Functional Homogenization Effect of Urbanization on Bird Communities

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Abstract: *We studied the community richness and dynamics of birds in landscapes recently affected by urbanization to test the prediction that biotic communities living in degraded landscapes are increasingly composed of generalist species. We analyzed bird communities in 657 plots monitored by the French Breeding Bird Survey from 2001 to 2005, accounting for the probability of species detection and spatial autocorrelation. We used an independent land-cover program to assess urbanization intensity in each FBBS plot, from 1992 to 2002. We found that urbanization induced community homogenization and that populations of specialist species became increasingly unstable with increasing urbanization of the landscape. Our results emphasize that urbanization has a substantial impact on the spatial component of communities and highlight the destabilizing effect of urbanization on communities over time. These results illustrate that urbanization may be a strong driving force in functional community composition and that measuring community homogenization is a powerful tool in the assessment of the effects of landscape changes and thus aides sustainable urban planning.*

Keywords: breeding bird survey, community dynamics, community homogenization, habitat disturbance, probability of detection, species specialization, urbanization

Efecto de la Homogeneización Funcional de la Urbanización sobre Comunidades de Aves

Resumen: *Estudiamos la riqueza y dinámica de la comunidad de aves en paisajes afectados recientemente por la urbanización para probar la predicción de que las comunidades bióticas que viven en paisajes degradados están compuestas cada vez más por especies generalistas. Analizamos las comunidades de aves en 657 cuadrantes monitoreados por el Monitoreo de Aves Residentes de Francia (MARF) de 2001 a 2005, considerando la probabilidad de detección de las especies y la autocorrelación espacial. Utilizamos un programa independiente de cobertura de suelo para evaluar la intensidad de la urbanización en cada cuadrante MARF, de 1992 a 2005. Encontramos que la urbanización indujo la homogenización de la comunidad y que las poblaciones de especies especialistas fueron más inestables a medida que incrementó la urbanización del paisaje. Nuestros resultados enfatizan que la urbanización tiene un impacto sustancial sobre los componentes espaciales de las comunidades y resaltan el efecto desestabilizador de la urbanización sobre las comunidades a largo plazo. Estos resultados ilustran que la urbanización puede ser una importante fuerza en la determinación de la composición de la comunidad funcional y que la medición de la homogeneización de la comunidad es una herramienta poderosa para la evaluación de los efectos de los cambios en el paisaje y, por lo tanto, ayuda a la planificación urbana sustentable.*

Palabras Clave: dinámica de la comunidad, especialización de especies, homogeneización de la comunidad, monitoreo de aves residentes, perturbación del hábitat, urbanización

Introduction

Measuring whether and how communities differ in or shift among species composition and diversity is crucial for predicting the consequences of habitat loss and environmental degradation. Nevertheless, the effects of disturbance on species may differ strongly according to the particular disturbance measured, its intensity in space and time, as well as the species considered (Newmark 2006). Human-generated environmental disturbances are often considered only in terms of the species that are affected negatively, yet any given perturbation will likely benefit at least some species (McKinney & Lockwood 1999). In this respect the specialist–generalist concept is relevant in assessing how and which species are affected in communities subjected to human disturbance (Kithahara et al. 2000). Indeed, habitat specialist species are theoretically expected to be highly sensitive to habitat loss or perturbation, whereas generalist species should be less affected or could even benefit from the local disappearance of specialists (Owens & Bennett 2000; Marvier et al. 2004; Julliard et al. 2006). Therefore, in considering the comprehensive ensemble of species, several authors have recently focused on the process leading to the replacement of many specialist species by a few generalist species. This phenomenon, so-called functional homogenization, is generally quantified as a spatial increase in community similarity over time (Olden & Poff 2004; Olden 2006).

Among the large-scale perturbations that may profoundly influence communities' fates, urbanization is considered the most severe and is occurring unchecked worldwide (Vitousek et al. 1997; Pauchard et al. 2006). Urbanization is generally accompanied by many activities and settlements that dramatically affect the abundance and diversity of species (Chace & Walsh 2006). Urbanization includes the replacement of any habitat with built-up features and the development of human-related infrastructures (e.g., roads, railways, gardens). This process is complex and scale-dependent (Blair 2004), rendering the generalization of particular findings difficult (Clergeau et al. 2006). That urbanization is a major cause of biotic homogenization has been highlighted recently (McKinney 2006; Smart et al. 2006). Nevertheless, most of the ecological mechanisms involved in natural communities facing such large-scale perturbations remain unclear.

In particular, communities' fates in human-degraded environments have generally been investigated using static variables, such as the size of residual fragments after habitat destruction and fragmentation (Crooks et al. 2004), whereas explicit consideration of the dynamic processes associated with large-scale perturbations has been rare. Yet local landscape change can only be comprehended when it is considered in its general geographical context and with all its related dynamics. Patterns of change are different for the countryside near major

cities, metropolitan villages, and remote rural villages; thus, communities are not affected with the same rapidity (Antrop 2004).

Similarly, as habitats undergo human-induced fragmentation, it is important to investigate associated changes in species diversity and community similarity, not only in space, but also over time (Boulinier et al. 1998a; Tworek 2003; Marzluff 2005; Newmark 2006). For instance, changes in landscape structure, such as an increase in urban patches, alter the ability of some organisms to disperse. This leads to the prediction that communities composed of species with specific habitat requirements should have higher local extinction and turnover rates, whereas widespread and broadly tolerant species should, on the contrary, benefit from landscape disturbance and demonstrate higher stability (Dall & Cuthill 1997; Krauss et al. 2003). To our knowledge, these predictions have not been supported empirically in communities facing urbanization.

To examine these predictions, data from large-scale monitoring programs may be useful as long as the sampling process allows one to account for potential biases. In particular, two shortcomings of monitoring design have been discussed (Yoccoz et al. 2001; Newmark 2006), but are often ignored. First, comparisons across species are often invalid because different species have different detection probabilities (Thompson 2002; Buckland et al. 2005). This bias is well addressed by the capture–recapture framework through the use of appropriate estimators that account for heterogeneity in species detectability for both animal (Boulinier et al. 1998b; Nichols et al. 1998a, b; Hines et al. 1999) and plant surveys (Kéry 2004). Second, large-scale data sets generally have a clear spatial structure that induces spatial autocorrelation in ecological variables (Carroll & Pearson 2000; Selmi & Boulinier 2001). In these cases species richness and composition measured in each community may be influenced by distance between samples so that the monitored plots are not independent replicates (Selmi et al. 2002). This spatial structure can mask or enhance relationships among biological responses and explanatory variables and may, as a result, lead to identification of false relationships (Liebhold & Gurevitch 2002). In disturbed or built-up landscapes, spatial structure may be particularly important because the composition and richness of a given community are often related to its distance from human infrastructure and the fact that urbanization is generally not randomly distributed.

We tested the hypothesis that strong habitat perturbation induced by urbanization increases homogenization of communities and temporal instability of specialist species. We tested these two predictions on data from the French Breeding Bird Survey (FBBS), which accounts for detection probability and spatial dependence among the plots. The use of bird data is particularly useful because

birds are one of the best-studied classes of organisms and exhibit a diverse range of ecological functions (Sekercioglu 2006).

Methods

Data Collection

The FBBS, initiated in France in 2001, is conducted by skilled volunteer ornithologists who count birds under the same protocol. The survey consists of a standardized survey of more than 1000 2×2 km plots selected from a national grid of 136,501 possible plots. A given plot is randomly selected within a fixed 10-km-radius circle of a locality proposed by the observer (i.e., 1 plot is randomly selected among 80 possible plots). Such random selection ensures that varied habitats are surveyed (including farmland, forest, suburbs, and cities).

The data for a given point count are validated if the plot is monitored by the same observer twice in the spring, once before and once after 8 May, with 4–6 weeks between sampling events. These counts are repeated on approximately the same date (± 7 days) each year. This double sampling is carried out to detect both early and late-breeding species. Each observer conducts 10-point counts within the 2×2 km plot and records every individual seen or heard within 5 minutes exactly. The survey must start at the same time of the day (± 15 minutes within 1–4 hours after sunrise). In addition, the 10-point counts must be fixed, monitored in the same order, be at least 300 m apart, and be distributed evenly across habitats by the observer.

Each plot is therefore randomly selected, but the 10-point counts are chosen by the observer according to the relative landscape composition within the 2×2 km plot and to each plot's accessibility. The same observer monitors the same points following this protocol each year.

Species Selection

Each of the species detected in the FBBS was classified as either a specialist or nonspecialist (Table 1). We based this classification on the species classification by Gregory et al. (2005), which was built to calculate Pan-European common bird indicators. This European classification categorizes 48 species as specialists or nonspecialists and was based on the *European Breeding Bird Atlas* (Hagemeijer & Blair 1997), *Birds in Europe* (Tucker & Heath 1994), and national BBS coordinators' assessments of the proportion of each species' national population breeding in a given habitat type (farmland, woodland, park and garden). Among the 48 species, 22 and 28 species were, respectively, classified as nonspecialist and specialist species at the European level.

To establish a similar list in France, we excluded 2 species among the 22 classified as nonspecialist at the European level because they were too rare to be reliably monitored by the FBBS (*Anthene noctua, Emberiza schoeniclus*). We then selected 20 specialist species to ensure that the specialist and nonspecialist species group included the same number of species. We determined the proportion of each specialist species' population that occurs in farmland, woodland, or park and garden in France.

A species was considered a specialist for a given habitat type if its relative density was higher in this habitat than in others. We ranked species according to the difference in their relative density for a given habitat and other habitats and excluded the six species for which this difference was the lowest. In doing so, we excluded, among the 26 species classified as specialist at the European level, the 6 species that had the lowest preference for a given habitat type (*Muscicapa striata, Streptopelia turtur, Sturnus vulgaris, Sylvia atricapilla, Sylvia communis, Troglodytes troglodytes*).

Community Richness and Dynamic Estimates

To estimate species richness and community dynamic parameters while taking species-detection probability into account, we considered the 10 FBBS point counts within each plot as local sampling replicates of the community within the geographical unit (i.e., the 4 km^2 FBBS plot). The matrix of presence and absence of detected species over the 10 sampling units was processed from the combination of the two sampling events (a species was considered present if detected on at least one sampling event) for each of the 20 specialist species and 20 nonspecialist species. Estimation of community-dynamic parameters followed the methods for estimation of temporal variation in species richness, local turnover, and extinction rates when not all species are detected (Nichols et al. 1998a). These estimations, based on capture–recapture models, were made in the program COMDYN (Hines et al. 1999). This program was specifically built to compute species richness and parameters of community dynamics and thus to account for heterogeneity in species' detectability (model Mh and the associated jackknife estimator). This model was the most frequently selected for estimation of bird-community species' richness (Boulinier et al. 1998b) and the most relevant for use with the FBBS under heterogeneous sampling conditions (Jiguet et al. 2005). In FBBS plots where few species were recorded, probability of detection was poorly estimated and lead to unreliable estimates of richness and dynamic parameters. Thus, to make the capture–recapture model perform adequately, we retained FBBS plots monitored for at least 2 years during 2001–2005 and in which at least six species of each community were detected each year. We analyzed the 657 BBS plots that fulfilled these conditions (Fig. 1).

Table 1. Specialization and major natural-history traits for the 40 bird species examined in this study of the homogenization effects of urbanization.*

Common name	Scientific name	Specialization category	Diet	Nesting place	Migration status	Breeding habitat
Long-tailed Tit	*Aegithalos caudatus*	S	I	C	1	W
Skylark	*Alauda arvensis*	S	O	G	1	F
Tree Pipit	*Anthus trivialis*	S	I	G	2	W
Linnet	*Carduelis cannabina*	S	G	G	1	F
Goldfinch	*Carduelis carduelis*	S	G	C	1	F
Quail	*Coturnix coturnix*	S	O	G	2	F
Yellowhammer	*Emberiza citrinella*	S	O	G	1	F
Jay	*Garrulus glandarius*	S	O	C	1	W
Red-backed Shrike	*Lanius collurio*	S	I	C	2	F
Corn Bunting	*Emberiza calandra*	S	O	G	1	F
Coal Tit	*Parus ater*	S	O	C	1	W
Tree Sparrow	*Passer montanus*	S	O	C	1	F
Common Redstart	*Phoenicurus phoenicurus*	S	I	C	2	W
Chiffchaff	*Phylloscopus collybita*	S	I	G	2	W
Dunnock	*Prunella modularis*	S	I	G	1	W
Goldcrest	*Regulus regulus*	S	I	C	1	W
Whinchat	*Saxicola rubetra*	S	I	G	2	F
Song Thrush	*Turdus philomelos*	S	O	C	1	W
Mistle Thrush	*Turdus viscivorus*	S	O	C	1	W
Lapwing	*Vanellus vanellus*	S	I	C	1	F
Sparrowhawk	*Accipiter nisus*	NS	R	C	1	W
Buzzard	*Buteo buteo*	NS	R	C	1	W
Greenfinch	*Carduelis chloris*	NS	G	C	1	W
Woodpigeon	*Columba palumbus*	NS	G	C	1	F
Carrion Crow	*Corvus corone*	NS	O	C	1	F
Jackdaw	*Corvus monedula*	NS	O	C	1	F
Great-spotted Woodpecker	*Dendrocopos major*	NS	O	C	1	W
Robin	*Erithacus rubecula*	NS	I	G	1	W
Hobby	*Falco subbuteo*	NS	R	C	2	F
Kestrel	*Falco tinnunculus*	NS	R	C	1	F
Chaffinch	*Fringilla coelebs*	NS	O	C	1	W
Swallow	*Hirundo rustica*	NS	I	C	2	F
Wryneck	*Jynx torquilla*	NS	I	C	2	W
Yellow Wagtail	*Motacilla flava*	NS	I	G	1	F
Blue Tit	*Parus caeruleus*	NS	O	C	1	W
Great Tit	*Parus major*	NS	O	C	1	W
Willow Warbler	*Phylloscopus trochilus*	NS	I	G	2	W
Magpie	*Pica pica*	NS	O	C	1	F
Garden Warbler	*Sylvia borin*	NS	O	C	2	W
Blackbird	*Turdus merula*	NS	O	C	1	W

*Key: S, specialist species; NS, nonspecialist species; I, insectivore; G, granivore; O, omnivore; R, raptor; C, canopy nester; G, ground nester; 1, short-distance migrant or resident; 2, long-distance migrant; W, woodland, park, or garden breeder; F, farmland breeder.

Community dynamics were characterized by two estimators that addressed changes in year-to-year community composition: the rate of local extinction and the rate of local turnover. The rate of local extinction between time t and $t+1$ was computed as one minus the survival rate of local species, which was the proportion of species, among those detected at time t, that were estimated to still be present at time $t+1$ (Nichols et al. 1998a; Boulinier et al. 2001). Similarly, the rate of local turnover was computed as the proportion of species at $t+1$ estimated to be locally new since time t (Nichols et al. 1998a; Boulinier et al. 2001). Because this turnover rate was conditioned on the species still present at time $t+1$, it was a function of both local extinction and colonization and reflected dis-

similarity between communities at t and $t+1$. The measures used to describe community dynamics and richness were not independent; rather, they each focused on different but complementary aspects of the community.

Measuring Local Homogenization and Relative Community Stability

Biotic homogenization is multifaceted and can cause misleading interpretation if not clearly defined (Olden 2006). For instance, one widely used method of quantifying homogenization between communities is to calculate similarity indices (e.g., Jacard index) between communities (Kühn & Klotz 2006). Nevertheless, such indices have
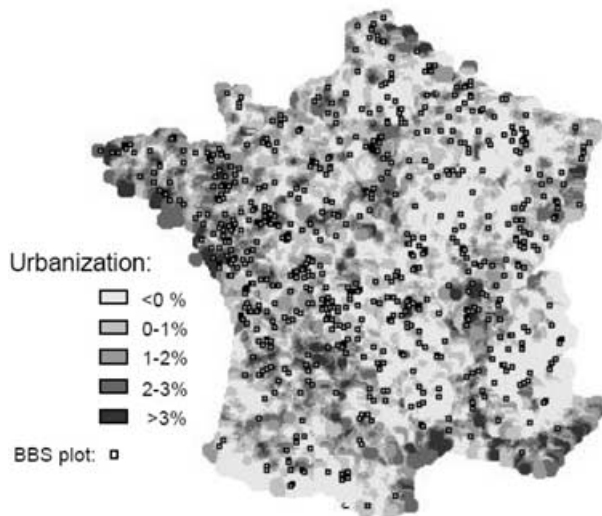
*Figure 1. Spatial distribution of urbanization from 1992 to 2002 across France. Each dot represents a plot monitored at least 2 years between 2001 and 2005 by participants in the French Breeding Bird Survey (*n = 657*).*

no explicit link with the identity or the ecological traits of species. We built a measure of the homogenization process with two explicit constraints. First, we sought an index of community homogenization that would measure the replacement of specialist species by generalist species. This homogenization index is a special case of functional homogenization (Olden 2006) and is expected to increase when urban-sensitive species are replaced by species better adapted to human environments. Second, we wanted a measure that would be easy to employ in monitoring programs. Estimates of richness obtained for generalist and specialist communities for a given year in a given FBBS plot were considered as paired observations (Doherty et al. 2003). Thus, we computed the homogenization index ($\hat{H}$) in each FBBS plot each year as the proportion of generalist species (*g*):

$$\hat{H} = \frac{\hat{S}g}{\hat{S}g + \hat{S}s},\qquad (1)$$

where $\hat{S}g$ and $\hat{S}s$ were respectively estimates of specialists and generalists species richness (provided by COM-DYN). This calculation accounted for variation in species detectability.

The relative stability ($\hat{E}$) of specialist species within each community was computed each year as the difference in local extinction rates between specialist and generalist communities for each FBBS plot:

$$\hat{E} = \hat{E}s - \hat{E}g,\qquad (2)$$

where $\hat{E}s$ and $\hat{E}g$ were respectively estimates of local extinction rates of specialist and generalist species. Finally,

we computed the difference in local turnover rate estimates, $\hat{T}$ between specialists and generalists. We then averaged each parameter ($\hat{H}$, $\hat{E}$, and $\hat{T}$) for each plot over the study period.

Indicators of Landscape Dynamics

France has developed TERUTI, a program specifically designed to estimate the change in land-use through space and time. TERUTI is a systematic survey of the entire country (including Corsica) that has 15,500 cells of 2 × 2 km squares. In each cell 36 sample points are regularly distributed 300 m from each other. Each point has been surveyed and characterized according to its physical characteristics among a standardized list. All urban features (e.g., parking area, cemetery, railway, highway) are grouped in one urban category. All other categories that contain all nonurban features are grouped in one nonurban category (Agreste 2003). Using this binary classification (urban and nonurban), we calculated the proportion of urban points in each TERUTI cell, both in 1992 and 2002 (in the 14,892 cells monitored in metropolitan France, i.e., excluding Corsica). We then calculated an urbanization index for each cell as the difference in the proportion of points classified as urban between 1992 and 2002. Negative urbanization could occur in a given cell if human settlements were removed between 1992 and 2002. This land-cover survey offered an excellent opportunity to examine variation in the fate of biodiversity because it incorporated quantitative estimates of large-scale landscape dynamics, rather than limiting analyses to a static gradient of urban density.

To assign an urbanization index to each FBBS plot, we used a kriging spatial interpolation model. Kriging modeled the spatial autocorrelation, which was then used to obtain unbiased predictions, thus providing the optimal variable interpolation at unsampled sites (Cressie 1993; Ashraf et al. 1997).

Farmland, forest, and urban settlements were likely to be affected by urbanization in different ways. For instance, we expected that urbanized habitats would contain more generalist species (McKinney 2006). Therefore, to control statistical analysis of the principal habitat type in each FBBS plot in 1992, we used CORINE land cover, which is a national georeferenced database that represents the entire country by means of contiguous polygons classified into four different land-cover categories (urban, farmland, forest, and wetland). We overlaid each FBBS square on this land-cover database and computed the sum of CORINE polygon areas. For each plot we considered the habitat category with the highest area score the principal habitat type for the plot. Each FBBS plot was thus classified as urban, farmland, forest, or wetland. The FBBS, CORINE, and TERUTI surveys were independent but had the same spatial resolution.

Data Analysis

We searched for potential relatedness among species induced by our species selection. This analysis was conducted to establish whether our homogenization measure was driven by particular traits shared by specific species. We used Moran's I statistic for each taxonomic level (genus, family, order) to test whether closely related taxa were more likely to be similarly classified as specialists (Lockwood et al. 2002). Then we compared the proportion of birds belonging to the specialist and nonspecialist groups sharing the same nesting preference (ground or canopy nesters), diet (predator, insectivorous, granivorous, and omnivorous), migration strategy (resident or short- or long-distance migrants), or the most-usual breeding area (woodland, park and garden, or farmland area). We used a chi-square test and correction for continuity to make the latter comparisons.

We sought to determine whether community parameters (i.e., homogenization, difference in bird species turnover, and difference in extinction rate) were related to urbanization, controlling for habitat type (i.e., urbanization effect was tested but was adjusted for habitat as a factor), and accounting for spatial autocorrelation. We used generalized least-square (GLS) models that accommodated spatial dependence between FBBS plots. A GLS model is a linear-mixed model that allows specification of spatial dependence in the error associated with each sample estimate as a random effect and thus computation of appropriate least-square regression coefficients (Pinhero & Douglas 2000). We conducted these GLS analyses in three steps. First, we used linear models that assumed no spatial structure between errors (we transformed homogenization to arc-sine square root so that homogenization in all analyses would meet assumptions of the parametric tests).

We used semivariograms of the standardized residuals of this previous analysis to investigate spatial autocorrelation structure. The semivariogram is a plot of the semivariance between residuals according to the distance between samples (Fortin et al. 2002). We selected the best-fitting semivariogram and the corresponding parameters (range and nugget) to model the spatial structure in a complete GLS model, with spatial structure as a random effect, habitat as a factor, and community parameter as a dependant variable.

To detect potential nonlinear relationships, we plotted previous regression models with global additive mixed model (GAMM), which is analogous to the GLMM, but can handle nonlinear data structures and nonmonotonic relationships between the response and explanatory variables (Guisan et al. 2002). In these plots urbanization was considered a smoothed term. Taxonomic autocorrelation, GLS and GAMM were completed respectively in the ape, nlme, and mgcv package of R statistical software (version 1.9.1., R Developpement Core Team 2004).

Results

Specialization was not autocorrelated at the family (Moran's $I = 0.06$, $p = 0.63$) or genus level ($I = -0.04$, $p = 0.95$). In other words, our specialization classification was not clustered according to these taxonomic levels. Taxonomic autocorrelation was positive at the order level ($I = 0.15$, $p = 0.01$), but this pattern was weakened by the highly skewed proportion of species belonging to the Passeriform order (31 species among 40). The proportion of raptors, insectivores, graminovores, and omnivores did not differ between specialist and nonspecialist species ($\chi^2 = 5.14$, 3 df, $p = 0.16$). The proportion of resident and long-distance migrant species did not differ among the two groups of species ($\chi^2 = 0$, 1 df, $p = 1$). Similarly, no strong difference occurred between the proportion of specialist and nonspecialist species that were ground or canopy nesters ($\chi^2 = 2.97$, 1 df, $p = 0.08$) or among species mostly breeding in farmland (or in nearby farm structures), woodland, or park and gardens ($\chi^2 = 0$, 1 df, $p = 1$). Thus, the generalist and specialist communities were similar with respect to a number of natural-history traits.

Urbanization throughout the country increased significantly between 1992 and 2002, with a mean difference of 0.0176 in the number of TERUTI sample points per cell that were classified as urban (95% CI 0.016–0.018). This difference represented a 25% increase in the surface of urban CORINE polygons across the entire country.

This increase in urbanization was not randomly distributed over a large spatial scale. A coarse gradient of positive urbanization from east to west was detected (Fig. 1). At a regional scale, urbanization mostly affected the areas around major cities and the Mediterranean coast.

As predicted, the habitat-controlled model that tested the relationship between homogenization and urbanization showed that more-homogenized communities were associated with more-urbanized landscapes (spatial model: $t_{653} = 3.74$, $p < 0.001$; Fig. 2a). The smoothed plot of this relationship was bounded: the proportion of generalist species increased with the intensity of urbanization but remained constant at the highest disturbance level.

The estimated richness of generalist species was on average 14.6 (0.35 SE) for a survey plot, whereas the estimated richness of specialist species was on average 12.5 (0.75 SE). On average, specialist species had a 54% higher annual extinction rate per survey plot (0.090, 0.003 SE) than generalist species (0.058, 0.002 SE), with a mean difference, specialist minus generalist, of 0.031. As predicted this difference increased with the intensity of urbanization ($t_{653} = 8.91$; $p < 0.0001$; Fig. 2b). Similarly, specialist species had on average a 63% higher local turnover rate per survey plot (0.085, 0.003 SE) than generalist species (0.052, 0.002 SE), with a mean difference, specialist minus generalist, of 0.033, and this difference also increased
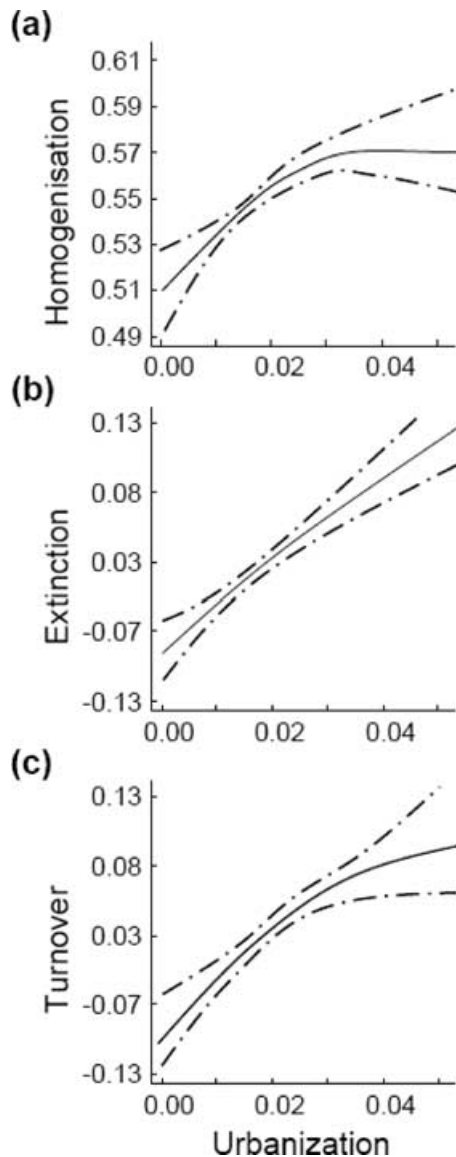
Figure 2. Smoothed relationships between bird community parameters and urbanization. (a) Relationship between homogenization (proportion of generalist species) computed on each FBBS plot from 2001 to 2005 and recent disturbance induced by urbanization, measured between 1992 and 2002 (with standard error limits in dashed lines). The same relationship is plotted for (b) mean local extinction rate difference (specialist minus generalist) and (c) mean local turnover rate difference (specialist minus generalist). All plots were drawn with global additive mixed models.

with the intensity of urbanization ($t_{653} = 8.14$; $p < 0.001$; Fig. 2c).

The estimated probability of detecting species (detectability) was higher for generalist species than for specialist species (respectively 0.85 ± 0.004 SE and $0.80 \pm$ 0.005 SE; paired *t* test: $t_{656} = 7.88$; $p < 0.0001$). Generalist species occurred in higher proportions than specialists. On average, bird communities were comprised of 56% generalist and 44% specialist species ($t_{657} = 147.3$ $p < 0.0001$).

Discussion

Urbanization significantly increased (+1.7%) in France between 1992 and 2002. If this increase seems relatively small in terms of metropolitan France's total land surface, because about 7% of the area of France (38,014 km² out of 549 192 km²) was composed of urban settlements in 1992, it represents in fact a 28% increase in terms of urbanized habitats. Moreover, our results showed that urbanization was widespread throughout the country. In fact, even if urbanization used to be typically restricted to the surroundings of cities, it now also affects rural settings (Antrop 2004).

Such perturbation was expected to affect communities differently according to the species considered because environments with higher variability are expected to favor generalist species, whereas specialist species should be favored in relatively constant environments (Futuyma & Moreno 1988; Jonsen & Fahrig 1997; Marvier et al. 2004). Accordingly, we found that functional homogenization was positively linked with community urbanization. This relationship was bounded, suggesting that the highest urbanization level communities were mainly composed of ubiquitous generalist species and that, at this stage, the relative specialist–generalist composition remained constant. Furthermore, specialist species had lower detection probability than generalist species. This result underlines the need to account for the fact that probability of detection could vary among species when examining the impact of landscape disturbance on communities (Newmark 2006). If our species classification had resulted in the grouping of species sharing the same specific trait, other confounding factors could have led to such patterns. Nevertheless, we found no evidence of a strong relatedness among species either induced by taxonomic autocorrelation or by major natural-history traits. We are confident therefore that our homogenization measure reflected species sensitivity to urbanization based on their ability or inability to thrive in degraded landscapes.

Specialist species had significantly higher local extinction and turnover rates than generalist species, suggesting that specialist species were more inclined to local extinction followed by recolonization. This pattern could be expected if, for example, the designation of specialist and nonspecialist species were only a function of apparent general abundance patterns and no further consideration had been paid to detectability issues. Indeed, species with lower densities are expected to experience higher levels of local extinction (Hanski, 1999). Thus, we stress that the

dynamic estimates accounted for variation in detectability among species and thus accounted for such difference among communities.

Yet, the extinction-rate estimator was based on the number of species detected at time t +1 that were already detected previously. If these species were more detectable at time t (e.g., because individuals within those species were more abundant), these species are likely to be more detectable the following year (Nichols et al. 1998a). This could induce an additional hidden bias in extinction rates, leading toward lower values, despite the use of the capture–recapture model. In our particular case this bias could be a problem if, for instance, generalist species were systematically more abundant than specialist species, which could induce a systematic underestimation of extinction rates for generalist species. This bias was recently studied empirically (Alpizar-Jara et al. 2004) and with simulation models (Jenouvrier & Boulinier 2006). Results from these studies showed that this bias was very weak and that the capture–recapture methodology designed to account for heterogeneity in species-detection probability was performing well, even in cases of covariance between species detectability and probability of local extinction.

Contrasts in dynamic parameters between specialist and nonspecialist species are thus likely to be based on ecological response of communities to environmental disturbance. In a constant environment one may expect that specialist species will have higher fitness in their specific habitats. Therefore, a specialist species present in a habitat a given year, on average, should have a higher probability of being detected in the same habitat the following year. This high probability of detection means that change in dynamic parameters should be low for specialist species at the community level. Nevertheless, our results showed that the environment was not constant and was strongly affected by urbanization. Therefore, we believe our results regarding changing environmental parameters support the hypothesis that, in the context of current global changes, specialist species are more at risk than generalist species (Julliard et al. 2004). The positive relationship we found between local extinction and turnover rates of specialist species and increasing urbanization supports this conclusion. These results also support the idea that because generalist species use various habitat types in the landscape matrix, they are less at risk than species that are more dependent on one or a few habitat types (Brouat et al. 2004).

We assessed community homogenization and the relative temporal stability of specialist versus nonspecialist species over a short time span (2001–2005). This time span did not match our measure of landscape urbanization (1992–2002). Although the impact of ecological perturbations is usually detectable over longer time periods (Newmark 2006), urbanization dramatically modifies

landscapes in ways that often greatly exceed forest disturbance or changes in farmland practices. Land modifications induced by urbanization are long term and intensify with time so that there is generally no opportunity for successional recovery (McKinney 2006; Marzluff & Ewing 2001). Therefore, it is likely that the immediate effect of urbanization on communities is strong but that the full effects of this disturbance can be subjected to time lags of several years. Our classification of species as specialist or nonspecialist illustrated the effects of urbanization, even in short time lags.

Variables other than specialization, such as body mass, are good predictors of potential responses to human disturbance across species (Blumstein et al. 2005), and different species are vulnerable to different risks (Owens & Bennett 2000). For instance, predators are generally more vulnerable to perturbation than herbivores. McGill et al. (2006) emphasize the relevance of using functional trait measures in community ecology. We suggest that grouping species a priori according to a specific trait that is expected to be sensitive to environmental disturbance could provide valuable community metrics to test scientific predictions.

Our results showed that dynamic parameters reflecting community stability are worth considering and that urbanization likely leads to both a larger spatial distribution of generalist communities and an increase in specialist instability over time. The homogenization measure we used has the great advantage of being calculable with presence–absence data and therefore being available for existing monitoring programs. A more quantitative measure of species' specialization, based on species density across habitats, was recently proposed (Julliard et al. 2006). Such a quantitative measure was shown to be highly valuable in quantifying the spatial segregation of bird species and could enable refinement of the quantitative link between homogenization and urbanization.

Finally, because urbanization was not randomly distributed in space, we suggest that the use of spatial models may be crucial in community-pattern investigations (Legendre 1993; Selmi et al. 2002; Heikkinen et al. 2004). Indeed, when considering ecological processes in which landscape disturbance is likely to be correlated spatially and where dispersal processes are expected to explain some of the observed pattern, accounting for spatial autocorrelation may be more statistically appropriate and ecologically meaningful (Selmi & Boulinier 2001).

Management Implications

Decision makers need clear information about the driving forces shaping community composition in space and time (Balmford et al. 2005). Our results support the hypothesis that urbanization leads to the replacement of specialist species by more generalist species within communities

(McKinney 2006) and a relative decrease in specialists' temporal stability. McKinney and Lockwood (1999) stress the importance of identifying present-day patterns of biotic homogenization for establishing proactive conservation planning. Our results suggest that using presence–absence data from large-scale monitoring programs could be a useful tool with which to derive trends of biotic homogenization and to provide a simple quantification of how biodiversity and human activities interact. Moreover, to be effective, conservation planning must be based on information derived from well-designed studies along the entire spectrum of land uses, from wilderness to the places where people live and work (Miller & Hobbes 2002). Similar assessments of functional homogenization are already possible at a wide array of scales in many countries, where such data sources are now available for animal and for plant species (Smart et al. 2006).

Homogenization is one of the most prominent forms of biotic impoverishment worldwide and is likely to cause negative genetic, functional, and evolutionary impacts on communities (Olden et al. 2004). Our results showed that this symptom of biodiversity loss is perceptible when considering common species. Landscape and urban planning should therefore encompass the protection of mainstream specialist species and not be limited to rare and endangered native species. The concept, vision, values, and utility of rural land is nowadays largely defined by people living and working in the city (Antrop 2004). Considering how urban-sprawl effects vary across species in future urban planning could help in the development of simple guidelines for more-sustainable urban development. In particular, specialist species are expected to have higher fitness than generalists in stable environments. The simple protection of nonurban areas within the urbanized landscapes should counterbalance the colonization of human-altered landscapes by generalist species. Moreover because specialist species are expected to be more limited by dispersal abilities than generalists (Krauss et al. 2003; Marvier et al. 2004), connection among nonurban patches within the urbanized matrix should also help prevent local extinction of specialist species.

Management of landscape changes, including the new complex and urbanized ones, is urgently needed, and conservation planning must specifically address the issue of human settlement to underline the value of unprotected lands for nature conservation (Miller & Hobbes 2002). Assessing whether the protection of several aspects of traditional landscapes (e.g., in regional nature parks in France) where human pressure is high is effective in limiting community homogenization should be a promising step forward. Because human infrastructures are threatening biodiversity worldwide and will increase in the future, conservation biologists should enlarge the scope of their investigations to nature in the areas where people live.

Acknowledgments

Literature Cited

Agreste. 2003. Indicateurs paysagers élaborés à partir de l'enquête sur l'utilisation du territoire (TERUTI). Technical report N-151. SCEES, Paris.

Alpizar-Jara, R., J. D. Nichols, J. E. Hines, J. R. Sauer, K. H. Pollock, and C. S. Rosenberry. 2004. The relationship between species detection probability and local extinction probability. Oecologia **141:**652–660.

Antrop, M. 2004. Landscape change and the urbanization process in Europe. Landscape and Urban Planning **67:**9.

Ashraf, M., J. C. Loftis, and K. G. Hubbard. 1997. Application of geostatistics to evaluate partial weather station. Agriculture and Forest Meteorology **84:**255–271.

Balmford, A., P. Crane, A. Dobson, R. E. Green, and G. M. Mace. 2005. The 2010 challenge: data availability, information needs and extraterrestrial insights. Philosophical Transactions of the Royal Society B **360:**221–228.

Blair, R. 2004. The effects of urban sprawl on birds at multiple levels of biological organization. Ecology and Society **9**: Available from http://www.ecologyandsociety.org/vol9/iss5/art2/.

Blumstein, D. T., E. Fernandez-Juricic, P. A. Zollner, and S. C. Garity. 2005. Inter-specific variation in avian responses to human disturbance. Journal of Applied Ecology **42:**943–953.

Boulinier, T., J. D. Nichols, J. E. Hines, J. R. Sauer, C. H. Flather, and K. H. Pollock. 1998*a*. Higher temporal variability of forest breeding bird communities in fragmented landscapes. Proceedings of the National Academy of Science **95:**7497–7501.

Boulinier, T., J. D. Nichols, J. R. Sauer, J. E. Hines, and K. H. Pollock. 1998*b*. Estimating species richness: the importance of heterogeneity in species detectability. Ecology **79:**1018–1028.

Boulinier, T., J. D. Nichols, J. E. Hines, J. R. Sauer, C. H. Flather, and K. H. Pollock. 2001. Forest fragmentation and bird community dynamics: inference at regional scales. Ecology **82:**1159–1169.

Brouat, C., H. Chevallier, S. Meusnier, T. Noblecourt, and J.-Y. Rasplus. 2004. Specialization and habitat: spatial and environmental effects on abundance and genetic diversity of forest generalist and specialist *Carabus* species. Molecular Ecology **13:**1815–1826.

Buckland, S. T., A. E. Magurran, R. E. Green, and R. M. Fewster. 2005. Monitoring change in biodiversity throug composite indices. Philosophical Transactions of the Royal Society B **360:**243–254.

Carroll, S. S., and D. L. Pearson. 2000. Detecting and modeling spatial and temporal dependence in conservation biology. Conservation Biology **14:**1893–1897.

Chace, J. F., and J. J. Walsh. 2006. Urban effects on native avifauna: a review. Landscape and Urban Planning **74:**46–49.

Clergeau, P., S. Croci, J. Jokimäki, K.-J. Marja-Liisa, and M. Dinettic. 2006.

Avifauna homogenisation by urbanisation: analysis at different European latitudes. Biological Conservation **127:**336–344.

Cressie, N. 1993. Statistics for spatial data. Revised edition. John Wiley & Sons, New York.

Crooks, K. R., A. V. Suarez, and D. T. Bolger. 2004. Avian assemblage along a gradient of urbanization in a highly fragmented landscape. Biological Conservation **115:**451–462.

Dall, S. R. X., and I. C. Cuthill. 1997. The information costs of generalism. Oikos **80:**197–202.

Doherty, P. F. J., G. Sorci, J. A. Royle, E. J. Hines, J. D. Nichols, and T. Boulinier. 2003. Sexual selection affects local extinction and turnover in bird communities. Proceeding National Academy of Science **100:**5858–5862.

Fortin, M.-J., M. R. T. Dale, and J. ver Hoef. 2002. Spatial analysis in ecology. Pages 2051–2058 in A. H. El-Shaarawi and W. W. Piegorsh, editors. Encyclopedia of environmetrics. Chichester, United Kingdom.

Futuyma, D. J., and G. Moreno. 1988. The evolution of ecological specialization. Annual Review of Ecology and Systematic **19:**207–233.

Gregory, R. D., A. van Strien, P. Vorisek, A. W. G. Meyling, D. G. Noble, R. P. B. Foppen, and D. W. Gibbons. 2005. Developping indicators for European birds. Philosophical Transactions of the Royal Society B **360:**269–288.

Guisan, A., T. C. Edwards, and J. T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distribution: setting the scene. Ecological Modelling **157:**89–100.

Hagemeijer, E. J., and J. M. Blair. 1997. The EBCC atlas of European breeding birds: their distribution and abundance. Poyser, London

Hanski, I. K. 1999. Metapopulation ecology. Oxford University Press, New York.

Heikkinen, R. K., M. Luoto, R. Virkkala, and K. Rainio. 2004. Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural-forest mosaic. Journal of Applied Ecology **41:**824–835.

Hines, J. E., T. Boulinier, J. D. Nichols, J. R. Sauer, and K. H. Pollock. 1999. COMDYN: software to study the dynamics of animal communities using a capture-recapture approach. Bird Study **46:**209–217.

Jenouvrier, S. and T. Boulinier. 2006. Estimation of local extinction rates when species datectability covaries with extinction probability: is it a problem? Oikos **113:**132–138.

Jiguet, F., O. Renault, and A. Petiau. 2005. Estimating species richness with capture-recapture models in heterogeneous conditions: choice of model when sampling in heterogeneous conditions. Bird Study **52:**180–187.

Jonsen, I. D., and L. Fahrig. 1997. Response of generalist and specialist insect herbivores to landscape spatial structure. Landscape Ecology **12:**185–197.

Julliard, R., F. Jiguet, and D. Couvet. 2004. Common birds facing global changes: what makes a species at risk? Global Change Biology **10:**148–154.

Julliard, R., J. Clavel, V. Devictor, F. Jiguet, and D. Couvet. 2006. Spatial segregation of specialists and generalists in bird communities. Ecology Letters 9:1237–1244.

Kéry, M. 2004. Extinction rate estimates for plant populations in revisitation studies: importance of detectability. Conservation Biology 18:570–574.

Kithahara, M., K. Sei, and K. Fujii. 2000. Patterns in the structure of grassland butterfly communities along a gradient of human disturbance analysis based on the generalist/specialist concept. Population Ecology **42:**135–144.

Krauss, J., I. Steffan-Dewenter, and T. Tscharntke. 2003. Local species immigration, extinction, and turnover of butterflies in relation to habitat area and habitat isolation. Oecologia **442:**591–602.

Kühn, I., and S. Klotz. 2006. Urbanization and homogenization—comparing the floras of urban and rural areas in Germany. Biological Conservation **127:**292–300.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology **74:**1659–1673.

Liebhold, A. M., and J. Gurevitch. 2002. Integrating the statistical analysis of spatial data in ecology. Ecography **25:**553–557.

Lockwood, J. L., G. J. Russel, J. L. Gittleman, C. C. Daehler, M. L. McKinney, and A. Purvis. 2002. A metric for analysing taxonomic patterns of extinction risk. Conservation Biology **16:**1137–1142.

McGill, B. J., B. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution **21:**178–185.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation **127:**247–260.

McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution **14:**450–453.

Marvier, M., P. Kareiva, and M. G. Neubert. 2004. Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. Risk Analysis **24:**869–878.

Marzluff, J. M. 2005. Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human-dominated landscapes. Urban Ecosystems **8:**157–177.

Marzluff, J. M., K. Ewing, 2001. Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. Restoration Ecology **9:**280–292.

Miller, J. R., and R. J. Hobbs. 2002. Conservation where people live and work. Conservation Biology **16:**330–337.

Newmark, W. 2006. A 16-year study of forest disturbance and understory bird community structure and composition in Tanzania. Conservation Biology **20:**112–134.

Nichols, J. D., T. Boulinier, J. E. Hines, K. H. Pollock, and J. R. Sauer. 1998a. Estimating rates of local species extinction, colonization, and turnover in animal communities. Ecological Applications **8:**1213–1225.

Nichols, J. D., T. Boulinier, J. E. Hines, K. H. Pollock, and J. R. Sauer. 1998b. Inference methods for spatial variation in species richness and community composition when not all species are detected. Conservation Biology **12:**1390–1398.

Olden, J. D. 2006. On defining and quantifying biotic homogenization. Global Ecology and Biogeography **15:**113–120.

Olden, J. D., and N. L. Poff. 2004. Clarifying biotic homogenization. Trends in Ecology & Evolution **19:**282–283.

Olden, J. D., N. L. Poff, M. B. Douglas, M. E. Douglas, and K. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology & Evolution **19:**18–24.

Owens, I. P. F., and P. M. Bennett. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proceeding of the National Academy of Science **97:**12144–12148.

Pauchard, A., M. Aguayo, E. Peña, and R. Urrutia. 2006. Multiple effects of urbanization on the biodiversity of developing countries: the case of a fast-growing metropolitan area (Concepción, Chile). Biological Conservation **127:**272–281.

Pinhero, J. C., and M. B. Douglas 2000. Mixed-effects models in S and S-PLUS. Springer, New York.

R Development Core Team. 2004. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available from http://www.R-project.org (accessed September 2006).

Sekercioglu, Ç. H. 2006. Increasing awareness of avian ecological function. Trends in Ecology & Evolution **21:**464–471.

Selmi, S., and T. Boulinier. 2001. Ecological biogeography of Southern Ocean islands: the importance of considering spatial issues. The American Naturalist **158:**426–437.

Selmi, S., T. Boulinier, and R. Barbault. 2002. Richness and composition of oasis bird communities: spatial issues and species-area relationships. The Auk **119:**533–539.

Smart, S. M., K. Thompson, R. H. Marrs, M. G. Le Duc, L. C. Maskell, and L. G. Firbank. 2006. Biotic homogenization and changes in species diversity across human-modified ecosystems. Philosophical Transactions of the Royal Society B **273:**2659–2665.

Thompson, W. L. 2002. Towards reliable bird surveys: accounting for individuals present but not detected. The Auk **119:**18–25.

Tucker, G. M., and M. H. Heath. 1994. Birds in Europe: their conservation status. Birdlife International, Cambridge, United Kingdom.

Tworek, S. 2003. Local extinction, colonisation and turnover rates of breeding birds in fragmented landscapes: differences between migratory guilds. Ornis Fennica **80:**49–62.

Vitousek, P. M., H. A. Mooney, J. Lubchenko, and J. M. Melillo. 1997. Human domination of earth's ecosystems. Science **277:**494–499.

Yoccoz, N. G., J. D. Nichols, and T. Boulinier. 2001. Monitoring of biological diversity in space and time. Trends in Ecology & Evolution **16:**446–453.