Ecological Applications, 17(1), 2007, pp. 168–180

DETERMINANTS OF LOCAL EXTINCTION AND TURNOVER RATES IN URBAN BIRD COMMUNITIES

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Abstract. Studying the effects of urbanization on the dynamics of communities has become a priority for biodiversity conservation. The consequences of urbanization are mainly an increased fragmentation of the original landscapes associated with a decrease in the amount of favorable habitats and an increased pressure of human activities on the remaining patches suitable for wildlife. Patterns of bird species richness have been studied at different levels of urbanization, but little is known about the temporal dynamics of animal communities in urban landscapes. In particular, urbanization is expected to have stronger negative effects on migratory breeding bird communities than on sedentary ones, which should lead to different patterns of change in composition. Using an estimation method accounting for heterogeneity in species detection probability and data collected between 2001 and 2003 within a suburban area near the city of Paris, France, we tested whether these communities differ in their local extinction and turnover rates. We considered the potential effects of patch size and distance to Paris' center as a measure of the degree of urbanization around the patches. As expected, local rates of extinction and turnover were higher for migratory than for sedentary species, and they were negatively related to patch size for migratory species. Mean species richness of the sedentary species increased during the study period and their local turnover rate was negatively related to the distance to the urban core, showing a trend to colonize the most urban patches. These results highlight the very dynamic nature of the composition of some local bird communities in fragmented habitats and help to identify factors affecting colonization and extinction.

Key words: bird species richness; colonization; community dynamics; detection probability; fragmentation; France; migratory birds; sedentary birds; urbanization.

INTRODUCTION

The destruction and fragmentation of continuous habitats into smaller and isolated patches take place all over the world, and the associated habitat changes represent a global threat to biodiversity (Wilcox and Murphy 1985, Caughley 1994, Wilcove et al. 1998, Harrison and Bruna 1999). An extreme case of fragmentation occurs in urban landscapes, where the remaining green patches are mainly parks that can be extremely limited in size and number. As greater numbers of people live in cities and as urbanization is increasing on all continents, restoration, preservation, and enhancement of biodiversity in such landscapes has become more important (Savard et al. 2000). It is thus becoming critical to study how ecological processes and human activities interact to drive the dynamics of biodiversity in urban landscapes (Marzluff 2001, McKinney 2002). Patterns of use of urban patches by wildlife can provide important insight (Hostetler and Knowles-Yanez 2003), although teasing apart the roles of factors potentially acting within and among patches remains to be done, especially at the level of communities.

Several studies have used naturally occurring spatial gradients of urbanization observed in the surrounding areas of cities to investigate potential changes in species richness and composition associated with increasing levels of human disturbance (Matson 1990, McDonnell and Pickett 1990, Blair 1996, 1999, Clergeau et al. 1998, Cam et al. 2000, Alberti et al. 2001, Crooks et al. 2004). Nevertheless, studies in urban contexts have rarely considered factors affecting the temporal variability in community composition, despite its need for a full understanding of the effect of urbanization on biodiversity. Processes determining the richness, composition, and dynamics of communities occur at various scales (Ricklefs and Schluter 1993), and estimates of local extinction and turnover rates can be useful to tease them apart. In terms of spatial scale, the effects may be local or regional, with extinction and colonization being more or less facilitated by the proximity of other patches holding viable communities. In terms of temporal scale,

Manuscript received 18 November 2005; revised 5 May 2006; accepted 8 May 2006. Corresponding Editor: T. R. Simons.

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a dynamic equilibrium state with local extinctions compensating for local colonizations may exist (Nichols et al. 2006), but there also may exist some transitional time during which an overall increase or decrease in the number of species may occur. It is within this context that predictions about rates of local change of bird communities as a function of fragmentation and level of urban disturbance can be tested. For species expected to be negatively affected by habitat fragmentation and other effects associated with urbanization, one can predict a decreasing species richness in the long term and higher rates of local extinction and turnover on smaller time scales. This may be due to a higher probability of having local extinctions followed by (re-)colonizations, because higher local extinction rates provide the opportunity for higher turnover rates (see Boulinier et al. [2001] for the same reasoning at a larger spatial scale). Conversely, for species not affected or positively affected by urbanization, one can predict more stable communities, with constant or increasing species richness in the long term. Investigating the properties of the temporal dynamics of metacommunities is also important as it may help to identify instances of extinction debts, i.e., when some species not regionally extinct yet have the potential to go extinct due to their situation relative to their extinction threshold (Hanski and Ovaskainen 2002).

The more urbanized regions are often associated with both small patches and reduced amount of suitable habitats (Fernández-Juricic 2000*a*), which limits our potential ability to test for a specific effect of habitat fragmentation per se (Fahrig 2003). Indeed, a distinction is usually made between fragmentation per se and habitat loss (Fahrig 1999, 2003, Haila 1999, Hanski 1999). However, both often occur together, and it is sometimes difficult to distinguish the two processes (Kupfer et al. 2006), especially in highly fragmented landscapes. In this context, patch size seems a reasonable measure of broad-sense habitat fragmentation in urban landscapes. Large suitable urban patches have been shown to host higher numbers of species than small ones (Tilghman 1987, Jokimäki 1999, Bolger et al. 2000, Fernández-Juricic 2000*b*, Park and Lee 2000), confirming that the response of bird species can differ according to fragmentation (Van Dorp 1987, Wiens 1994, Boulinier et al. 2001, Tworek 2002, 2003). The response of bird species may also differ according to urbanization pressure in the surrounding matrix and associated levels of human disturbance that can be related to the distance of patches to the urban core in the case of the presence of an urban gradient. Finally, the response may vary among species, as for instance a relative success of ubiquitous species has been reported in highly urbanized areas (Beissinger and Osborne 1982, Clergeau et al. 1998, Blair 2001).

The island biogeography theory (MacArthur and Wilson 1967, Rosenzweig 1995) and the metapopulation concept (Hanski and Simberloff 1997) have been useful frameworks to study the impact of habitat fragmentation on bird communities (Andrén 1994, Wiens 1994) and especially the species–area relationship in urban landscapes (Tilghman 1987, Park and Lee 2000). Considering community composition, temporal changes are the result of year-to-year dynamics of presence on urban patches, i.e., local extinction and local colonization, which may depend on local and regional characteristics, but also on population size. Higher probabilities of extinction are expected in smaller populations (MacArthur and Wilson 1963, 1967, Boyce 1992) as smaller populations are less resistant to demographic stochasticity. Moreover, a weak heterogeneity of habitat in small patches (leading to a lower availability of resources) and higher edge effects may particularly influence changes in species composition (Fahrig and Merriam 1994, Nilon et al. 1995). In particular, a decrease of patch size may be associated with the replacement of native vegetation by human settlement, and this may affect extinction and colonization events (Marzluff 2005).

Sedentary birds have been reported to be less disadvantaged than migratory birds by surrounding human developments (Friesen et al. 1995, Hennings and Edge 2003, Miller et al. 2003). Several reasons may explain that. Migratory species may have constraints on local recolonization following the local loss of breeders on the smaller patches. Also, local populations of sedentary species may often be larger than migratory ones on smaller patches, notably because of their lower requirement for particular breeding sites. Sedentary species may also be more accustomed to coping with constant surrounding disturbances due to human activities. Finally, sedentary species may select nesting sites before the arrival of migratory species, which may increase their competitiveness (Jokimäki and Suhonen 1998). Comparing the dynamics of these two groups is interesting as it may help to further understanding of how much local richness is affected by (re-)colonization after local extinction (i.e., "rescue effect"; see Brown and Kodric-Brown 1977) and thus how important dispersal from larger patches is.

Correlative studies cannot necessarily tease apart the role of different factors. However, multiple regression using factors describing different characteristics associated with the local patches can help to infer which of these factors may be important. In this study, we tested associations between rates of change in community composition of migratory and sedentary birds and two potentially independent factors expected to affect bird communities, namely patch size and a measure of the urbanization around patches. We used presence–absence data of breeding bird species on a series of patches in a suburban area next to the city of Paris, France, over a three-year period (2001–2003) to test a series of a priori predictions related to these variables.

In studies based on direct counts, it is likely that not all species are detected in the sampled communities and variation in detection probabilities can lead to invalid inferences about community dynamics (Yoccoz et al. 2001). The inability to detect all species present in a sampled area is accepted as a recurrent methodological problem (Boulinier et al. 1998*b*), and ecologists increasingly attempt to consider the fact that detection probabilities <1 may induce biased estimates of community parameters (Burnham and Overton 1979, Nichols and Conroy 1996, Boulinier et al. 1998*a*, 2001, MacKenzie et al. 2002, 2003, Royle and Nichols 2003, Bailey et al. 2004). Variation in species detection probability may arise from variation in abundance of each species, but also from other factors affecting detectability of individuals of different species (e.g., size, color of plumage, vocalizations). In particular, the detectability of sedentary and migratory species can be expected to be different according to the date of sampling in the breeding season. Thus, in order to estimate the local rate of change in the composition of sedentary and migratory communities, we used recently proposed estimators and patterns of detection/nondetection of species over a series of sampling occasions of each local community (Nichols et al. 1998). This approach enabled us to take into account potential differences in detectability between patches and years, but also between the groups of species considered. Using estimates of community parameters for each patch also allowed us to account for potential spatial covariance in the data (Selmi and Boulinier 2001, Lichstein et al. 2002, Hawkins and Porter 2003). This study is among the first that we know of to explore the temporal dynamics of sedentary and migratory birds using such relevant estimation methods in an urban landscape.

For the two groups of bird species (migratory and sedentary), we predicted higher species richness on larger patches. Higher mean changes in species composition, i.e., higher local extinction rate (proportion of species going locally extinct) and higher turnover rate (proportion of locally new species), were expected for migratory species in the studied urban landscapes due to their more limited tolerance for human disturbance (Friesen et al. 1995, Nilon et al. 1995, Hennings and Edge 2003). We also predicted higher local extinction and turnover rates for the migratory species on smaller patches and on more urbanized patches, i.e., on patches situated closer to Paris, mainly due to reduced connectivity among patches with increasing urbanization. Regarding sedentary species, we expected stable or increasing species richness during the study period and little effect of patch variables.

METHODS

Study area

The study was carried out in the Seine-Saint-Denis northeastern suburbs of Paris, France. The entire study area is highly urbanized and covers ~236 km^2. The mean human population density is high (5855 inhabitants/km^2 in 1999; Institut National de la Statistique et des Etudes Economiques INSEE, *available online*)[4] but lower than in Paris (20 164 inhabitants/km^2 in 1999; INSEE). Patches suitable for wildlife are mainly urban parks (see Plate 1). A few remaining woodlands and temporarily unused patches are also scattered across this area. Patches potentially suitable for breeding-bird communities were identified using an aerial photograph and field observations (A. Husté). Reliable data on the breeding bird communities were collected in a large proportion of the patches ($n = 67$) available within the whole study area (>80% of the patches of the study area; Husté et al. 2006). The estimates of the rates of change in community composition were computed for each patch between 2001 and 2003, and the size of the patches used in the analyses ranged from 0.4 to 450 ha.

Data collection

Patch size and the geographic coordinates of the centroid of each patch were obtained using color aerial photographs provided by the Institut Géographique National (taken in 2000) and the Geographic Information System (GIS) ArcView 3.2 (ESRI 1996). 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, located in the center of Paris. Using color aerial photographs at a scale of 1:5000 and ArcView 3.2 (ESRI 1996), polygons with the same cover types were delimited by hand. That way, we built a land cover map of the study area defining three types of covers around the patches: urban (i.e., buildings and roads), residential (i.e., residential areas), and green (i.e., remaining islands of vegetation including other studied patches; see McKinney 2002). Then we measured the proportion of the type "urban" around each patch using a circular area with a radius of 1000 m and Spatial Analyst for ArcView 3.2 (ESRI 1996). This distance has already been used as a relevant distance to characterize the local effect of urbanization on bird communities (Bolger et al. 1997, Mörtberg 2001, Donnelly and Marzluff 2004).

Bird communities within the 67 sampled patches were surveyed using point counts during the breeding seasons of 2001 and 2003. In order to account for differences in the breeding phenology of the species, we followed Blondel et al. (1970, 1981) adapted to account for a potential heterogeneity in species detectability (Selmi and Boulinier 2003). For each year and each patch, two series of counts were thus conducted at two different times of the breeding season. Each patch was visited (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). During each visit, five-point counts of 10 min each were conducted within each patch early in the morning and

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[4] ⟨http://www.insee.fr⟩

only under good meteorological conditions (O'Connor and Hicks 1980). This level of sampling effort was chosen as we expected bird species to be relatively easily detected because of the low number of species potentially present and the good fieldwork conditions within urban patches (e.g., rarely dense vegetation potentially decreasing the chance of detecting some species). The sampling was done at the same time for the two groups of species considered in this study, i.e., species were classified a posteriori into two groups depending on their migratory behavior, sedentary vs. migratory species (see Table 1 and Le Maréchal and Lesaffre 2000). Only regular breeders in the study area were considered (Le Maréchal and Lesaffre 2000), and waterbirds (e.g., *Anas platyrhynchos*, *Fulica atra*, *Gallinula chloropus*) were excluded from the analyses.

The point counts were conducted so that they were homogeneously distributed within each patch and their localization within the patch was maintained between visits and years. During each count, the observer recorded all of the birds heard or seen in the surroundings at unlimited distances. The absence of limited sampling distance during point counts may have contributed to an increase in the heterogeneity of species detection as it allows a higher detection of species whose movements and vocalizations are detectable at larger distances without increasing the detectability of species whose movements and vocalizations are mostly detectable at smaller distances. Detection probability was not directly corrected by the sampling distance, but this should not be a problem given the approach we used. Each year, the data of the breeding season (two visits per year) within each patch were grouped into five cumulative lists of detected species to make lists of species detected on five sampling "occasions" per patch (Nichols and Conroy 1996, Boulinier et al. 1998*b*).

Estimation of community dynamic parameters

The parameters of the community dynamics associated with each patch (species richness, extinction rate, and turnover rates) were estimated using the data from the cumulative lists of recorded species and a capture–recapture type of approach that accounts for situations in which not all species are detected (Burnham and Overton 1979, Boulinier et al. 1998*a*, Nichols et al. 1998). The species detection probability was defined as the probability that at least one individual of the species was detected during a sampling occasion, given that the species is present in the sampled area (Boulinier et al. 1998*b*, Nichols et al. 1998). Following Boulinier et al. (1998*b*), species richness estimates and detection probabilities were obtained using the jackknife estimator associated with model M(h) (Burnham and Overton 1978, 1979, Otis et al. 1978). This model assumes a heterogeneity in detectability among species and among patches and years. Estimates of extinction and turnover rates between 2001 and 2003 were performed using the estimators proposed by Nichols et al. (1998). The local

Table 1. List of the sedentary and migratory species used in the analyses following Le Maréchal and Lesaffre (2000).

Common name	Scientific name
Sedentary species	
Gray Partridge	*Perdix perdix*
Great Spotted Woodpecker	*Dendrocopos major*
Lesser Spotted Woodpecker	*Dendrocopos minor*
Eurasian Green Woodpecker	*Picus viridis*
Rock Pigeon	*Columba livia*
Common Woodpigeon	*Columba palumbus*
Eurasian Collared Dove	*Streptopelia decaocto*
Common Kestrel	*Falco tinnunculus*
Long-tailed Tit	*Aegithalos caudatus*
Eurasian Skylark	*Alauda arvensis*
European Goldfinch	*Carduelis carduelis*
European Greenfinch	*Carduelis chloris*
Short-Toed Treecreeper	*Certhia brachydactyla*
Eurasian Jackdaw	*Corvus monedula*
Hooded Crow	*Corvus corone corone*
Rook	*Corvus frugilegus*
Yellowhammer	*Emberiza citrinella*
Reed Bunting	*Emberiza schoeniclus*
European Robin	*Erithacus rubecula*
Eurasian Jay	*Garrulus glandarius*
White Wagtail	*Motacilla alba alba*
Marsh Tit	*Parus palustris*
Crested Tit	*Parus cristatus*
Great Tit	*Parus major*
Blue Tit	*Parus caeruleus*
House Sparrow	*Passer domesticus*
Black-billed Magpie	*Pica pica*
Hedge Accentor	*Prunella modularis*
Common Goldcrest	*Regulus regulus*
Wood Nuthatch	*Sitta europaea*
Common Starling	*Sturnus vulgaris*
Eurasian Blackbird	*Turdus merula*
Winter Wren	*Troglodytes troglodytes*
Migratory species	
Common Cuckoo	*Cuculus canorus*
Common Swift	*Apus apus*
European Turtle Dove	*Streptopelia turtur*
Marsh Warbler	*Acrocephalus palustris*
Tree Pipit	*Anthus trivialis*
Eurasian Linnet	*Carduelis cannabina*
Northern House Martin	*Delichon urbica*
Chaffinch	*Fringilla coelebs*
Melodious Warbler	*Hippolais polyglotta*
Barn Swallow	*Hirundo rustica*
Grasshopper Warbler	*Locustella naevia*
Common Nightingale	*Luscinia megarhynchos*
Spotted Flycatcher	*Muscicapa striata*
Coal Tit	*Parus ater*
Eurasian Tree Sparrow	*Passer montanus*
Black Redstart	*Phoenicurus ochruros*
Common Redstart	*Phoenicurus phoenicurus*
Willow Warbler	*Phylloscopus trochilus*
Eurasian Chiffchaff	*Phylloscopus collybita*
Wood Warbler	*Phylloscopus sibilatrix*
Eurasian Bullfinch	*Pyrrhula pyrrhula*
European Serin	*Serinus serinus*
Lesser Whitethroat	*Sylvia curruca*
Garden Warbler	*Sylvia borin*
Greater Whitethroat	*Sylvia communis*
Blackcap	*Sylvia atricapilla*
Mistle Thrush	*Turdus viscivorus*
Song Thrush	*Turdus philomelos*

Note: The study was carried out in the Seine-Saint-Denis northeastern suburbs of Paris, France.

extinction rate between 2001 and 2003 was defined as the proportion of species present in 2001 that were not present in 2003. This quantity is conditioned on species detected in 2001 and uses the model M(h) to estimate how many of these species are still present in 2003 (Nichols et al. 1998):

$$1 - \hat{\phi}_{2001-2003} = 1 - \frac{\hat{M}^{R_{2001}}_{2003}}{R_{2001}}$$

where ϕ is the survival rate of local species, which is the ratio of the number of species estimated to be present in 2003 among those detected in 2001 ($\hat{M}^{R_{2001}}_{2003}$), over the number of species detected in 2001 (R_{2001}). There are several definitions of the turnover in community ecology. According to Nichols et al. (1998), we chose to define the local turnover rate as the proportion of species in 2003 that were locally new since 2001. This quantity is conditioned on species detected in 2003 and uses the model M(h) to estimate how many of them were not present in 2001 (Nichols et al. 1998):

$$1 - \hat{\phi}_{2003-2001} = 1 - \frac{\hat{M}^{R_{2003}}_{2001}}{R_{2003}}$$

where ϕ is the survival rate with data placed in reversed time order, which is the ratio of the number of species estimated to be present in 2003 that were not present in 2001 ($\hat{M}^{R_{2003}}_{2001}$) over the number of species detected in 2003 (R_{2003}). This definition of the turnover rate considers extinction and colonization events and reflects changes of the considered community during the study period (Nichols et al. 1998). The performance of these estimators has been shown to be good (Alpizar-Jara et al. 2004, Jenouvrier and Boulinier 2006). The use of such estimators is recommended in most field situation as detection probabilities often vary among species, time period, and sites.

Our sampling was designed in such a way that we were able to characterize each community via a series of spatial replicates (Nichols and Conroy 1996). The use of spatial replicates relies on the assumption that the community is closed over the series of sampling occasions. We feel that this assumption is reasonable because if a species is present in a patch at a given time, it has a non-null probability of being detected on each point count conducted in that patch at that time (Kendall 1999). We are thus assuming that there is one community per patch and not a strong heterogeneity in the distribution of species within each patch. Such an assumption is usually made in studies in which local species richness is related to patch size or other characteristics, notably when species accumulation curves across samples are used in a way that can confound partial sampling due to detectability issues and spatial heterogeneity in species distribution (e.g., see Cam et al. [2002*a*, *b*] and Gray et al. [2004] for discussions of these issues). Microhabitat differences within a patch could be expected to prevent some species from being easily detected in some areas within a patch, i.e., the probability of detection for a given species might vary across sampling occasions. Such a consideration was investigated by Jiguet et al. (2005), who found that the M(h) model and its associated jackknife estimator were reliable in estimating local community parameters even when habitats were heterogeneous within sampling units. We also tested whether estimates of dynamic parameters varied according to the number of sampling occasions (5 vs. 20 spatial sampling occasions) on one large patch out of the 67 considered patches in which a larger sampling effort had been made. It appeared that the different levels of sampling effort did not change much the estimates obtained, and the estimates using lower sampling effort were not particularly smaller. This result may be explained by the fact that estimated detection probabilities using a lower sampling effort were not clearly lower than using a higher sampling effort.

Only 37 patches were used for most of the analyses presented here because we were constrained to estimate community dynamic parameters for local communities of sufficient sizes (Fig. 1). Indeed, as we estimated dynamic parameters for sedentary and migratory species independently, the number of species was sometimes very low for one of these groups, which makes it difficult to estimate extinction and turnover rates using a community level approach (Nichols et al. 1998, Doherty et al. 2003*a*). In order to ensure meaningful estimates of the rates of change in community composition, we kept only patches in which a minimum number of species ($n = 7$) was detected in 2001 and 2003. Model M(h) fit the data well for the 37 considered patches (76% of P values of the goodness-of-fit tests > 0.05 for the two groups of species). Detection probabilities were high and similar for the two groups in 2001 (sedentary species, $p_{2001} = 0.88 \pm 0.01$; migratory species, $p_{2001} = 0.87 \pm 0.02$; paired t test, $t = 0.38$, $P = 0.704$, $n = 37$), but significantly different in 2003 (sedentary species, $p_{2003} = 0.87 \pm 0.02$; migratory species, $p_{2003} = 0.81 \pm 0.02$; paired t test, $t = 2.19$, $P = 0.035$, $n = 37$). This underlined potential biases that could have been induced by using simple counts directly and the necessity to take into account detection probabilities when estimating species richness and community dynamic parameters. All parameter estimates were computed using freely available COMDYN software (Hines et al. 1999). Data are given as means ± SE.

Data analyses

Estimated species richness and the independent variables were log-transformed ($x + 0.5$) to ensure normality of residuals. Homoscedasticity of variances was also verified. To ensure that the distance to Paris was a reliable measure of the degree of urbanization, we calculated the correlation between the distance of each patch to Paris' center and the proportion of the "urban" cover type around it. These two variables were indeed

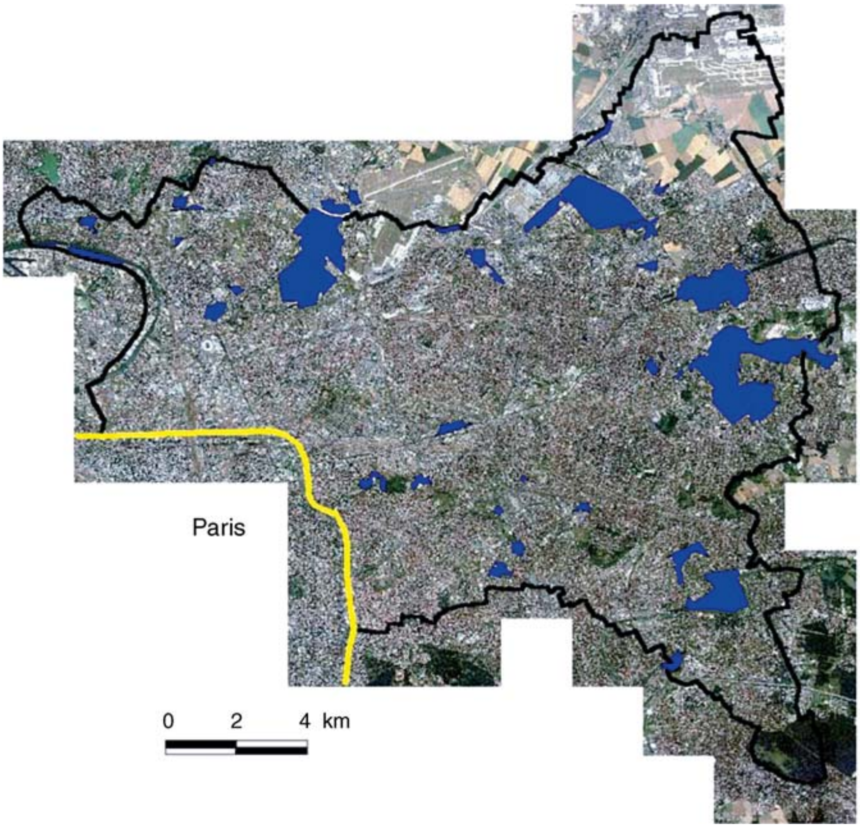

FIG. 1. The study area, located to the immediate northeast of Paris, France, and the location of the 37 sampled patches. The yellow enlarged line shows the border of the city of Paris. Copyright © Institut Géographique National–Paris; reproduced with permission.

negatively correlated (Pearson: $r = -0.70$, $P < 0.001$, $n = 37$), suggesting the presence of an urban gradient and confirming the fact that the distance to Paris was a reasonable measure of the degree of urbanization. A comparable relationship was found when including all the sampled patches (Pearson: $r = -0.76$, $P < 0.001$, $n = 67$). We used paired t tests to compare mean estimated species richness in 2001 vs. 2003, extinction rate vs. turnover rate, and parameters for sedentary species vs. migratory species. Statistical analyses were performed using the SAS statistical package (SAS Institute 1996).

For each bird group, multiple regression analyses were used to test whether bird species richness and parameters describing the rates of change in composition were related first to patch size, the degree of urbanization around patches, and their interaction and then to patch size, the distance to Paris center (as a measure of urbanization), and their interaction. When the interaction was not significant, we dropped it, and results showing the model with only patch size and the distance to Paris' center were reported. Patch size was correlated neither to the degree of urbanization around patches (Pearson: $r = -0.15$, $P = 0.365$, $n = 37$) nor to the distance to Paris' center (Pearson: $r = 0.15$, $P = 0.367$, $n = 37$). We first used a standard regression model assuming independence among model errors, but in order to account for a potential spatial dependence in the data points, we further used a model assuming that errors were correlated and that their covariance was a function of the distance separating patches (Littell et al. 1996; see Selmi and Boulinier [2001], Lichstein et al. [2002], Selmi et al. [2002], and Hawkins and Porter [2003] for examples of applications to ecological data). The regression analyses were performed using the MIXED procedure (Littell et al. 1996) of the SAS statistical package (SAS Institute 1996). Spatial covariance parameters (sill, range, and nuggets; Littell et al. 1996) were estimated using semivariograms plotted with the VARIOWIN program (Pannatier 1996). We used Akaike's Information Criterion (AIC) to compare the parsimony of the models and their fit to the data. For AIC differing by >2, the most parsimonious model was the model with the lowest AIC value (Burnham and Anderson 1998). Because in several instances the standard errors of estimates of community parameters were estimated to be 0 (instances in which the detection probability was estimated to be 1), we did not weight the regression by the inverse of the variance of sampling errors of these parameters in the analyses. We agree that taking into account the relative uncertainty in these

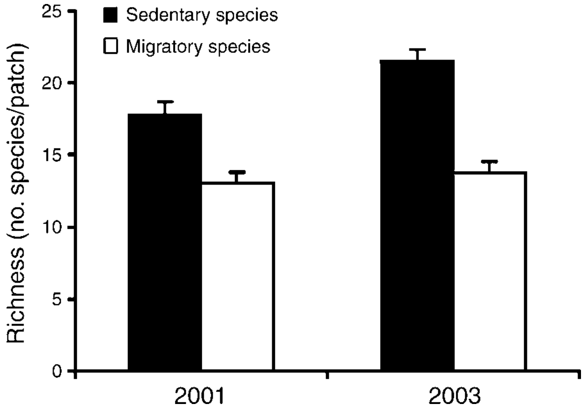

FIG. 2. Species richness (mean + SE) for sedentary and migratory bird species in 2001 and 2003.

estimates would have been useful but we did not find a simple way to do so. The use of a hierarchical modeling approach (Thogmartin et al. 2004, Royle and Dorazio 2006) could be a way to solve this issue but it would have needed specific developments beyond the scope of the current paper.

Finally, in order to test whether the difference between the community parameters of the two groups (species richness, local extinction, and turnover rates) varied with patch size and distance to Paris, we performed regression analyses with the differences between the two groups as dependent variables and patch size and distance to Paris as explanatory variables. This MANOVA framework provided a way to test for an expected difference in the slope of the relation between community parameters and patch characteristics (Boulinier et al. 1998*a*, 2001).

RESULTS

Thirty-three sedentary and 28 migratory species were detected on at least one of the 37 patches over the study period (2001–2003). In 2001, the estimated mean species richness per patch was significantly higher (17.82 ± 0.85 species/patch) for sedentary species than for migratory species (13.05 ± 0.77 species/patch; paired t test, $t = 7.36$, $P < 0.001$, $n = 37$; Fig. 2). This difference in species richness was also observed in 2003 (sedentary, 21.50 ± 0.80 species/patch; migratory, 13.75 ± 0.79 species/patch; paired t test, $t = 7.87$, $P < 0.001$, $n = 37$; Fig. 2). Mean species richness of sedentary species significantly increased by 21% during the study period (paired t test, $t = 3.97$, $P < 0.001$, $n = 37$), while it was stable ($P > 0.05$) for migratory species.

Species richness

All analyses showed that species richness and extinction and turnover rates were not related to the variable measuring the degree of urbanization around patches (all $P > 0.05$), thus only results involving patch size and distance to Paris' center are reported below.

The results of multiple regressions on species richness showed that spatial covariance models were not more parsimonious than standard regression models (ΔAIC > 2). In 2001, as predicted, species richness of migratory species was positively related to patch size (slope = 0.11 ± 0.03 [mean ± SE], $F_{1,34} = 13.34$, $P < 0.001$). It was not related to the distance to Paris (slope = 0.30 ± 0.17, $F_{1,34} = 3.13$, $P = 0.086$). These relationships were confirmed in 2003 (patch size, slope = 0.12 ± 0.03, $F_{1,34} = 12.61$, $P = 0.001$; distance to Paris, slope = 0.07 ± 0.17, $F_{1,34} = 0.19$, $P = 0.667$). As also predicted, species richness of sedentary species was positively related to patch size (slope = 0.09 ± 0.02, $F_{1,34} = 12.99$, $P = 0.001$) and tended to be positively related to the distance to Paris (slope = 0.28 ± 0.14, $F_{1,34} = 3.94$, $P = 0.055$) in 2001, i.e., species richness of sedentary species was higher on larger patches and on patches situated farther away from Paris. In 2003, species richness of sedentary species was positively related to both patch size (slope = 2.65 ± 1.00, $F_{1,33} = 6.99$, $P = 0.012$) and the distance to Paris (slope = 3.23 ± 1.23, $F_{1,33} = 6.85$, $P = 0.013$) and negatively related to the interaction between the two variables (coefficient = −0.27 ± 0.10, $F_{1,33} = 6.81$, $P = 0.013$). In 2003, species richness of sedentary species was indeed higher on large patches near Paris, but the relationship was much weaker on patches farther away from Paris.

Nevertheless, overall, the relationships between species richness and patch size and between species richness and the distance to Paris did not differ for sedentary and migratory species in 2001 (MANOVA framework, patch size, $F_{1,34} = 0.18$, $P = 0.667$; distance to Paris, $F_{1,34} = 0.00$, $P = 0.959$), as well as in 2003 (patch size, $F_{1,34} = 0.01$, $P = 0.935$; distance to Paris, $F_{1,34} = 2.20$, $P = 0.147$).

Extinction and turnover rates

Local extinction rates between 2001 and 2003 ranged from 0.00 ± 0.00 to 0.30 ± 0.15 and from 0.00 ± 0.00 to 0.49 ± 0.21 for sedentary and migratory species, respectively. As predicted, the mean extinction rate for sedentary species was small (0.03 ± 0.01) and significantly lower than for migratory species (0.20 ± 0.03; paired t test, $t = 6.62$, $P < 0.001$, $n = 37$; Fig. 3). The proportion of locally new species (turnover rate) ranged from 0.00 ± 0.03 to 0.51 ± 0.15 and from 0.00 ± 0.00 to 0.43 ± 0.16 for sedentary and migratory species, respectively. The mean turnover rates of sedentary species (0.14 ± 0.02) and migratory species (0.19 ± 0.02) were not significantly different (paired t test, $t = 1.81$, $P = 0.078$, $n = 37$; Fig. 3).

The results of multiple regressions of local rates of change in composition as a function of habitat variables showed that spatial covariance models were also not more parsimonious than standard regression models (ΔAIC > 2). As predicted, local extinction rate was negatively related to patch size for migratory species (slope = −0.04 ± 0.02, $F_{1,34} = 4.91$, $P = 0.033$): the

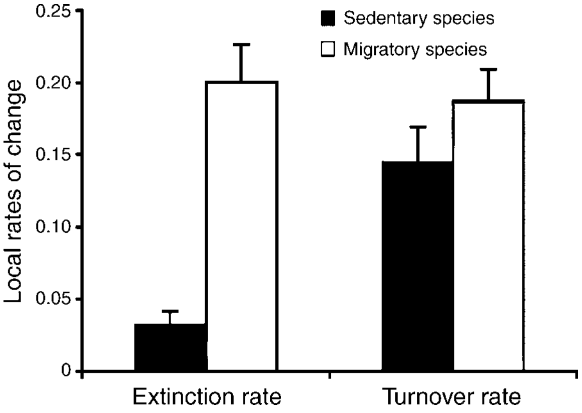

FIG. 3. Local rates of change (extinction and turnover rates; mean + SE) of sedentary and migratory bird species.

smaller the patch, the higher the local extinction rate (Fig. 4a). Conversely, local extinction rate was not related to the distance to Paris (slope = 0.10 ± 0.10, $F_{1,34}$ = 1.09, P = 0.305). Similarly, local turnover rate was higher on small patches than on large ones (slope = −0.04 ± 0.01, $F_{1,34}$ = 8.41, P = 0.006; Fig. 4b), and there was no relationship between the local turnover rate and the distance to Paris (slope = −0.00 ± 0.08, $F_{1,34}$ = 0.00, P = 0.965).

For sedentary species, the extinction rate was neither related to patch size (slope = 0.00 ± 0.01, $F_{1,34}$ = 0.34, P = 0.564) nor to the distance to Paris (slope = 0.00 ± 0.04, $F_{1,34}$ = 0.00, P = 0.962). The turnover rate for these species was not related to patch size (slope = −0.02 ± 0.02, $F_{1,34}$ = 1.56, P = 0.220), but was negatively related to the distance to Paris (slope = −0.19 ± 0.09, $F_{1,34}$ = 4.42, P = 0.043), showing that the proportion of locally new species between 2001 and 2003 was the highest on patches closer to Paris than on patches farther away. Some of the sedentary species thus colonized the most urban patches over the three-year study period.

The relationship between extinction rates and patch size differed between sedentary and migratory species (MANOVA framework, $F_{1,34}$ = 6.47, P = 0.016), while the one between the extinction rate and the distance to Paris did not differ between the two groups ($F_{1,34}$ = 1.14, P = 0.293). The difference of the local extinction rates between sedentary and migratory species was low on larger patches, but was high on smaller ones, where the local extinction rate of migratory species was higher. The relationships between the local turnover rate and patch size did not differ between sedentary and migratory species ($F_{1,34}$ = 2.01, P = 0.165), while the one between the turnover rate and distance to Paris differed between the two groups ($F_{1,34}$ = 4.52, P = 0.041). The difference of local turnover rates between the two

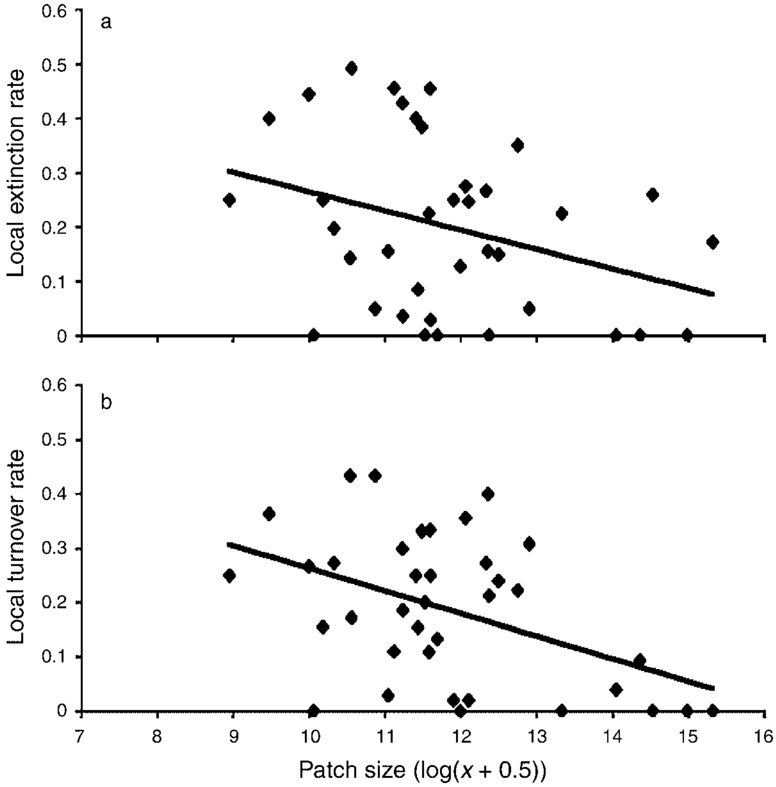

FIG. 4. Relationships between (a) local extinction rate and (b) local turnover rate and patch size for migratory bird species (n = 37 patches).

PLATE 1. The urban park of La Courneuve, France. Photo credit: A. Husté.

groups was low on patches located farther from Paris, but was high on patches located closer to Paris, where local turnover rate (proportion of new species) of sedentary species was higher.

DISCUSSION

As predicted, species richness of both migratory and sedentary birds was lower on smaller patches than larger patches. Rates of local extinction and turnover were higher for migratory species than sedentary species, and those rates were negatively related to patch size. Local extinction and turnover rates of migratory species nevertheless showed relatively similar values, leading to constant mean species richness between 2001 and 2003. Species richness and local turnover rates for sedentary species were related to both patch size and the distance to Paris, but local extinction rates were low on all patches for these species. Overall, the mean local turnover rate of sedentary species was high because relatively high values were recorded on the small patches closer to Paris, reflecting a local increase in sedentary species richness during the study period.

The results suggest a negative correlation between levels of urbanization and habitat suitability for migratory species. Different factors could explain the high temporal variability in the composition of migratory bird communities in urbanized landscapes. In the study area, the effects of patch size on the dynamics of the migratory species could be explained by the fact that the local abundance of these species may have been smaller than it was for sedentary ones. Extinction probability may indeed be related to population size (Bellamy et al. 1996), meaning that smaller populations located on smaller patches may be more vulnerable to extinction as a result of stochastic processes (MacArthur and Wilson 1963, 1967, Boyce 1992). Moreover, smaller patches may be associated with higher densities of urban nest predators (e.g., *Felix catus* and *Canis familiaris*) along habitat edges (Opdam 1991). Migratory species are indeed more sensitive to nesting habitat changes than sedentary species (Newton 2004). Finally, patch heterogeneity is well known to decrease with patch size (Freemark and Merriam 1986, Donnelly and Marzluff 2004), and in urban landscapes, smaller patches often lack specialized habitats that sensitive species require (Jokimäki and Suhonen 1998).

Studies in more natural landscapes have already reported differences in the relationships between community dynamic parameters and landscape structure for a priori sensitive species compared to nonsensitive ones (forest birds, Boulinier et al. 1998*a*, 2001; forest butterflies, Krauss et al. 2003; migratory birds, Bennett et al. 2004). Our results suggest that similar patterns may be observed in urban landscapes (Jokimäki and Suhonen 1998), as the dynamics of migratory species was related to patch size while it was not for sedentary ones.

High extinction and turnover rates can induce high temporal variability in species richness (Boulinier et al. 1998*a*, 2001). However local (re-)colonizations can balance extinctions leading to stable mean local richness, as we observed for migratory species. The occurrence of (re-)colonizations implies that dispersal of individuals, among patches within the study area or from outside the study area, plays an important role in maintaining local species richness. Dispersal of individuals is a key process in fragmented landscapes, and its effect depends notably on both the grain and extent of suitable habitat patches and the mean dispersal distance of individuals (Wiens 1994, Villard et al. 1995, Gilpin 1996). If at the scale considered, dispersal is affected by the distance between patches, we would expect higher extinction rates but lower turnover rates on smaller or more isolated patches. This was not the case in the current study, in which high estimated turnover rates indicated that local extinctions could be followed relatively rapidly by local (re-)colonizations. These findings illustrate how maintaining a sufficient density of suitable habitat patches in urban landscapes could enable individuals dispersing from surrounding landscapes to preserve local species richness.

Several sedentary species (e.g., *Pica pica*, *Turdus merula*, *Passer domesticus*) found in most European cities are known to be well adapted to human activities and to take advantage of urban landscapes (e.g., via access to food supply, nesting sites on buildings; Clergeau et al. 1998, Jokimäki and Suhonen 1998, Marzluff 2001, Fernández-Juricic et al. 2003). This may explain the high colonization rates of sedentary species on patches located close to Paris, irrespective of patch size. However, it also highlights that other sedentary species, even if less adapted to urban landscapes, are probably able to succeed in maintaining themselves in these disturbed environments. Among them, some forest species such as *Parus caeruleus*, *Parus major*, or *Parus palustris* are increasingly abundant in parks and gardens where they regularly use feeding dishes (Jokimäki et al. 1996, Virkkala 2004).

Urban gradients can have different structures (Alberti et al. 2001). The studied urban area presents a typical monocentric structure, with the degree of urbanization around each patch being negatively correlated to the distance to Paris' center. Interestingly, community parameters of sedentary species were found to be related to the distance to Paris' center, but not to the degree of urbanization around each patch, suggesting that the position of a patch in this gradient is more relevant for birds than the actual surrounding degree of human disturbance. Contrary to other measures of urbanization (e.g., proportion of buildings around patches, Rottenborn 1999, Lim and Sodhi 2004; density of human population, Jokimäki and Suhonen 1998, Lim and Sodhi 2004), the distance of each patch to Paris' center described the level of development in the surrounding landscape at a larger scale, which could explain some of the results. The fact that, contrary to previous studies (Friesen et al. 1995, Rottenborn 1999), species richness and changes in community composition of migratory species were related neither to the distance to Paris' center nor to the degree of urbanization around patches could be due to the high dispersal ability of these species relative to the size of the study area (236 km^2) and to the high overall level of urbanization in the study area (Fig. 1).

The issue of taking into account heterogeneity in detection probabilities among species, time, and locations is clearly critical in studies using monitoring data of biodiversity (birds, Selmi et al. 2002, Doherty et al. 2003*a*, *b*; amphibians, Bailey et al. 2004, Dodd and Dorazio 2004; plants, Kéry 2004). The fact that such approaches make various assumptions cannot be a reason for not using them altogether, as in most cases the estimates would be biased. The methodological approach we used enabled us to estimate the parameters of community change while accounting for heterogeneity in species detection probability. It relies on the assumption of closure of each community over a series of sampling occasions used as replicates to characterize each community at a given time (Nichols et al. 1998). With the design we followed, the assumption of the temporal closure of the community is reasonable, but the spatial closure may be discussed. In particular, a heterogeneity of habitats among spatial sampling occasions could lead to variability in occurrence and detection probabilities of species among occasions, at least at large scales (e.g., Dorazio and Royle 2005). Nevertheless, due to the relatively low spatial heterogeneity and the high openness of most of the habitats of the urban patches considered, we do not think that this was an issue in the current study. An empirical study by Jiguet et al. (2005) further showed in a comparable situation that such an approach was still reliable even when communities were sampled across heterogeneous habitats.

The conclusions we report cannot be extrapolated to patches where very small numbers of species had been detected (i.e., less than seven). Nevertheless, the extinction–colonization processes studied are likely to be comparable, or even more dramatic, in the more extreme cases involving communities with very low numbers of species detected. In particular, the effect of patch size on the probability of local extinction of migratory species is likely to hold for the situations that we did not consider in the analyses. Analyses of the proportion of occupied patches could be conducted on a species-by-species basis using recently available methods (MacKenzie et al. 2002, 2003) as this could complement our perception of the dynamics of patch occupancy in urbanized landscapes (Donnelly and Marzluff 2004). It would nevertheless imply making different assumptions, notably in terms of specifying potential variables affecting detection probability and dynamics of occupancy. Our results highlight that patch size would be a covariate of prime importance to be considered in such analyses.

Only few studies on the local change in the composition of animal communities in urban landscapes have been conducted thus far. Yet, in these dynamically changing landscapes, such studies have a great value in terms of conservation, as they should further our understanding of the manner in which communities are likely to respond to environmental changes. In particular, our results stress the very dynamic nature of the migratory bird communities and the importance of dispersal to explain how local turnover rates on small patches can compensate for local extinction rates. In this study, the approaches used allowed us to account for a heterogeneity in the probability of detecting species and for potential spatial covariance effects that could be prevalent in heterogeneous landscapes affected by human activities. The use of such approaches on landscapes subjected to various levels of fragmentation and human disturbance is necessary to complement our understanding of the response of animal communities to alteration of the environment. In particular, our study points out the need for better understanding of factors affecting dispersal processes in this context.

ACKNOWLEDGMENTS

We thank J. M. Marzluff, J. A. Royle, M. Kéry, C. Jimenez, L. Riffaut, C. Biard, and anonymous reviewers for useful comments on earlier versions of the manuscript and the observers of the LPO (Ligue pour la Protection des Oiseaux) for their assistance in the collection of the data. This work was supported by the Conseil Général de la Seine-Saint-Denis, the CNRS, and the French Biodiversity Institute (IFB).

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