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Determinants of bird community composition on patches in the suburbs of Paris, France

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ABSTRACT

The ecological processes responsible for the spatial assemblages of breeding bird communities in urban landscapes are more and more investigated. Indeed, understanding these processes is imperative to plan relevant management policies. We investigated breeding bird communities on 67 patches in the suburbs of Paris, France. We examined the role of patch characteristics and geographic distance between patches in determining similarity between bird assemblages. To do this, we proposed a new SØrensen similarity index based on estimators of change in community composition taking into account the detection probability of species. The patch occupancy by sedentary and migratory species was also estimated to compare their sensitivity to urbanization. Patches close to each other supported more similar bird assemblages, suggesting an effect of the spatial distribution of patches on bird dispersal and a posteriori on local community composition. Accounting for spatial location of patches, bird assemblage similarity was related to the similarity of the surrounding level of urbanization but not to the similarity of patch size or to the similarity of patch vegetation. The mean estimated occupancy rate of sedentary species was higher than that of migratory species in the whole study area. While sedentary species occupied patches surrounded by both moderate and high levels of urbanization, migratory ones primarily occupied patches surrounded by moderate levels of urbanization. Human choices in degrees, styles, and extent of urbanization, including designation and design of patches within an urban matrix, affect the composition of local bird communities.

1. Introduction

Despite the reduced number and diversity of suitable patches for wildlife in cities, biodiversity in urban landscapes has an underestimated conservation value (Savard et al., 2000) and notably for birds (Bolger et al., 1997; Finland: Jokimäki, 1999; Spain: Fernandez-Juricic, 2000a; Sweden: Mörtberg and Wallentinus, 2000; Korea: Park and Lee, 2000; USA: Blair, 2001; Australia: Parsons et al., 2003; Singapore: Lim and Sodhi, 2004). These studies have mainly focused on local and regional factors that determine species richness and bird composition. More recently, the role of temporal dynamics of bird communities in determining avian composition was highlighted (Fernandez-Juricic, 2004; Husté and Boulinier, 2007). These investigations identified ecological processes determining the composition of bird assemblages on urban patches. Therefore they can also inform management plans that seek to maintain reasonable local levels of biodiversity in the present context of increasing urbanization all over the world (Marzluff, 2001).

Fragmentation of continuous habitats into smaller isolated patches impacts the local and regional richness (Fahrig, 2003). Moreover the individual movements between patches may be a determinant of the maintenance of local diversity in fragmented landscapes. Models such as metapopulation models (Hanski and Gilpin, 1997) and source-sink metapopulation models (Pulliam, 1988; Hanski and Gilpin, 1991; Hanski and Simberloff, 1997) have been proposed. The dispersal abilities of species and the permeability of the surrounding landscape may be crucial to maintain local diversity, but may be particularly reduced in highly anthropogenic landscapes (Fahrig and Merriam, 1994). Therefore, patches close to each other are expected to share more species than patches situated further apart.

Human disturbances can create new biotopes that provide habitats useful for very few animal and plant species (i.e., sandpits, quarries, factories; Purger, 2001). Furthermore, human activities can also produce patches with both low habitat quality and omnipresent disturbances such as noise, pollution, pedestrians. Finally, patch habitat quality can vary in time leading to species-specific responses. Some species will colonize patches after cessation of

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disturbances (Chacón and Cavieres, 2008), whereas others will leave these patches (burrowing bird species: Heneberg (2009); farmland birds: Farina (1997) and Reif et al. (2008)). In urban landscapes, patches with lower habitat quality are often situated in the more disturbed areas (Fernandez-Juricic, 2000a) and investigating how species respond to the presence of an urban gradient may help to consider differences in patch characteristics (Bennett et al., 2004).

All bird species do not tolerate urban constraints in the same way (Blair, 1996). 'Urban avoiders', are intolerant to urban constraints and are confined in natural remnants. 'Urban adapters', are able to maintain populations at intermediate levels of urbanization. Finally, 'urban exploiters' are able to maintain populations in highly urbanized regions. These species are recorded in numerous cities all over the world. Overall, tolerance to urbanization may also be species-specific. Some species, such as *Turdus merula* in Europe, are able to maintain distinct populations in both cities and forests (Partecke et al., 2006). Others, such as *Sturnus vulgaris,* react differently in different countries. In Central Europe, this species appears to be an urban adapter (Croci et al., 2008) while in Canada it was described as urban exploiter (Clergeau et al., 1998). Generally, urbanization appears to modify bird communities by both increasing the number of species that are 'urban exploiters' and leading to a biotic homogenization (Blair, 2001; Clergeau et al., 2006; McKinney, 2006; Evans et al., 2009).

Migratory birds have been reported to be more disadvantaged in urban environments than sedentary ones (Friesen et al., 1995; Hennings and Edge, 2003; Miller et al., 2003; Lim and Sodhi, 2004; Kark et al., 2007; Croci et al., 2008). Every year, migratory species have to recover specific breeding sites that they may lose to sedentary species (Jokimäki and Suhonen, 1998). Moreover sedentary species have more opportunities to adapt to urban constraints and are therefore more apt to occupy and defend their breeding and foraging sites (Kark et al., 2007).

In this study, we investigated the role of patch characteristics (i.e., patch size, patch vegetation and surrounding urbanization) in determining local assemblages of bird communities in a suburban area of Paris (France). First, we considered the compositional similarity of bird communities. It can be assessed using various indices that are often calculated assuming that all species have been detected. However, as noted by Chao et al. (2005), this could bias the results of analyses as the non-detection of a part of the community may lead to an underestimation of similarity (i.e., apparent higher dissimilarity). Using series of sampling occasions in each assemblage, it is nevertheless possible to compare the composition of assemblages between spatial locations while accounting for undetected species (Nichols et al., 1998; Cam et al., 2000; Chao et al., 2005). Here, we propose a way to compute the classical SØrensen index to compare assemblages using lists of detected/undetected species on series of occasions and accounting for potential heterogeneity in the probability of detecting species (Boulinier et al., 1998). Using the modified SØrensen index, we investigated the correlation between bird composition and local patch characteristics. We used statistical approaches that explicitly incorporated the spatial configuration of the studied urban system in the analyses in order to test whether similarities between local bird compositions were related to similarities in local patch characteristics or to the geographic distance between patches. Similarity in patch size and patch vegetation were expected to be associated with low differences in species composition (Goldstein et al., 1986; Jokimäki, 1999; Fernandez-Juricic, 2000a), as well as similarity in surrounding levels of urbanization (Blair, 1996; Clergeau et al., 1998; McKinney, 2002; Crooks et al., 2004). If comparable results have been reported in other urban landscapes, this is the first time that heterogeneity in the probability of detecting species is explicitly estimated and taken into account in such analyses (see Cam et al. (2000) for a discussion on these issues). Second, we investigated how bird communities are shaped in urban landscapes. We tested the difference of sensitivity to urbanization between migratory and sedentary birds by comparing occupancy rates of the two groups in the urban studied area. We used a method that allowed us estimating occupancy rate of species, i.e., the proportion of patches that are occupied by a species (MacKenzie et al., 2002), when detection probability is less than one. We predicted a higher proportion of patches occupied by sedentary species in the area the closest to the urban core.

2. Materials and methods

2.1. Study area

The study was carried out in the northeastern suburbs of Paris, France (48°54′N, 2°29′W). The entire study area is highly urbanized and covers about 236 km^2. The mean density of human population is high (5855 inhabitants/km^2 in 1999; data issued from the Institut National de la Statistique et des Etudes Economiques, http://www.insee.fr) but lower than in Paris (20164 inhabitants/km^2 in 1999; INSEE). We defined as an individual patch, every fragment of vegetation that was entirely delimited and surrounded by urbanization and where the level of disturbances due to human activities was limited compared to the surrounding urban matrix. Such suitable patches for wildlife were mainly urban parks and private gardens (i.e., managed patches). There were also unmanaged patches consisting of one remaining woodland and a few areas temporarily unused by humans. Patches were identified using color aerial photographs (i.e., orthophotos) from 1999 (supplied by the Institut Géographique National) and field observations (A. Husté). We surveyed breeding bird communities in 2003 and we sampled all study area patches to which we had access. Omitted patches were mainly private gardens. Our study covered therefore a large proportion of the patches available within the whole study area ($n = 67$, >80% of available patches in the study area; Fig. 1; Husté et al., 2006). Patch size was calculated using color aerial photographs and the Geographical Information System (GIS) ArcView 3.2 (ESRI, 1996). It ranged from 0.4 to 450 ha (see Fig. 1). 11.94% of patches were smaller than 1 ha, while 50.75% were 1–10 ha and 25.37% were 10–40 ha. Finally 11.94% of patches were larger than 100 ha and were generally situated at the periphery of the studied area.

2.2. Collection of habitat data

Using the color aerial photographs at a scale of 1:5000 and Arcview 3.2 (ESRI, 1996), we built a land cover map of the study area defining three types of cover around the patches: urban (i.e., block-of-flats and industries), residential (i.e., considered as suburban with detached flats and single-family housing) and green (i.e., remaining islands of vegetation including other studied patches) (see Marzluff et al., 2001). Polygons with the same cover types were delimited by hand. Then, the proportion of the urban type around each patch was measured using buffers with a radius of 1000 m and situated only outside the patches. Analyses were computed using Spatial Analyst for Arcview 3.2 (ESRI, 1996). The distance of 1000 m is commonly used to investigate the local effects of urbanization when investigating bird communities (Bolger et al., 1997; Mörtberg, 2001; Donnelly and Marzluff, 2004). Moreover, Reijnen et al. (1997) suggested that the estimated distance from traffic disturbing birds could not exceed 1000 m. The distance between each patch and the urban core was defined as the distance separating the centroid of the patch and the cathedral of Notre Dame, situated in the center of Paris. The urban cover variable

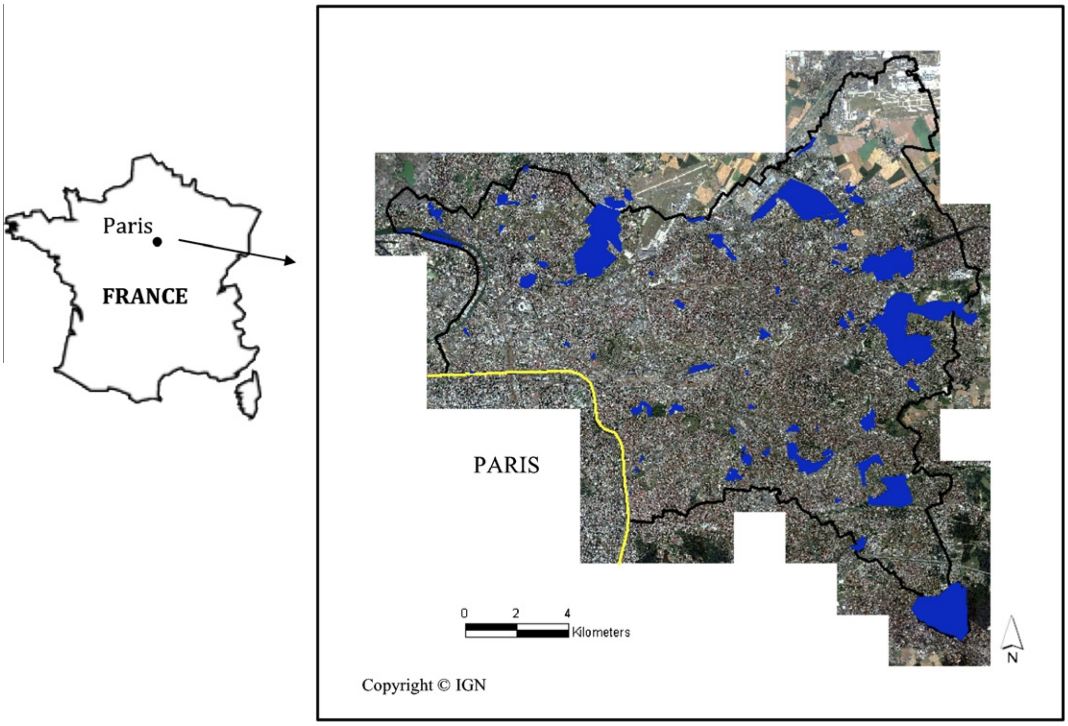

Fig. 1. Map of the study area located to the immediate north-east of Paris, France, and the location of the study patches. The yellow enlarged line shows the border of the city of Paris.

was strongly negatively correlated with the distance between each patch and Paris center (Pearson $r = -0.75$, $P < 0.001$, $n = 67$). Therefore, the urban cover variable was a satisfactory measure of the urbanization level (McKinney, 2002) and the study area presented an urban gradient with a typical monocentric structure from Paris center to suburbs (Alberti et al., 2001; see Fig. 1).

Vegetation data were collected by a single observer (S. Filoche) from July to October 2001. We used data from 2001 as it was the most recent data available in the study area. Within each patch, five 100 m^2-sample units along a transect were used. Distance between the 100 m^2-sample units was defined according to patch size so that they were uniformly distributed. Moreover, distance separating one sample unit to another in a patch was always the same. Six local vegetation variables were measured: cover of trees (%), number of tree species, cover of shrubs (%), number of shrub species, cover of herbaceous plants (%), number of herbaceous plant species. For each patch, a mean value was calculated for each variable. Vegetation characteristics are presented in Table 1 according to four classes of patch size. Our constant sampling effort regardless of patch size was justified by the fact that the percentage of each vegetation cover type was not significantly different between the four classes of patch size (Kruskal–Wallis tests: $P > 0.05$).

2.3. Bird survey

Bird communities were surveyed during the breeding season of 2003. We verified that the urban matrix had not drastically changed between 1999 and 2003. We also verified that the vegetation and the management of the considered patches had not drastically changed between 2001 and 2003. The study was conducted on sedentary species (i.e., species that remain in the study area all year) and migratory ones (i.e., migrant breeders that leave the study area during the winter). Only regular breeders in the study area were considered (Le Maréchal and Lesaffre, 2000). In order to account for differences in species phenology, we conducted counts within each patch at two different times of the breeding season (Blondel et al., 1970, 1981; Selmi and Boulinier, 2003a). Each patch was visited twice: (1) in May to ensure the efficient sampling of sedentary breeding birds and (2) in June to ensure the efficient sampling of migratory breeding birds that settle late in the breeding season (see Blondel et al., 1970). Surveys were made during weekdays early in the morning (i.e., between sunrise and 3 h later) and only under good meteorological conditions (O'Connor and Hicks, 1980). During each visit to a patch, 5-point counts of 10 min each were conducted. Point counts were homogeneously distributed in each patch, i.e., the distance between point counts varied according to patch size. Therefore, sampling points were closer in smaller patches than in larger ones. Such sampling design is currently used with capture–recapture approaches (Husté and Boulinier, 2007; Cherkaoui et al., 2009). It may pose the problem of a more likely double counting in the smaller patches compared to the larger ones (Cherkaoui et al., 2009) when considering abundance data. However, all the approaches used in this study considered only presence/absence data. The same sampling points were used dur-

Table 1
Summary of patch vegetation characteristics. Patches have been divided into four classes according to their size. Mean values are given ±SE.

Patch size	Number of patches	Mean cover of herbaceous plants (%)	Mean cover of shrubs (%)	Mean cover of trees (%)	Mean number of herbaceous plants	Mean number of shrub species	Mean number of tree species
<1 ha	8	66.33 ± 11.05	4 ± 2.24	14.37 ± 6.97	14.62 ± 1.27	0.2 ± 0.14	0.46 ± 0.16
1–10 ha	34	80.46 ± 3.23	8.28 ± 2.06	17.50 ± 3.38	15.60 ± 1.26	0.55 ± 0.14	0.92 ± 0.16
10–40 ha	17	81.25 ± 2.93	12.84 ± 3.22	28.94 ± 4.70	16.64 ± 0.92	0.8 ± 0.23	1.48 ± 0.20
>40 ha	8	80.37 ± 5.67	23.87 ± 8.05	37.62 ± 12.97	15.38 ± 2.61	1.67 ± 0.34	2.05 ± 0.51

ing each visit. During each count, the observer recorded all birds heard or seen in the surroundings at unlimited distances. For each sampling point, data from the first and the second visits in 2003 were pooled into cumulative lists of detected species. Therefore we obtained five cumulative lists of species corresponding to the five sampling points within each patch (Nichols and Conroy, 1996; Boulinier et al., 1998): a species was considered present on a sampling point if it was present on at least one of the two temporal events. Our sampling design provided data to characterize each community via a series of spatial replicates (Nichols and Conroy, 1996). Similarly to temporal replicates, this approach relies on the assumption of community closure over the series of sampling occasions. This assumption seems reasonable because if a species is present on a patch at a given time, it is likely to have a non-null probability of being detected on each point count conducted on that patch at that time (Kendall, 1999). Waterbirds (e.g., *Anas platyrhynchos, Fulica atra, Gallinula chloropus*) and night-active species were excluded from the analyses.

2.4. Similarity of bird assemblages

Similarity in species composition between pairs of patches was investigated by calculating the SØrensen similarity index (Jongman et al., 1995). This index measures similarity of species between two communities but does not take abundances into account:

$$Sor = 2C/(A + B),$$

where C is the number of species shared by the two considered patches, and A and B are the species richness of the two considered patches. Values of *Sor* vary between 0 and 1, 0 suggesting that the two patches have no common species and 1 meaning that the two patches have similar species composition.

To estimate species richness for each patch and calculate the number of common species to all pairs of patches, we used presence–absence data from our cumulative lists of species and estimators based on capture–recapture approaches (Burnham and Overton, 1979; Boulinier et al., 1998; Nichols et al., 1998). Following Boulinier et al. (1998), estimated species richnesses were obtained using the jackknife estimator corresponding to model M (h) (Burnham and Overton, 1978, 1979; Otis et al., 1978). This model assumes heterogeneity in detectability among species. The total number of species common to both patches within each pair considered was calculated using their estimated species richness and the estimated proportion of species "lost" when going from one patch to the other, i.e., spatial extinction rates (Nichols et al., 1998). Following Nichols et al. (1998), each spatial extinction rate was conditioned on the species detected in one of the two patches under consideration (e.g., patch A) and used the model M (h) to estimate how many of these species were still present in the second patch (e.g., patch B). The spatial extinction rate may be estimated as the complement of the spatial 'survival' rate (Nichols et al., 1998):

$$1 - \hat{\phi}_{BA} = 1 - \frac{\widehat{M}_B^{R_A}}{R_A},$$

where $\hat{\phi}_{BA}$ is the estimated survival rate of local species (i.e., the probability that a species present in a patch A at a time is also present in a patch B at that time). This estimated survival rate is the ratio of the number of species estimated to be present in the patch B among those detected in the patch A ($\widehat{M}_B^{R_A}$), over the number of species detected in the patch A (R_A). $\widehat{M}_B^{R_A}$ is computed by conditioning on the subset of species actually observed in the patch A (R_A) and then estimating the number of these species that were also present in the patch B. The performance of the estimators used has been shown to be good (Alpizar-Jara et al., 2004; Jenouvrier and Boulinier, 2006). Their use may be crucial as detection probabilities often vary among species, time period and sites. Estimations of bird species richness (i.e., $\widehat{N}_A$ and $\widehat{N}_B$), $\widehat{M}_B^{R_A}$, $\widehat{M}_A^{R_B}$, $\hat{\phi}_{BA}$ and $\hat{\phi}_{AB}$ were computed using COMDYN software (Hines et al., 1999), which implements a procedure of selecting an interpolated estimator from the series of jackknife estimators of different orders (see Burnham and Overton, 1978, 1979). The estimated total number of species shared by patches A and B was thus defined as:

$$C_e = (\widehat{N}_A\hat{\phi}_{AB} + \widehat{N}_B\hat{\phi}_{BA})/2,$$

where $\widehat{N}_A$ and $\widehat{N}_B$ are the estimated species richness on patches A and B respectively, $\hat{\phi}_{AB}$ the spatial 'survival' rate of local species between patches B and A, and $\hat{\phi}_{BA}$ the spatial 'survival' rate of local species between patches A and B. Finally, the SØrensen index was calculated as:

$$Sor = (\widehat{N}_A\hat{\phi}_{AB} + \widehat{N}_B\hat{\phi}_{BA})/(\widehat{N}_A + \widehat{N}_B).$$

Our sampling design considered 5-point counts per patch whatever the size of the patch. In large patches, higher habitat heterogeneity may be predicted leading to potential variability in occurrence and detection probabilities of species among occasions (e.g., Dorazio and Royle, 2005). Nevertheless, the relatively low spatial heterogeneity of habitats and the high openness of most of the habitats of the considered patches suggest that this should not be an issue in the current study. Moreover, the capture–recapture model M (h) and the associated jackknife estimator are now used with confidence to obtain estimates of local community dynamics parameters whatever sampling conditions and notably in both homogeneous and heterogeneous habitats (Jiguet et al., 2005; Husté and Boulinier, 2007; Cherkaoui et al., 2009). Finally, a larger sampling effort was made in one large patch of 320 ha out of the 67 considered to investigate a potential effect of sampling effort and heterogeneity in microhabitats among sampling occasions. Four groups of 5-point counts were performed in this patch (i.e., a total of 20 spatial sampling occasions). The final 5-point counts selected from the 20 conducted, were chosen so that they were homogeneously distributed within the patch. In this patch, a different sampling effort (5 vs. 20 spatial sampling occasions) did not change the estimates of dynamics parameters (Husté and Boulinier, 2007). Moreover, a SØrensen index was estimated for this patch to compare bird assemblages using the 15 additional point counts or the subset of 5-point counts. The estimated SØrensen index was equal to 1, meaning that, as predicted, we could not distinguish between the species assemblages computing using 15 or 5-point counts.

The local breeding bird composition of a community can result from characteristics of the local patch considered, but also from space-related factors introduced by other environmental variables not identified in the model. Mantel tests were used to determine relationships between similarities in bird composition, patch characteristics and spatial distances between patches (Legendre and Fortin, 1989). Mantel analyses test correlations between two matrices (simple Mantel test) or between two matrices while controlling for the effect of a third matrix (partial Mantel test). We built four matrices of similarity and 1 matrix of geographical distance between all pairs of patches. (1) A matrix of bird composition similarity was performed using the SØrensen Index. (2) A matrix of vegetation similarity was performed using the distribution of patches in the PC1–PC2 space. We first calculated a matrix of Euclidian distances in vegetation structure between pairs of patches. Then, this distance matrix was converted into a similarity matrix according to the method developed by Casgrain and Legendre (2001; $S_{AB} = 1 - D_{AB}$ for patches A and B, where S_{AB} et D_{AB} are respectively the similarity index and the Euclidian distance between patches A and B). (3) Similarly, two matrices of patch size similarity and surrounding level of urbanization similarity (measured by the urban cover type) were obtained using a matrix of Euclidian distances converted into a similarity matrix. (4) Finally, a matrix of Euclidian distances between pairs of patches was calculated using coordinates of the patch centroids. The Mantel *r* statistic was tested for significance by 999 permutations according to Hope's method (1968; see Manly, 1997). Calculations of matrices and computations of simple Mantel and partial Mantel tests were performed using the "R 4.0" package (Casgrain and Legendre, 2001).

2.5. Patch occupancy by sedentary and migratory species

Species were classified into two groups depending on their migratory behavior, sedentary vs. migratory species (Le Maréchal and Lesaffre, 2000; Table 2). Because of an urban gradient in the study area, we attempted to test the hypothesis that the position of a patch in this urban gradient may affect its local characteristics and therefore its attractiveness for birds. To do this, patches were divided into two groups of different levels of urbanization according to the distance to the center of Paris. The first group ($n = 32$, noted HU in our analyses) contained patches surrounded by high urbanization i.e., patches situated at a distance lower than 12 km from Paris' center. The second group ($n = 35$, noted MU in our analyses) contained patches surrounded by moderate urbanization i.e., patches situated further than 12 km from Paris. A distance of 12 km was chosen to ensure the same number of patches within each group. We used a likelihood based-method proposed by MacKenzie et al. (2002) to estimate the proportion of area occupied (PAO) by each species, i.e., the probability a patch is occupied for each species. This method is similar to traditional closed-population methods using capture–recapture data. It helps to consider situations when the detection probabilities of species are less than one. Therefore the history of detection/non-detection for each species is used to compute the likelihood model for the observed data set, which is then maximized to obtain maximum likelihood estimates of the parameters. This approach is based on a series of assumptions: (1) the community of each patch is considered as "closed" during the study period (i.e., the five cumulative lists of detected species realized from the two series of counts are assumed to be replicates of the same community), (2) the investigator uses a sampling design to detect species and all species are correctly identified and (3) the detection probability of a species on one patch is independent of the detection probability of the same species on other patches (MacKenzie et al., 2002). We estimated the PAO for sedentary and migratory species independently in each of the two groups of patches using the freely available PRESENCE program (http://www.proteus.co.nz). We assumed that species presence probability and conditional probability of detection were constant over time, i.e., between the five sampling occasions in a patch, and patches (see MacKenzie et al., 2002). Therefore, we considered that the highest source of heterogeneity in detection probability was mainly due to varying detectability among species (e.g., song, abundance, color of plumage). As suggested by MacKenzie et al. (2002), we did not include in the analyses the PAO of species very close or equal to 1 when the detection probability was low (<0.15; Table 2).

Data were systematically tested for normality condition using the Shapiro–Wilk test. We used *t*-tests to compare local characteristics between patches of the two groups (HU vs. MU). We used *t*-tests and Wilcoxon signed rank tests to compare respectively the mean detection probability and the mean proportion of patches occupied by sedentary and migratory species in the study area. Then, for each group of birds considered independently, Wilcoxon

Table 2
List of regular breeding birds detected in 2003 and their detection probabilities considering only analyses on all 67 patches. Species have been ordered according to decreasing detection probabilities. Waterbirds and night-singer species have been omitted. According to Le Maréchal and Lesaffre (2000), species were classified into sedentary and migratory groups. Species followed by '*' indicate species not included in the analyses considering all 67 patches. Species followed by '†' indicate species not included in the analyses considering the two groups of patches separately (i.e., HU vs. MU). Abbr: species name abbreviations.

Sedentary species			Migratory species		
Scientific names	Abbr	Pdetec ± SE	Scientific names	Abbr	Pdetec ± SE
Turdus merula	Tmer	0.98 ± 0	*Cuculus canorus*	Ccan	0.80 ± 0.18
Columba palumbus	Cpal	0.90 ± 0.02	*Acrocephalus palustris*	Apal	0.80 ± 0.18
Sturnus vulgaris	Svul	0.87 ± 0.02	*Sylvia atricapilla*	Satr	0.80 ± 0.02
Parus major	Pmaj	0.86 ± 0.02	*Phylloscopus collybita*	Pcol	0.76 ± 0.02
Prunella modularis	Pmod	0.83 ± 0.02	*Fringilla coelebs*	Fcoe	0.72 ± 0.03
Troglodytes troglodytes	Ttro	0.83 ± 0.02	*Apus apus*	Aapu	0.70 ± 0.03
Pica pica	Ppic	0.81 ± 0.02	*Turdus philomelos*	Tphi	0.62 ± 0.03
Passer domesticus	Pdom	0.79 ± 0.02	*Carduelis cannabina*	Ccan	0.55 ± 0.05
Carduelis chloris	Cchl	0.75 ± 0.02	*Hippolais polyglotta*	Hpol	0.53 ± 0.07
Corvus corone corone	Ccor	0.74 ± 0.02	*Sylvia communis*	Scom	0.51 ± 0.06
Cyanistes caeruleus	Ccae	0.70 ± 0.03	*Serinus serinus*	Sser	0.50 ± 0.04
Certhia brachydactyla	Cbra	0.59 ± 0.04	*Phylloscopus trochilus*	Ptro	0.45 ± 0.05
Picus viridis	Pvir	0.56 ± 0.04	*Luscinia megarhynchos*	Lmeg	0.44 ± 0.14
Erithacus rubecula	Erub	0.55 ± 0.03	*Phoenicurus ochruros*	Poch	0.44 ± 0.04
Sitta europaea	Seur	0.52 ± 0.06	*Turdus viscivorus*	Tvis	0.42 ± 0.05
Carduelis carduelis	Ccar	0.48 ± 0.04	*Delichon urbica*	Durb	0.42 ± 0.04
Alauda arvensis	Aarv	0.46 ± 0.11	*Hirundo rustica*	Hrus	0.37 ± 0.06
Parus palustris†	Ppal	0.44 ± 0.14	*Passer montanus*	Pmon	0.26 ± 0.06
Dendrocopos major	Dmaj	0.44 ± 0.05	*Sylvia borin*†	Sbor	0.24 ± 0.08
Emberiza schoeniclus	Esch	0.42 ± 0.12	*Streptopelia turtur*†	Stur	0.17 ± 0.10
Garrulus glandarius	Ggla	0.40 ± 0.04	*Sylvia curruca*†	Scur	0.14 ± 0.12
Aegithalos caudatus	Acau	0.38 ± 0.05	*Muscicapa striata*†	Mstr	0.14 ± 0.09
Regulus regulus	Rreg	0.35 ± 0.06	*Pyrrhula pyrrhula*†	Ppyr	0.10 ± 0.06
Columba livia	Cliv	0.35 ± 0.09	*Anthus trivialis*†	Atri	0.09 ± 0.08
Streptopelia decaocto	Sdec	0.35 ± 0.04	*Locustella naevia**†	Lnae	0.00 ± 0
Dendrocopos minor	Dmin	0.34 ± 0.04	*Parus ater**†	Pate	0.00 ± 0
Motacilla alba alba	Malb	0.27 ± 0.07	*Phoenicurus phoenicurus**†	Ppho	0.00 ± 0
Falco tinnunculus	Ftin	0.12 ± 0.05			
Parus cristatus†	Pcri	0.11 ± 0.10			

signed rank tests were used to investigate whether the mean proportion of patches occupied by each species was significantly different between the two groups of patches (HU vs. MU). Statistical analyses were performed using SAS 8.2 (SAS Institute, 1996).

3. Results

3.1. Patch vegetation characteristics

Because vegetation data were highly correlated, we performed a Principal Component Analysis (PCA) to summarize them into a few independent factors. The first two factors accounted for 68.38% of the total variance. PC1 (45.88% of the total variance) could be interpreted as an axis of an increase in diversity and abundance of trees and shrubs (Table 3). PC2 (22.50% of the total variance) could be interpreted as an axis of an increase in diversity and abundance of herbaceous plants (Table 3).

3.2. Patch characteristics according to the urban gradient

The mean proportion of urbanization surrounding the patches of the HU group was significantly higher (0.77 ± 0.02 SE) than that of the patches of the MU group (0.52 ± 0.03 SE; *t*-test: $t = 7.11$, $P < 0.001$). Patches of the HU group were significantly smaller (18.5 ha ± 10.00 SE) than patches of the MU group (45.6 ha ± 16.21 SE; *t*-test: $t = 2.11$, $P = 0.039$; after log-transformation of patch size to ensure normality). Considering vegetation using the distribution of patches in the PC1–PC2 space, the diversity and abundance of trees and bushes (i.e., PC1) were significantly higher in patches of the MU group (0.26 ± 0.19 SE) than patches of the HU group (−0.28 ± 0.14 SE; *t*-test: $t = 2.29$, $P = 0.025$).

3.3. Relationships between breeding bird assemblages, habitat and space

Similarity in bird composition was not correlated with patch size similarity and patch vegetation similarity, even after accounting for the effect of geographical distance ($P > 0.05$; Table 4). Analyses performed on the two groups of patches independently (HU vs. MU) provided the same results (see Supplementary Tables S1 and S2). However, as expected, similarity in bird composition was positively correlated with similarity in the level of urbanization around the patches ($r_M = 0.181$, $P = 0.004$; Table 4). This correlation held true after controlling for the effect of geographical distance ($r_{Mp} = 0.161$, $P = 0.012$; Table 4). Bird composition similarity was negatively correlated with geographical distance between patches ($r_M = -0.103$, $P = 0.024$; Table 4). Both patch size similarity and level of urbanization around patches were negatively correlated to geographical distance between patches ($r_M = -0.127$, $P = 0.032$ and $r_M = -0.262$, $P = 0.001$ respectively; Table 4).

Table 3
Results of the principal components analysis of the six descriptors characterising the vegetation structure of the patches, $n = 67$.

Variables	PC1	PC2
Number of tree species	0.910**	−0.047
Cover of trees (%)	0.757**	−0.329**
Number of shrub species	0.765**	0.528**
Cover of shrubs (%)	0.791**	0.095
Number of herbaceous plant species	−0.040	0.885**
Cover of herbaceous plants	−0.372**	0.409**
Eigenvalues	**2.75**	**1.35**
Variance explained (%)	**45.88**	**22.50**
Cumulative variance (%)	**45.88**	**68.38**

** $P < 0.01$.

Table 4
Results of Mantel (above diagonal) and partial Mantel tests (below diagonal) conducted successively for local (vegetation structure and area) and regional (surrounding urbanization) variables.

	Bird similarity	Vegetation similarity	Geographic distance
Vegetation structure (n = 67)			
Bird similarity	–	0.089	−0.103*
Vegetation similarity	0.084	–	−0.055
Geographic distance	−0.098*	−0.046	–
Patch area (n = 67)			
Bird similarity	–	0.120	−0.103*
Patch area similarity	0.108	–	−0.127*
Geographic distance	−0.089*	−0.116*	–
Surrounding urbanization (n = 67)			
Bird similarity	–	0.181**	−0.103*
Urban similarity	0.161*	–	−0.262**
Geographic distance	−0.058	−0.249**	–

* $P < 0.05$.
** $P < 0.01$.

3.4. Effects of urbanization on bird composition

As suggested by MacKenzie et al. (2002), species for which both the PAO was very close or equal to 1 and their probability of detection was low were excluded from the analyses. In such situations, the level of information collected on species presence/absence is small and the model is not able to distinguish between a patch where the species is genuinely absent and a patch where the species has merely not been detected. Considering analyses on all 67 patches, three migratory species were not included (see species followed by ‘*’ in Table 2). Estimated probabilities of detection of the remaining species varied between 0.09 ± 0.08 SE and 0.80 ± 0.02 SE and between 0.11 ± 0.10 SE and 0.98 ± 0 SE for migratory and sedentary species respectively. The mean detection probability of migratory species (0.46 ± 0.05 SE) was not significantly different than that of sedentary species (0.56 ± 0.04 SE; *t*-test: $t = -1.55$, $df = 1$, $P = 0.128$). The estimated proportions of occupied patches varied between 0.015 ± 0.015 SE and 0.912 ± 0.035 SE and between 0.047 ± 0.048 SE and 1 ± 0 SE for migratory and sedentary species respectively. As expected, the mean estimated proportion of patches occupied by migratory species (0.41 ± 0.06 SE) was significantly lower than occupancy by sedentary species (0.60 ± 0.06 SE; Wilcoxon signed rank test: $P = 0.017$). It suggests that migratory species did not occupy all types of patches in the study area.

Considering analyses on patch occupancy in the two groups of patches (i.e., HU vs. MU), nine migratory species and two sedentary ones were not included (see species followed by ‘†’ in Table 2). Considering the remaining migratory species only, the mean estimated proportion of patches occupied was significantly higher for patches of the MU group (0.48 ± 0.08 SE) than for patches of the HU group (0.41 ± 0.07 SE; Wilcoxon signed rank test: $P = 0.029$). *Sylvia atricapilla*, *Apus apus* and *Fringilla coelebs* occupied more than 90% of the patches. Seventy-two percent of the migratory bird species, and particularly *Phoenicurus ochruros* and *Phylloscopus trochilus*, preferentially occupied patches situated more than 12 km from Paris (i.e., patches surrounded by moderate urbanization; Fig. 2).

Considering the remaining sedentary species only, the mean estimated proportion of patches occupied was not significantly different between the two groups of patches (MU: 0.67 ± 0.06 SE; HU: 0.63 ± 0.07 SE; Wilcoxon signed rank test: $P > 0.05$; Fig. 2). It suggests that the level of urbanization may not greatly affected the distribution of these species in the study area. *Corvus corone corone*, *T. merula and Columba palumbus* were present on all patches. Other species such as *Prunella modularis*, *S. vulgaris*, *Cyanistes caeruleus*, *Parus major*, *Passer domesticus*, *Pica pica* and *Troglodytes troglodytes* occupied more than 90% of the patches. Forty-four

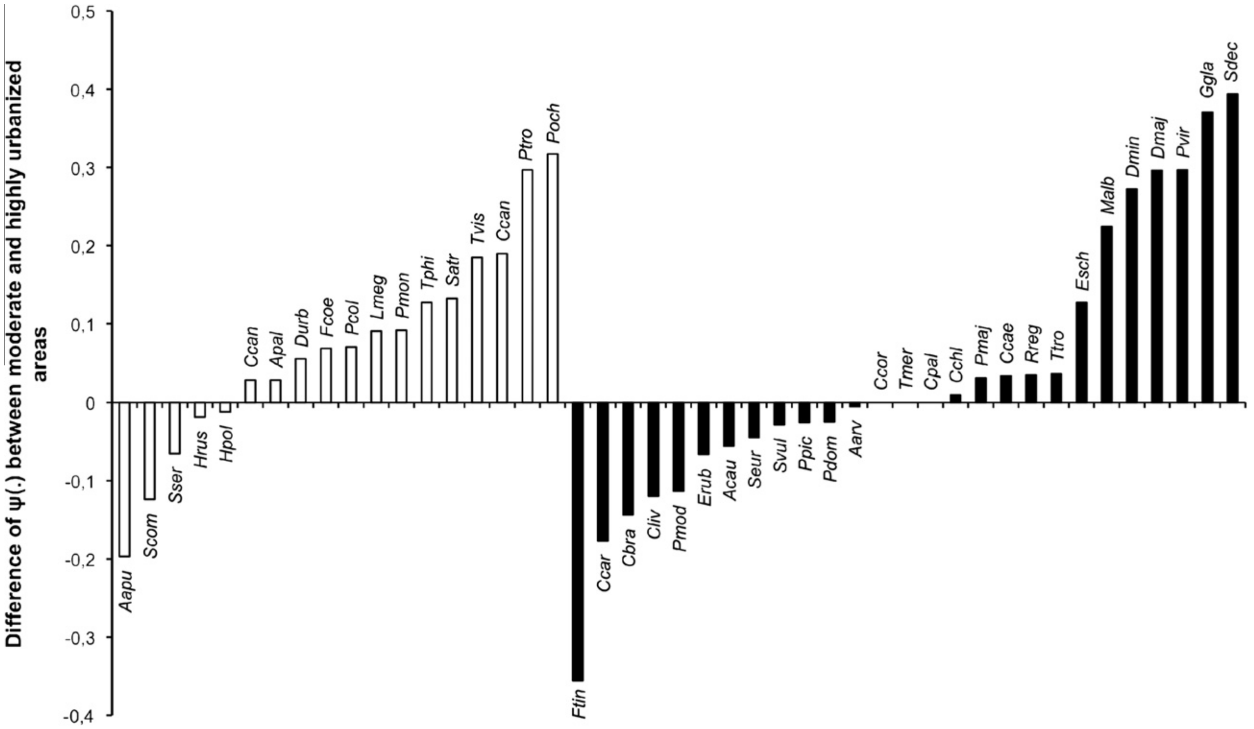

Fig. 2. Difference of estimated proportion of patches occupied $\psi(\cdot)$ between patches situated at more than 12 km from Paris' center and patches situated closer than 12 km from Paris' center. Positive values mean that $\psi(\cdot)$ are higher in patches situated at larger distances from Paris. Negative values mean that $\psi(\cdot)$ are higher in patches situated next to Paris. Open bars represent migratory species and filled bars represent sedentary species. Species name abbreviations are given in Table 1.

percent of the sedentary bird species, and particularly *Falco tinnunculus*, preferentially occupied patches surrounded by high urbanization (Fig. 2). The same proportion, and particularly *Streptopelia decaocto*, *Garrulus glandarius*, *Picus viridis*, *Dendrocopos major*, *Dendrocopos minor* and *Motacilla alba alba*, preferentially occupied patches surrounded by moderate urbanization (Fig. 2).

4. Discussions and conclusions

In the studied urban landscape, the similarity in composition between breeding bird assemblages was not related to the similarity in local patch characteristics such as patch size and vegetation structure. However, the similarity between breeding bird assemblages was related to the similarity in the level of surrounding urbanization and the spatial distribution of patches. Our results showed that sensitivity to urbanization varied according to bird guilds, notably between migratory and sedentary species. Indeed, migratory birds preferentially occupied patches surrounded by moderate urbanization while sedentary ones occurred equally in patches surrounded by moderate or high urbanization.

Previous studies have used urban gradients to investigate the consequences of increasing urbanization on bird communities (Jokimäki and Suhonen, 1993; Blair, 1996, 1999). However, ecological mechanisms driving bird community assemblages according to different levels of anthropogenic disturbances still need to be investigated. In this study, local assemblages were affected by both the surrounding level of urbanization and space-related factors not identified in the model. These factors could be due to higher probability of species exchange between patches closer to each other. First, bird compositions of two patches were more similar when the considered patches were surrounded by similar level of urbanization. Therefore, the urban gradient in the study area is likely to play a determining role in shaping bird assemblages. Second, bird compositions of two patches were more similar when the considered patches were close to each other. Such spatial pattern has rarely been considered in urban environments but it should be taken into account, particularly when attempting to understand the role of dispersal in the structure and dynamics of bird communities (Selmi and Boulinier, 2001, 2003b).

The size and the vegetation structure of urban patches have often been shown as causal factors for species richness and abundance of birds (Goldstein et al., 1986; Tilghman, 1987; Park and Lee, 2000; Husté et al., 2006). This can be explained by the fact that diversity and availability of resources (i.e., food and nest sites) usually depend on the overall level of habitat quality, which may be related to the size and vegetation structure of patches. Moreover, such patch characteristics are often linked to urbanization intensity. Indeed, as highlighted by previous studies (Blair, 1996, 1999; Crooks et al., 2004), patches with highest species richness are themselves often situated in areas with moderate levels of urbanization, often corresponding to residential areas. In these areas, the amount of parks and yards may be high and their vegetation composed primarily of ornamental plants and planted trees and bushes. On the contrary, patches situated in areas with high levels of urbanization are often surrounded by intense human development with high densities of residential and commercial buildings. Pavements usually replace all native habitats. In the study area, our results showed that urbanization leads to a spatially structured distribution of the considered patches. Indeed, patches with similar sizes were close to each other. Moreover, patches situated in highly urbanized areas were smaller and had lower diversity and abundance of trees and bushes. Yet, when considering bird composition, patches of similar size or with similar vegetation structure had different bird compositions while patches surrounded by the same levels of urbanization had similar bird composition. First, this result can be explained by varying persistence of species (Fahrig, 2001), particularly because requirements and sensitivity to disturbances of the considered species may vary according to constraints. Second, this situation involves determinant roles of both the urban gradient and dispersal in shaping bird assemblages.

The sensitivity to urbanization may vary dramatically between bird species (Mills et al., 1989; Blair, 1996; Germaine et al., 1998; Crooks et al., 2004; Lim and Sodhi, 2004). The distribution of birds in these environments may result from a combination of several life-history traits (Kark et al., 2007; Croci et al., 2008). As seen above, changes due to human development may directly affect resources on which each bird species may depend within a given patch. Not all species react the same way to the constraints imposed by the surrounding urbanization, and responses of birds to urbanization depend on species-specific patterns. As expected, sensitivity to urbanization varied between migratory and sedentary species confirming that migratory status is a strong biological trait influencing bird sensitivity to urbanization (Bennett et al., 2004; Kark et al., 2007; Croci et al., 2008).

In the study area, a large number of the migratory species preferentially occupied patches situated in areas with moderate levels of urbanization. This result can be explained in different ways. First, patches surrounded by moderate levels of urbanization were larger in the study area. These patches are therefore less exposed to human disturbances along habitat edges (e.g., road traffic, predators such as *Felix catus* and *Canis familiaris*). Second, the majority of these species are avoider or adapter species preferring moderately disturbed patches that are also the most heterogeneous (Blair, 1996). Third, in the more urbanized areas where patches are scarce, the likelihood to find available patches with sufficient habitat quality is small. Desertion and resettlement every year decrease their likelihood to find suitable patches and mates. Consequently, migratory species are constrained in their distribution among patches and the year-to-year dynamics of occupation are likely to be critical. Finally, the ability of some migratory species to maintain viable communities from 1 year to the next in the most disturbed landscapes may be reduced because local breeding populations in extremely patchy habitats are too small (MacArthur and Wilson, 1967; Boyce, 1992; Gregory, 2000). This is corroborated by comparisons of local extinction and turnover rates of migratory and sedentary species in the same system of patches (Husté and Boulinier, 2007).

Interestingly, patch occupancy of a few migratory species (i.e., *Hirundo rustica*, *A. apus*, *Sylvia communis*, *Hippolais polyglotta* and *Serinus serinus*) was higher in highly urbanized areas, or equal in high and moderately urbanized areas. As reported in previous studies (Kark et al., 2007), urbanization favors species that are able to nest in building cavities. It also favors granivores, aerial insectivores and ground foraging insectivores. Therefore, these species are probably able to find nest sites and food in the more urbanized areas despite both the dominance of human infrastructures and the replacement of native vegetation by ornamental vegetation.

Our results showed that migratory status is a determinant trait to explain the distribution of species along an urban gradient. This can be explained by the fact that migratory status is behind temporal dynamics due to constraints of re-colonization by migratory species each year (Husté and Boulinier, 2007). However, other biological traits such as the ability to occupy territories and foraging sites may also be important factors shaping success in the most highly urban areas (Croci et al., 2008). Therefore, bird community organization in urban environments is probably the result of a combination of at least nesting behavior, feeding ecology, migratory status, and territory defense for breeding and foraging, each with specific states that contribute to tolerance of urban constraints.

Sedentary birds are distributed across the entire urban gradient in the study area. Moreover, sedentary species seem able to exist within the constraints due to urbanization since ten species occupied more than 90% of patches in the study area and 44% preferentially occupied patches surrounded by high levels of urbanization. Some sedentary species are successful in urban landscapes and have colonized cities all over the world (e.g., *P. domesticus*, *Columbia livia*, *Corvus corone corone*; Savard et al., 2000). They are considered as ‘urban exploiters’ and are repeatedly present in the most developed landscapes. Their success is related to their ability to use human presence to find their required resources. They can be very abundant (Clergeau et al., 1998; Marzluff, 2001) and are responsible for the biotic homogenization reported in most of the cities in the world (Clergeau et al., 2006; McKinney, 2006). In the entire study area, patch occupancy of sedentary species was higher than for migratory ones. According to the positive distribution–abundance relationship (Hanski, 1999; Selmi and Boulinier, 2004) i.e., widely distributed species are more abundant locally than the more localized ones, our results emphasize that sedentary species are likely more abundant locally in the studied urban area than migratory ones. Interestingly, few sedentary species, such as *M. alba alba*, *G. glandarius*, *D. minor*, *Dendrocopos major*, *P. viridis* and *S. decaocto*, require habitats that are less altered by human development and are therefore mostly present in the less urbanized patches. This result confirms that other biological traits than migratory status may also be relevant to tolerance of urban constraints.

Patch community similarity has been investigated in varied landscapes (Kadmon and Pulliam, 1993; Selmi and Boulinier, 2003b) and studies concluded that dispersal of individuals between patches might be an important factor. Dispersal may affect the probability of occupancy and contribute to determining the composition of local communities. However, the degree of isolation of patches (i.e., their spatial arrangement) can affect the probability of colonization of new habitat patches through its effect on the success of dispersal of individuals. Such studies are rare in urban landscapes because dispersal processes may seem insignificant due to the reduced scale of urban studies. Yet, we demonstrated here that dispersal could be significant in shaping urban bird communities even if the scale of the study was small (study area of 236 km^2). This consideration is of prime importance before implementation of management plans in urban landscapes. In particular, dispersal of migratory species seemed reduced between areas with high and moderate levels of urbanization. Two reasons can explain this result. First, reduced dispersal of migratory species can be explained by the fact that patches are more isolated and with insufficient habitat quality in the more urbanized areas. In the case of a presence of a pool of species in the extreme undisturbed part of the gradient (i.e., outside of our study area), our results suggest that dispersal could occur from this pool to moderately urbanized areas but not much further to the more urbanized areas (Cam et al., 2000; Clergeau et al., 2001). They also suggest that sedentary species may have both less stringent requirements for particular breeding sites and also get to select nesting sites before the arrival of migratory species, which may increase their competitiveness (Jokimäki and Suhonen, 1998). Second, the urban surrounding matrix in the more disturbed areas may represent a physical barrier for the dispersal of birds. Nevertheless, such a barrier effect is more often reported for taxa with reduced mobility (e.g., amphibians; Pellet et al., 2004). Overall our study did not consider green corridors such as wooded streets, though they may enhance bird movements by connecting otherwise isolated patches. However corridor quality may differ according to the particular habitat requirements of individual bird species and not all species occupied corridors in cities (Fernandez-Juricic, 2000b). Therefore specific investigations would be useful to study the probabilities of movement along corridors for each species.

In the study area, we showed a spatial organization of breeding bird communities due to the presence of an urban gradient, and especially for migratory species. The fact that the size and vegetation of patches did not affect bird compositions while the geographical location in the gradient did influence them, has a great value to conservation and management. Indeed, it suggests that whatever local patch characteristics may be in the more urbanized areas, some species will not be found in these patches because of their sensitivity to the surrounding urbanization. First, the mean size of patches situated in very urbanized landscapes is globally small compared to that of patches situated in moderately urbanized areas. Second, the surrounding urban disturbances are omnipresent even if habitat conditions are good for birds in such patches. Such considerations are of prime importance because they suggest that management plans in urban landscapes have to take into account the intensity of human activities and potentially, all urban patches cannot have the same conservation value. Moreover, at patch scale, bird assemblages may be influenced by specific patterns of co-occurrence of species. Investigating such patterns might help to understand more precisely the mechanisms that drive bird assemblages in urban landscapes. Finally, factors affecting bird detectability are complex and it is rare to detect all species in a study area. The probabilistic estimators we used, and our proposed modification of the SØrensen index may allow avoiding the typical assumption of species detection probabilities of 1. We think that they may be good candidates to assess dynamics and composition assemblages whatever the spatial and temporal scales, and the nature of the considered landscape.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.08.022.

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