeneity influence was greater (Fig. 4c). Ground nesters were negatively influenced by both the proportion of medium-height buildings (H2) and by the interaction

<table>
<thead>
<tr>
<th>Species richness</th>
<th>Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Insectivorous</td>
<td>0.46</td>
</tr>
<tr>
<td>Granivorous</td>
<td>0.38**</td>
</tr>
<tr>
<td>Omnivorous</td>
<td>0.32*</td>
</tr>
<tr>
<td>Ground nesters</td>
<td>0.47**</td>
</tr>
<tr>
<td>Shrub nesters</td>
<td>0.48**</td>
</tr>
<tr>
<td>Tree nesters</td>
<td>0.38*</td>
</tr>
<tr>
<td>Roof nesters</td>
<td>0.45**</td>
</tr>
</tbody>
</table>
between building heterogeneity and the proportion of low buildings in the cell (H1). When looking at the prediction curves, it appeared that the standard deviations overlapped the prediction curves, thus indicating that the relative cover of H1 and H2 buildings did not have a very great influence (Fig. 4d). The shrub nesters were only positively influenced by the proportion of shrubs in the cell. Tree nester abundance was positively influenced by the proportion of trees, the interaction between the IJI and the proportion of bare soil, and the interactions between building heterogeneity and the low and medium-height buildings (H1 and H2). The prediction curves revealed the same differences in abundance as for omnivorous species (Fig. 4e). Roof nester abundance was strongly negatively influenced by the IJI and the proportion of bare soil in the cell, and positively influenced by the interaction between these two variables. As predicted by the averaged predictions, when the bare soil cover decreased, the juxtaposition index only had a slightly positive influence on roof nester abundance (Fig. 4f).

Fig. 3. Percentage of each class of vegetation in each cell of Paris. The size of each chart is proportional to the percentage of total vegetation surface of the cell.

Fig. 4. Average predictions of the abundance of (a) insectivorous, (b) granivorous, (c) omnivorous, (d) ground nesters, (e) tree nesters and (f) roof nesters. The thin dashed lines are the standard deviations around the mean prediction. The bold lines are used to represent the prediction means for two values of (a) H2 cover, (c), (d) and (e) H1 and H2 cover, (b) shrub cover and (f) bare soil cover.
Table 3
Response patterns of feeding and nesting bird guilds (species richness) to urban metrics using Bayesian model averaging. Intercepts are not shown. PP indicates the posterior probability that the variable has a non-zero coefficient in the predictor model. Variables exhibiting evidence of being useful predictors are in bold.

<table>
<thead>
<tr>
<th>Guilds</th>
<th>Insectivorous</th>
<th>Granivorous</th>
<th>Omnidvoorous</th>
<th>Ground nesters</th>
<th>Shrub nesters</th>
<th>Tree nesters</th>
<th>Roof nesters</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean (SD) PP</td>
<td>Mean (SD) PP</td>
<td>Mean (SD) PP</td>
<td>Mean (SD) PP</td>
<td>Mean (SD) PP</td>
<td>Mean (SD) PP</td>
<td>Mean (SD) PP</td>
</tr>
<tr>
<td>IJ</td>
<td>0.002 (0.008)</td>
<td>12.6</td>
<td>0.003</td>
<td>3.1</td>
<td>-0.004 (0.016)</td>
<td>11.4</td>
<td>0.005</td>
</tr>
<tr>
<td>Baresoil</td>
<td>-0.81 (3.28)</td>
<td>14.9</td>
<td>0.601 (2.429)</td>
<td>17</td>
<td>-6.12 (3.33)</td>
<td>47.9</td>
<td>-3.34 (0.579)</td>
</tr>
<tr>
<td>Herb</td>
<td>-0.03 (0.48)</td>
<td>3.1</td>
<td>-3.785 (6.14)</td>
<td>38.7</td>
<td>3.21 (2.973)</td>
<td>21.8</td>
<td>1.34 (0.436)</td>
</tr>
<tr>
<td>Shrub</td>
<td>7.311 (4.067)</td>
<td>80.2</td>
<td>4.66 (7.166)</td>
<td>37.8</td>
<td>-0.127 (15.94)</td>
<td>43</td>
<td>3.017 (5.838)</td>
</tr>
<tr>
<td>Tree</td>
<td>-0.04 (0.443)</td>
<td>3.2</td>
<td>0.123 (1.03)</td>
<td>9.6</td>
<td>-3.72 (1.927)</td>
<td>9.1</td>
<td>1.28 (3.838)</td>
</tr>
<tr>
<td>H1</td>
<td>-0.02 (0.091)</td>
<td>1.9</td>
<td>-0.167 (0.11)</td>
<td>9.6</td>
<td>-0.372 (2.197)</td>
<td>9.1</td>
<td>-1.38 (3.383)</td>
</tr>
<tr>
<td>H2</td>
<td>1.273 (1.127)</td>
<td>60.9</td>
<td>2.134 (2.093)</td>
<td>61.9</td>
<td>0.879 (2.93)</td>
<td>12.3</td>
<td>-0.037 (7.244)</td>
</tr>
<tr>
<td>H3</td>
<td>-0.06 (0.059)</td>
<td>3.1</td>
<td>0.133 (1.30)</td>
<td>9.4</td>
<td>-1.01 (4.974)</td>
<td>8.1</td>
<td>1.01 (7.099)</td>
</tr>
<tr>
<td>Building heterogeneity</td>
<td>-0.01 (0.006)</td>
<td>3.0</td>
<td>-0.004 (0.016)</td>
<td>8.6</td>
<td>-0.003 (0.022)</td>
<td>6.3</td>
<td>-0.003 (0.044)</td>
</tr>
<tr>
<td>IJ x Baresoil</td>
<td>0.003 (0.04)</td>
<td>11</td>
<td>0.021 (0.039)</td>
<td>31</td>
<td>-0.09 (0.102)</td>
<td>54.1</td>
<td>-0.042 (0.072)</td>
</tr>
<tr>
<td>IJ x Herb</td>
<td>0.003 (0.05)</td>
<td>2.4</td>
<td>0.021 (0.009)</td>
<td>25.4</td>
<td>-0.102 (0.278)</td>
<td>33.4</td>
<td>0.023 (0.057)</td>
</tr>
<tr>
<td>IJ x Shrub</td>
<td>0.017 (0.042)</td>
<td>22.1</td>
<td>-0.009 (0.007)</td>
<td>64.5</td>
<td>0.001 (0.025)</td>
<td>47</td>
<td>0.031 (0.063)</td>
</tr>
<tr>
<td>IJ x Tree</td>
<td>0.004 (0.03)</td>
<td>3.2</td>
<td>0.001 (0.01)</td>
<td>4.8</td>
<td>0.044 (0.249)</td>
<td>46.5</td>
<td>-0.049 (0.282)</td>
</tr>
<tr>
<td>H1 x Shrub</td>
<td>-0.009 (0.042)</td>
<td>8.4</td>
<td>-0.007 (0.005)</td>
<td>6.3</td>
<td>-0.038 (0.362)</td>
<td>95.3</td>
<td>-0.094 (0.543)</td>
</tr>
<tr>
<td>Heterogeneity x H2</td>
<td>-0.079 (0.136)</td>
<td>29.2</td>
<td>-0.002 (0.02)</td>
<td>24.1</td>
<td>1.36 (0.533)</td>
<td>91.5</td>
<td>0.628 (0.802)</td>
</tr>
<tr>
<td>Heterogeneity x H3</td>
<td>-0.003 (0.006)</td>
<td>3.5</td>
<td>-0.003 (0.008)</td>
<td>3.4</td>
<td>-0.342 (0.829)</td>
<td>18.9</td>
<td>0.105 (0.747)</td>
</tr>
</tbody>
</table>
4. Discussion

The urbanisation process is known to involve less species richness in urban centres than in surrounding countryside (Clergeau, Jokimaki, & Savard, 2001; Sorace & Gustin, 2010; Turner, 2003). The role of the vegetation is also known (Husté, Selmi, & Boulinier, 2006) but is always studied using a large urban gradient. We show here that within a very small part of this urban–rural gradient, i.e. downtown or urban centre, land-use composition (proportion of different types of buildings and green spaces) and configuration (heterogeneity, relationship between patches) also have an influence on avifauna. However, contrary to previous studies on avifauna in urban areas, it appeared that the species richness of guilds was only slightly influenced by urban structure in the deeply urbanised city centre.

Based on the species richness data of bird guilds, it appeared that insectivorous species richness was little influenced by the organisation of tree areas, whereas their abundance was strongly influenced by the proportion of shrubs, this influence being stronger in areas with a high proportion of medium-height buildings. The majority of the literature on urban avifauna underlined the increase in insectivorous abundance in urbanised areas (Allen & O’Connor, 2000) or their indifference to urbanisation (Evans, Chamberlain, Hatchwell, Gregory, & Gaston, 2011). We show here that this sensitivity is also observed at a small scale within the city centre.

Richness of granivorous and omnivorous species was not affected by our metrics. Granivorous and omnivorous species are known to adapt well to urban environments (Lim & Sodhi, 2004; Chace & Walsh, 2006). For these two groups, the number of species remained similar and urban characteristics were of little importance. However, the abundance of these guilds was potentially increased in some parts of the city. The areas with Haussmann buildings (Jordan, 2004) and with a high proportion of shrubs, located close to other vegetation areas, were favourable to granivorous species. The omnivorous species were favoured by the heterogeneity of the building heights in areas with high cover of medium–height buildings. Consequently, granivorous species were influenced by the configuration of green spaces and omnivorous species by urban characteristics. Although Sorace and Gustin (2010) found a decreasing frequency of granivorous species when urbanisation increased, they also noted that this decline is due to their sensitivity to habitat fragmentation (see Ewers & Didham, 2006). Since our study took place in an already highly fragmented landscape, it is likely that another landscape-scale variable influenced the establishment of granivorous species, e.g., the presence of shrub cover offering suitable feeding and nesting places. The omnivorous species appeared to be better adapted to the wide range of potential habitats, even with a large heterogeneity of elements. Moreover, the large quantity of food potentially provided by humans in the city to the birds favours omnivorous birds (Lancaster & Rees, 1979; Jokimaki & Suohonen, 1998).

Surprisingly, the richness of shrub nester species is not influenced by spatial organisation, even if they are known to be very sensitive to urbanisation (Lim & Sodhi, 2004). Moreover, their abundance increased in areas with a large shrub cover. Thus, the detrimental effect of urbanisation on the shrub nester guild, leading to a higher rate of predation (Clergeau et al., 2006; Baker, Molony, Stone, Cuthill, & Harris, 2008), appeared to be potentially buffered by increasing the area covered with shrub. Increasing shrub density provides additional feeding resources as well as a secure nesting environment for shrub nesters.

Ground nesters are also known to suffer from high predation rates (Thaxter, Joys, Gregory, Baillie, & Noble, 2010) because the nesting environment is often exposed to the view of predators. Contrary to shrub nesters, none of the building or green space characteristics could prevent the detrimental effect of urbanisation on both the richness and abundance of this guild. We assumed that the south-eastern inner area of our study area, with their small private buildings and gardens, could have favoured the establishment of ground nesters. It turned out that this was not the case, perhaps because of the probable presence of domestic animals that prey on the ground nesters (Baker et al., 2008). However, the predictions of the abundance of this guild are not very conclusive because of the large variations around the mean. In addition, the abundance of ground nesters is already very low in our deeply urbanised areas and thus somewhat influenced by urban characteristics.

The tree nesters, nesting at greater heights than the other nesting guilds, are often viewed as better urban adapters (Huhta, Jokimaki, & Rahko, 1999; Clergeau et al., 2006). The proportion of trees in the surroundings did indeed increase both the richness and the abundance of tree nesters since it provided suitable nesting habitats. These birds also benefited from areas with large bare soil areas and equal spatial distribution of the three vegetation heights since they may provide suitable feeding areas. This nesting guild was also favoured by the urban structure of the city. Heterogeneity increased its abundance more rapidly when the cover of medium–height buildings was considerable. Moreover, medium–height buildings are likely to act as surrogate nesting habitats. Thus, the neighbouring presence of a large woody park with a high proportion of bare soil and surrounded by small private gardens is likely to have a positive influence on this guild.

Finally, if the roof nesters were negatively influenced by large amounts of bare soil, this negative effect was buffered by the presence of the different vegetation elements close to each other in the cell. It thus appeared that this nesting guild would benefit from advanced green space management since it requires both a low bare soil cover and an equal proportion of each type of vegetation, as long as each green element is close to the other. Such a nesting guild would probably be favoured by the presence of an urban park or semi-natural structures such as wasteland or unmanaged cemeteries.

5. Conclusions

The main findings of this paper are as follows. Out of the seven bird guilds considered, only one, the shrub nester, was not sensitive to either the building characteristics or the configuration of green spaces. The abundances of three guilds were mainly influenced by both the building proportion and the heterogeneity of this cover. The abundances of the three other guilds were mainly determined by the attributes of the green spaces in the surrounding area. It is thus likely that a simple urban management option such as varying the heights of buildings when constructing a new neighbourhood rather than clustering buildings of similar height will increase the abundances of bird species. In the same way, when designing urban green spaces, focusing on the spatial configuration of these spaces (especially their proximity) is likely to increase avifauna abundance. Thus, urban planning can also promote the abundance of bird species in the city centre. Nonetheless, as the species richness was barely influenced by the landscape metrics considered here, a challenging issue to tackle in designing these new neighbourhoods will be to ensure that these increases in abundance is not due to only a few species. Thus, taking into account other factors likely to influence the diversity itself, such as the inclusion of large, diverse semi–natural areas (Oliver et al., 2011), altogether with the building characteristics and urban green spaces configuration is key to maintain high level of local diversity within highly urbanised areas.

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Appendix A. Supplementary data


References


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