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Green infrastructures and ecological corridors shape avian biodiversity in a small French city

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Abstract

In the context of increasing urbanization, preserving urban biodiversity has become a priority because biodiversity appears to be a key element when evaluating the well-being of urban residents. Recently, urban management has relied on a 'renaturing' strategy to improve biodiversity, but the benefits of these policies remain debated. In this study, we evaluated the effects of urban land use and green corridors on (1) urban avian biodiversity, and (2) the presence of the most common (top 70%) and least common (bottom 30%) bird species. We surveyed bird diversity at 102 sites during the Spring in a small French city, and performed a PCA on several habitat structures (e.g. roads, houses, grassy areas) to determine the level of urbanization of each site. Then, we tested with GLMMs the effects of land use (PC1), distance to the edge of the city, and distance to the corridor on bird diversity. We found a positive effect of green infrastructures on bird species richness, and this effect was reinforced by the proximity to the green corridor. Thus, bird species richness and the presence of common species were positively impacted by the presence of green areas, the proximity to the city edge and the proximity to the green corridor. The presence of the green corridor contributed significantly to the presence of rare species, which emphasizes its role in promoting avian biodiversity. Green corridors are a key element of the urban landscape because they allow less common species to colonize cities, and thus enhance urban biodiversity.

Keywords Biodiversity · Bird species richness · Green infrastructures · Connectivity · Corridor · Urban planning

Introduction

Humans are modifying Earth's ecosystems at an unprecedented rate. Although urbanized areas represent only 3% of the world's surface area (United Nations 2012), more than 50% of humans currently live in cities. Importantly, this percentage is expected to increase and it is predicted that 60% of the world's population will live in urbanized areas in 2030 (United Nations 2016). In Europe, the urban population has already reached 70% of the total population (United Nations 2018) and improving the quality of life of urban populations is recognized as a priority of urban management policies. Contact with nature and biodiversity is essential to the wellbeing of urban residents (Aerts et al. 2018; Alberti 2015; Cox et al. 2017; Fischer et al. 2018; Puppim de Oliveira et al. 2011), and urban biodiversity is often used to determine the attractiveness of cities worldwide (Mondal and Das 2018; Romão et al. 2018).

Urbanization induces severe environmental changes, such as landscape fragmentation and alteration, which lead to a drastic reduction of natural habitats (i.e. forests, grasslands, wetlands) and a simultaneous increase of artificial and impervious surfaces (Forman 2014; Grimm et al. 2008; Seress and Liker 2015). Habitat fragmentation and alteration also constrain plant dispersion and reproduction and, consequently, directly affect resource availability and quality for wildlife (Alberti 2015; Aronson et al. 2014). Further, fragmentation and alteration limit the ability of animal communities to disperse, breed, and colonize the urban environment (Marzluff et al. 2008; Rebele 1994). Concomitantly with new sources of urban anthropogenic pollution (light, chemical, noise, etc.), these changes of habitat structure are associated with reduction and homogenization of biodiversity (Benítez-López et al. 2010; McKinney 2002; McKinney 2006; Newbold et al.

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2015). This phenomenon is especially striking in birds, and previous studies have notably reported that urbanization is associated with the disappearance of certain species in urban habitats, while other species increase (e.g. rock doves, starlings, house sparrows; Chace and Walsh 2006; Clergeau et al. 2006; Leveau 2019; Marzluff et al. 2001; Moller 2009; Seress and Liker 2015).

Avian biodiversity is often measured in urban landscapes because it is relatively easy to monitor (Ralph et al. 1995) and because it represents a good indicator of the suitability of the urban habitat for wildlife (Blair 1999). Therefore, assessment of avian biodiversity can shed light on the impact of land use management and urban planning on biodiversity. Previous studies have demonstrated that urban parks and green spaces can improve avian biodiversity (Aida et al. 2016; Aronson et al. 2014; Barth et al. 2015; Beninde et al. 2015; Chang et al. 2017; Filazzola et al. 2019; Ortega-Álvarez and MacGregor-Fors 2009). Similarly, higher building densities and larger areas of impervious surfaces are associated with lower avian diversity. Accordingly, avian species richness tends to be higher in moderately urbanized areas (i.e. suburbs) and to decrease toward the urban core (Blair 2001; Blair 2004; Chace and Walsh 2006; Seress and Liker 2015).

Recently, urban management has relied on a 'renaturing of cities' strategy to improve biodiversity, but the relative benefits of alternative policies remain debated (Connop et al. 2016; Garmendia et al. 2016; Snäll et al. 2016). Specifically, it has been suggested that all green spaces do not have similar value in terms of habitat suitability, and that highly fragmented, small, and isolated green spaces may be of limited ecological value relative to larger and more connected green spaces (Beninde et al. 2015; Bernat-Ponce et al. 2020; Lepczyk et al. 2017; Villaseñor et al. 2020). In the last decade, the development of connected green infrastructures and ecological corridors has been proposed as a way to improve the colonization of wildlife and, therefore, urban biodiversity (Filazzola et al. 2019; Vergnes et al. 2013). Many studies have demonstrated that such green corridors can enhance biodiversity (e.g. Beninde et al. 2015; Davies and Pullin 2007; Gilbert-Norton et al. 2010; Tewksbury et al. 2002; Vergnes et al. 2013). Particularly, previous studies have shown a positive effect of corridors on bird dispersion, abundance, and/or species richness (Gillies and CCS 2008; Kang et al. 2015; Shanahan et al. 2011; Stagoll et al. 2010). However, most other studies have focused on animals with a low dispersion ability, while neglecting birds, especially those living in urban landscape (Gilbert-Norton et al. 2010; Lepczyk et al. 2017; Resasco 2019). In addition, it is also important to test if the richness of species that are less common in cities (i.e. urban avoiders) could benefit from these green corridors to colonize urban territories. These riparian corridors are often composed of waterbodies (e.g. pond, rivers), which could bring important food and water resources for species which are especially constrained by the urban environment (Puppim de Oliveira et al. 2011), and may significantly improve urban biodiversity (Kang et al. 2015; Olden et al. 2004). Finally, considering the distribution of more and less common species from the edge to the core of the city could provide more information about the effectiveness of the corridor in enhancing bird diversity inside the city (LaPoint et al. 2015).

In this study, we evaluated the effects of urban land use and green corridors on avian biodiversity. In addition, we distinguished the least common species in cities (rare species) from the most common species, to see if they benefit differently from green infrastructures and corridors. To do so, we relied on a detailed survey of avian biodiversity (102 locations) during the Spring in a small city in Western France (Niort, ~60,000 inhabitants), which is surrounded by agricultural lands. Interestingly, this city has developed environmentally friendly management policies over the last decade, which are characterized by the creation of several green infrastructures (parks, vegetated roadsides) in the city and the protection of a large green corridor, which crosses the whole city (http://www.tvb-nouvelle-aquitaine.fr/IMG/pdf/fiche_niort.pdf). This corridor consists of a riparian corridor, with large vegetated river banks and surrounding parks, which insures the connectivity between several parts of the city and the surrounding rural areas (Fig. 1). This situation represents a unique opportunity to evaluate the effects of a large green corridor on avian biodiversity. In addition to the avian biodiversity assessment, we measured the detailed habitat structure of each census location (e.g. percentage of green space), its distance to the edge of the city, and its distance to the ecological corridor described above. Moreover, we measured the level of urban noise as a proxy of human disturbance, especially because urban noise can alter bird population densities (Francis et al. 2009). According to previous studies, we hypothesized that urban avian biodiversity, and particularly rare species, would benefit from (1) the presence of green infrastructures; (2) the proximity to the edge of the city, and associated agricultural areas and wetlands; and (3) the proximity to the green corridor, which connects the city to these non-urban habitats. Conversely, we hypothesized that urban avian biodiversity would be negatively impacted by artificial infrastructures and urban noise.

Materials and methods

Study area

Our study sites were located in Niort, a small city in France (human population: 59005, location in Western Europe: N 46°18′46.8 W 0°28′44.399). The city is 68.20 km^2, with elevations varying from 2 to 77 m and a temperate oceanic climate. Niort is characterized by the presence of residential

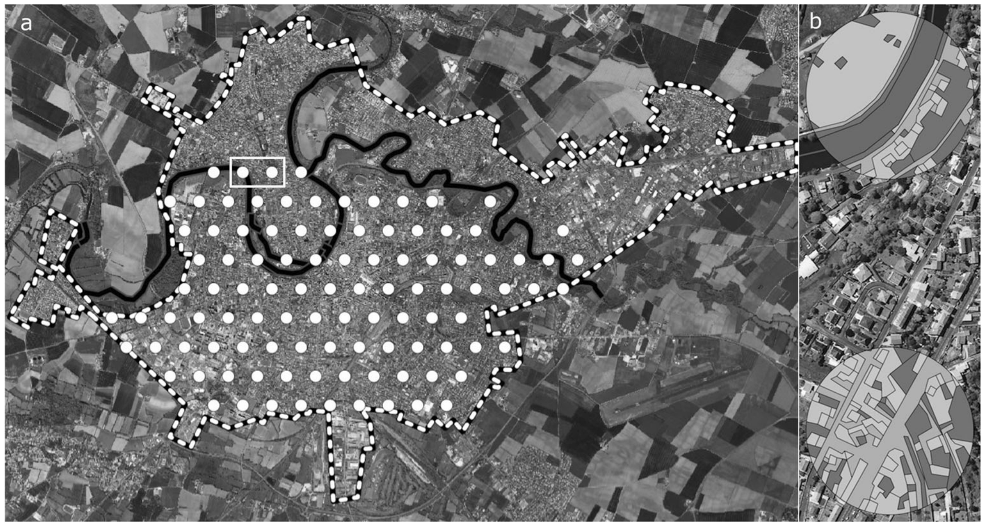

Fig. 1 (a) Location of the 102 sites in the city of Niort, France. Black line represents the green corridor, black and white dotted line represents the edge of the city. (b) Example of the characterization of habitat in two neighboring sites, one site (top circle) with relatively important green (light grey) and water (dark grey) surfaces, and another site (bottom circle) with more impervious surfaces

areas with numerous old (stone) houses and some modern buildings. It includes several green parks and a green corridor that crosses the city (the Sèvre Niortaise river and its vegetated banks, Fig. 1). The river banks are composed of many tall deciduous trees, conifers, and understory vegetation, whereas the green parks and gardens are essentially composed of herbaceous vegetation, hedges, and small trees. Niort is surrounded by agricultural lands and wetlands (Poitevin marshlands, Fig. 1).

Bird survey

Bird surveys were conducted in 2017 and adapted from the STOC – EPS protocol (Suivi Temporel des Oiseaux Communs - Echantillonnages Ponctuels Simples; Morelli et al. 2017b). In total, 102 sites were surveyed. All sites were located by using a grid (400 m between each site, Fig. 1). Three survey sessions were made: (1) from the 15th to the 31st of March, (2) from the 10th to the 25th of April, and (3) from the 9th to the 22nd of May. A mean of 9 sites were visited per day. Bird surveys were performed between 6 a.m. and 10 a.m. In each session, sites were surveyed in a different order and at a different hour within this time-slot, to avoid a potential bias on the number of birds and species observed. First, the observer counted the number of individuals seen per species within a 25-m radius for 5 min without moving. During the following 5 min, the observer moved within the 25-m circle and also counted the number of individuals seen per species. Then, the numbers of birds per species obtained in the two 5 min surveys were summed to obtain one final count per species and per site. Double counting may have occurred and is an unavoidable fact during most bird censuses. Thus, we used the same standardized technique at each site to limit a potential bias between sites and the effect of double counting on our results (Sutherland et al. 2004). Surveys were not performed when the weather could have affected the detectability of birds (rain or wind).

Habitat characterization

First, urban noise was recorded between 7 a.m. and 10 a.m. for 1 min using a numeric sonometer Voltcraft SL 200. The sonometer was located 2 m above the ground during the measurement session to avoid interferences. Two measurement sessions were conducted (1) from the 1st to the 5th of May, (2) from the 22nd to the 25th of May. The two sessions were highly repeatable ($R = 0.733$), so the mean noise intensity (dB) between the two sessions was calculated and used in the analyses.

Habitat characterization of all census sites was conducted using the open source geographic information system (QGIS Development Team 2017). For each of the 102 sites, habitat was characterized within a 100-m radius (Fig. 1), in order to characterize a sufficient surface area without overlap among neighboring sites. Six categories of habitat were defined: concrete surface (Road); flat roof building (Bat1, considered as a modern building); steep roof made of tiles (Bat2, considered as an old building); grassy area (Grass, area with a majority of understory vegetation); wooded area (Wood, area with a majority of tall vegetation); water (Water). Then, the percentage of surface for each habitat category was calculated for the 102 sites. We performed a principal component analysis (PCA) on these six variables, along with the noise values, to determine which habitat variables best describe the level of urbanization of each site, as in Blair (2004). The first principal component (PC1) accounted for 33.54% of the total variance, and was negatively correlated with Road ($r = -0.852$), Bat1 ($r = -0.707$) and Noise ($r = -0.651$), and positively correlated with Grass ($r = 0.604$). Thus, sites with negative PC1 values (majority of Road, Bat1 and Noise) had higher levels of urbanization than sites with positive PC1 values (majority of Grass).

To include a more precise measure of the ecological corridors in the habitat characterization, we defined two linear components: the green corridor (corresponding to the two rivers Sèvres and Lambon) and the edge of the city (Fig. 1). These components were chosen as source habitats for bird species, because they represent natural areas without urban constraints, and those from which species can colonize urban habitat. So, to understand the effect of source habitats on the presence of species in the city, we calculated the distance to the green corridor ($D_{corridor}$) and the distance to the edge (D_{edge}) for each site.

Diversity indices

For each site, we determined Niort's avian diversity using three indices: (1) species richness, (2) Shannon's diversity and (3) Simpson's evenness (Morris et al. 2014). Species richness (S) corresponded to the total number of bird species observed per site. Shannon diversity (H′) indicates the degree of diversity of the community, and Simpson's evenness (E) indicates if the abundance of individuals is relatively equal among species (Morris et al. 2014). These two indices were calculated according to the formulas from Shannon (1948) and Simpson (1949):

$$H' = -\sum P_i \ln(P_i) \quad (1)$$

$$E = \frac{1/\sum P_i^2}{S} \quad (2)$$

with P_i being the proportion of individuals that belong to species *i*. We obtained H' values between 0 and 3, with higher H' values indicating more bird diversity. We obtained E values between 0 and 1, with higher E values indicating a higher evenness in the community, while lower E values indicated that a few species dominate (Morris et al. 2014). The three diversity indices were calculated independently for each session of the survey (March, April and May). They were strongly correlated (S-H': r = 0.906; $p < 0.001$; S-E: r = 0.901; p < 0.001; H'-E: r = 0.996; p < 0.001), so we mainly discuss the results for Richness, as it remains the more commonly used index of diversity (Morris et al. 2014).

Statistical analyses

All statistical analyses and graphs were performed in R 3.4.3 (R Core Team 2016). First, spatial autocorrelation was checked using Mantel tests (Mantel 1967), based on a matrix of geographic distances (latitude, longitude) and a second matrix of differences in bird species richness among sampling sites, applying Monte Carlo permutations with 9999 randomizations (Oksanen et al. 2016). The 102 sites were treated as statistically independent observations because spatial autocorrelation was not detected ($r_m = 0.014$, $p = 0.244$).

We fitted generalized linear mixed models (GLMMs, Poisson distribution, log link function) to test the relationship between species richness and (1) habitat structure, (2) distance to the edge, and (3) distance to the green corridor. We used PC1, $D_{corridor}$, and D_{edge} as explanatory variables. Session (March, April, or May) was used as random factor to account for the non-independence of birds surveyed on the same site. We also fitted linear mixed models (LMMs, normal distribution, identity link function) to test the effects of habitat variables on Shannon diversity or Simpson's evenness. Model selections were performed using a backward stepwise approach starting from the most complex model and progressively eliminating interactions with $p > 0.100$. In addition, we used the second-order Akaike Information Criterion (AICc) to conduct model selections. Results from both approaches were similar and led to the selection of the same models. In the final models, all variance inflation factor (VIF) values were < 2, indicating that collinearity did not bias the model results (Graham 2003; Zuur et al. 2007). To see whether using PC1 values might mask effects of each habitat variable tested separately, we performed GLMMs with Road, Bat1, Bat2, Grass, Wood, Water or Noise as explanatory variable and Session as random factor (see Online Resource 1 for detailed results).

We also fitted GLMMs to separately test the effects of habitat variables on the less common and more common species. To do this, we first calculated the occurrence of species on the 102 sites during the 3 sessions combined (306 observations in total). We determined a rarity threshold using the Gaston's method (Leroy et al. 2012). Rarity threshold was fixed at 3, meaning that the rare species were observed only 3 times or less during the 306 observations. Among the 47 observed species, 14 were defined as "rare" (30% of the total number of species observed). The 33 other species were defined as "common" species (Online Resource 2). We fitted GLMMs on the richness of rare species, with PC1, $D_{corridor}$, and D_{edge} as explanatory variables, and Session as a random factor. In the same way, we fitted GLMMs on the richness of common species, with Session, PC1, $D_{corridor}$, and D_{edge} as explanatory variables. We chose the model selected by the backward stepwise approach for both rare and common species. To see if using PC1 values may mask the effects of each habitat variable tested separately, we performed GLMMs with Road, Bat1, Bat2, Grass, Wood, Water or Noise as explanatory variable and Session as random factor (Online Resource 1).

Results

Urban avian biodiversity

In total, 47 species were observed during the survey periods. Species richness was significantly correlated with PC1 and its interaction with $D_{corridor}$ (Table 1a). Specifically, bird species richness increased in sites with a higher PC1 value (i.e. higher Grass cover, lower Road and Bat1 cover, and lower Noise intensity), and this effect was stronger closer to the green corridor (Fig. 2). Shannon diversity and Simpson's evenness were significantly and positively correlated with PC1 but not with $D_{corridor}$ or its interaction with PC1, although the *p* value was almost significant (Table 1a). Species richness, Shannon diversity, and Simpson's evenness were significantly and negatively correlated with D_{edge}, with fewer species, lower diversity, and less evenness observed towards the center of the city (Table 1a).

Rare versus common species

Richness of rare species was significantly correlated with $D_{corridor}$ (Table 1b), with more species observed closer to the corridor (Fig. 3a). However, Session, PC1, and D_{edge} were not significantly related to the richness of rare species (Table 1b; Fig. 3b, c). Results for the richness of common species were similar to those for Niort's biodiversity (Table 1c).

Discussion

Our study highlights the importance of vegetation and green corridors for bird species in cities, because we found a positive effect of green infrastructures on bird species richness, which was reinforced by the proximity of a green corridor. Particularly, habitat connectivity appeared to be essential for rare species, because their richness was positively related to the proximity of the green corridor, but not by habitat variables (PC1) or the distance to the city edge. In contrast, the richness of common species was related to the three habitat variables. In total, 47 bird species were identified in Niort during our study. Niort is a small city compared to other French cities, and is characterized by "green" policies and urban planning. When we consider the entire city, from the urban core to suburban areas, Niort has a relatively high bird species richness compared to those reported in suburban areas of other French, Italian or Finnish cities (Clergeau et al. 2006). Therefore, this supports the idea that Niort's urban management may have a beneficial effect on bird biodiversity.

Table 1 Minimum adequate models to test the influence of the session and relevant habitat variables on (a) total bird species richness, Shannon diversity and Simpson's evenness (b) rare bird species richness, (c) common bird species richness

Test	Variable of interest	Explanatory variables[1]	Estimate ± SE	Z-value[2]	*P* value
a	Richness	Intercept	1.848 ± 0.095	19.430	< 0.001
		PC1	0.111 ± 0.031	3.587	< 0.001
		Distance to the corridor	−0.081 ± 0.043	−1.856	0.063
		Distance to the edge	−0.216 ± 0.051	−4.219	< 0.001
		PC1*Distance to the corridor	−0.060 ± 0.026	−2.337	0.019
	Shannon diversity	Intercept	2.165 ± 0.179	12.100	< 0.001
		PC1	0.170 ± 0.049	3.443	< 0.001
		Distance to the corridor	−0.105 ± 0.071	−1.486	0.1383
		Distance to the edge	−0.293 ± 0.081	−3.597	< 0.001
		PC1*Distance to the corridor	−0.079 ± 0.042	−1.890	0.060
	Simpson's evenness	Intercept	0.399 ± 0.030	13.302	< 0.001
		PC1	0.032 ± 0.009	3.465	< 0.001
		Distance to the corridor	−0.019 ± 0.013	−1.450	0.148
		Distance to the edge	−0.054 ± 0.015	−3.602	< 0.001
		PC1*Distance to the corridor	−0.014 ± 0.008	−1.872	0.062
b	Richness	Intercept	−1.450 ± 0.485	−2.987	0.003
		PC1	0.231 ± 0.172	1.340	0.180
		Distance to the corridor	−1.260 ± 0.458	−2.748	0.006
		Distance to the edge	−0.568 ± 0.384	−1.481	0.139
c	Richness	Intercept	1.818 ± 0.095	19.221	< 0.001
		PC1	0.107 ± 0.031	3.433	< 0.001
		Distance to the corridor	−0.067 ± 0.044	−1.536	0.124
		Distance to the edge	−0.209 ± 0.052	−4.047	< 0.001
		PC1*Distance to the corridor	−0.058 ± 0.026	−2.260	0.024

[1] Models were selected by using a stepwise approach starting from the full models and removing independent variables with P > 0.10

[2] t-value for Shannon diversity and Simpson's evenness

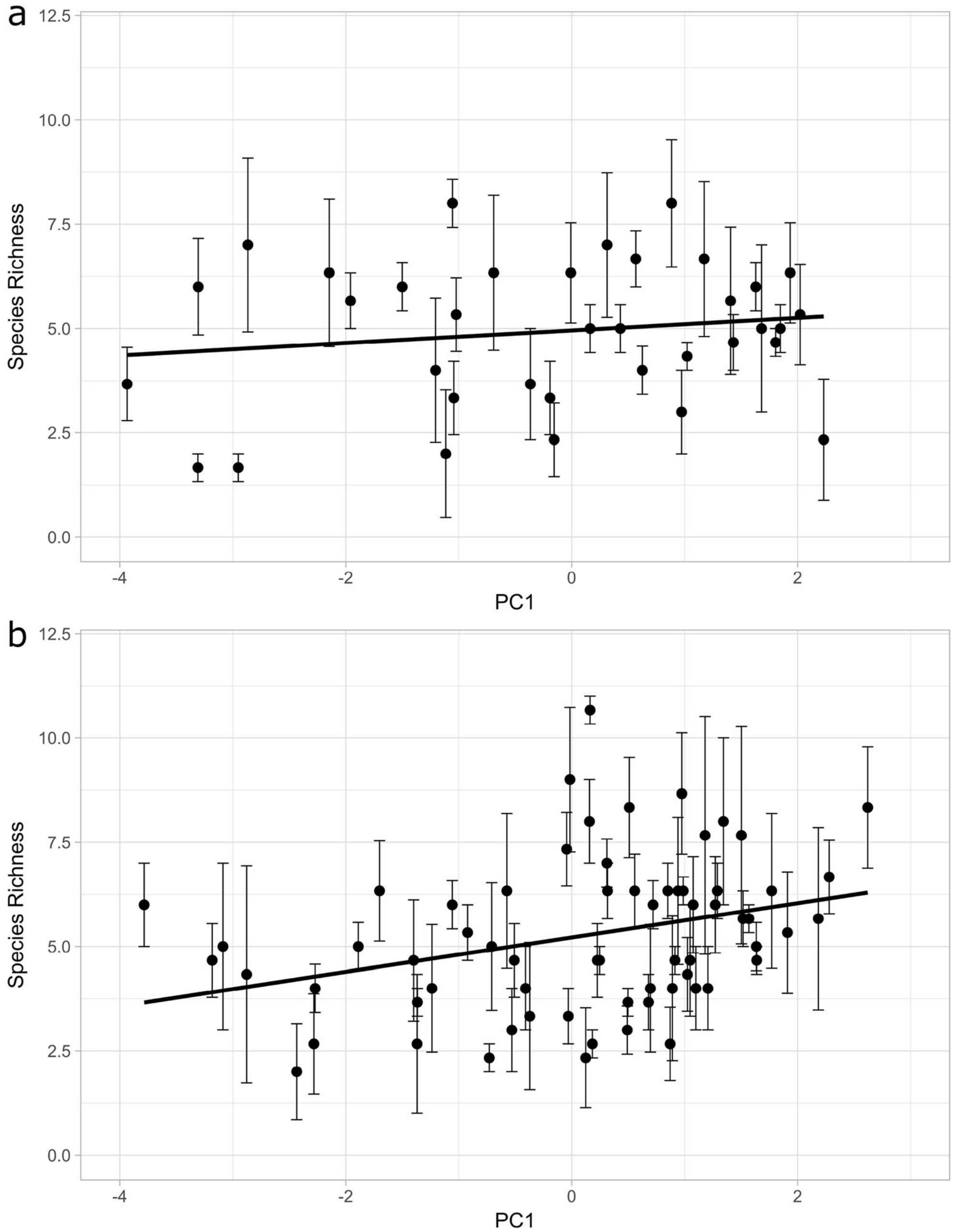

Fig. 2 Relationship between PC1 and species richness of bird species (mean ± SE) in Niort with (a) distance to the green corridor greater than 1 km (GLMM: $F_{1.107} = 0.234$; $p = 0.621$), (b) distance to the green corridor less than 1 km (GLMM: $F_{1.197} = 5.869$; $p = 0.014$). We present two graphs to better visualize the interactive effect of PC1 and distance to the corridor on bird species richness. The limit distance of 1 km was arbitrary selected to better visualize the stronger effect of PC1 on species richness on sites closer to the corridor. PC1 is negatively correlated with Road, Bat1 and Noise, and positively correlated with Grass

Benefits of vegetation for avian biodiversity

The positive correlation of bird species richness, Shannon diversity, and Simpson's evenness with understory vegetation cover in Niort confirmed the value of maintaining vegetation in cities (Chace and Walsh 2006; Faeth et al. 2011; Pirzio Biroli et al. 2020). Accordingly, previous studies have reported that bird species richness is higher in parks and gardens, compared to more urbanized areas, in a large number of cities (e.g. Aida et al. 2016; Barth et al. 2015; Blair 1996; Callaghan et al. 2019a). In our study, understory vegetation areas appeared to be particularly beneficial to common species (see Online Resource 2). Previous studies in Europe have shown that common species, such as house sparrows (*Passer domesticus*) and common starlings (*Sturnus vulgaris*), preferentially settle in urban sites with parks and gardens (Chamberlain et al. 2007; Morelli et al. 2018; Murgui 2009). Urban birds can find most of their food resources, which consist mostly of seeds and insects, in understory vegetation areas (Carvajal-Castro et al. 2019; Huang et al. 2015; Müller et al. 2018). Moreover, understory vegetation areas can provide material for nest building, such as grass, straw, and twigs (Anderson 2006; Mainwaring and Healy 2019). Even if tall vegetation was not integrated in the PC1, its effect was partially significant when tested on different bird species richness categories (see Online Resource 1). This supports the idea that

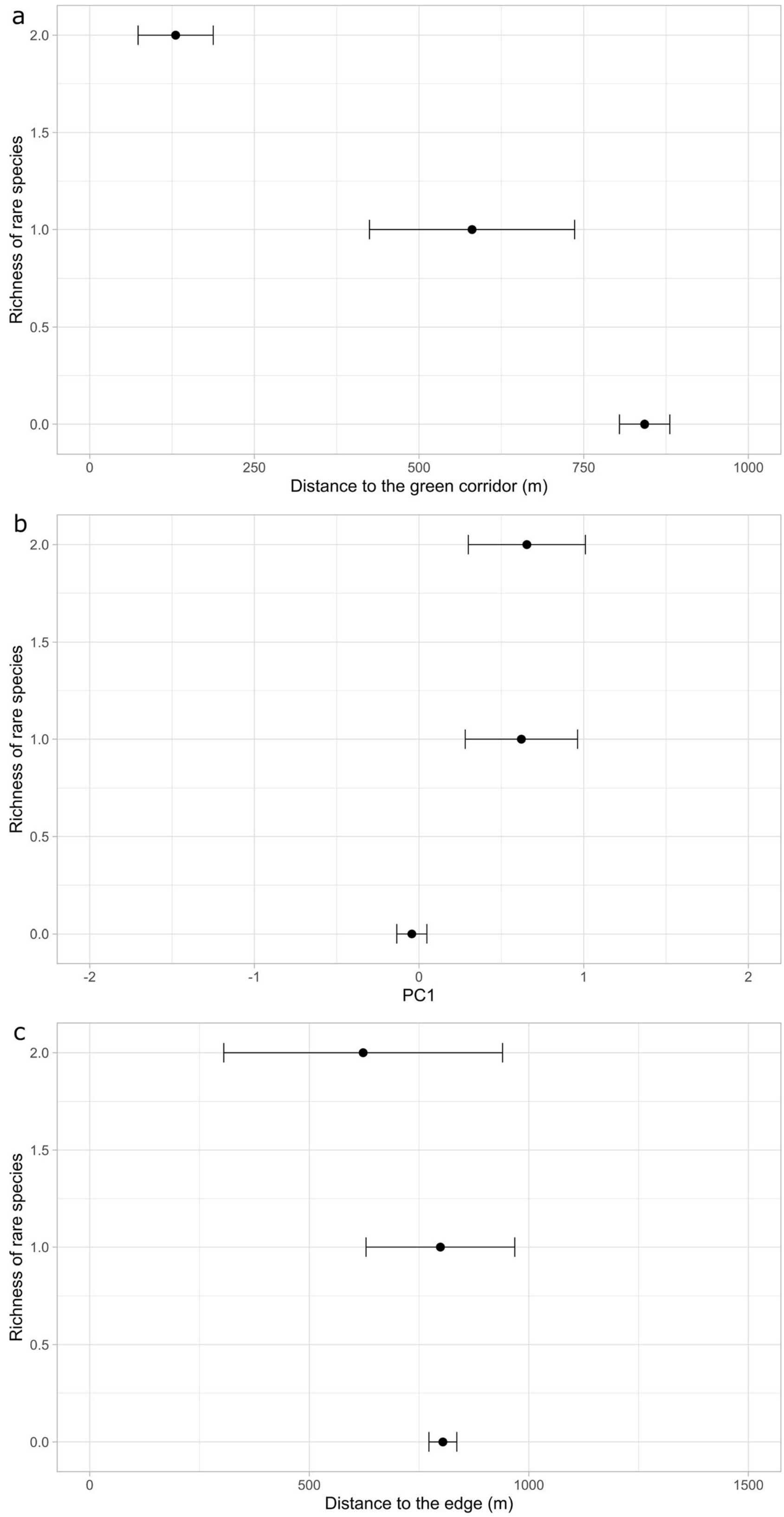

Fig. 3 Relationship between (a) the distance to the green corridor (mean ± SE), (b) PC1 (mean ± SE), (c) the distance to the city edge (mean ± SE) and species richness of rare bird species in Niort. The distance to the green corridor has a significant effect on species richness of rare bird species, but PC1 and the distance to the city edge are not related to species richness of rare species. PC1 is negatively correlated with Road, Bat1 and Noise, and positively correlated with Grass

the presence of tall vegetation in cities, notably trees and shrubs, is necessary for the reproduction of many bird species, especially for building their nests and for finding nesting material (Barth et al. 2015; Han et al. 2019; Moller 2009). High vegetation is also an important complementary food resource for insectivore and frugivore species, and offers shelters for many species (Aida et al. 2016; Barth et al. 2015; Stagoll et al. 2010).

Artificial urban areas can be detrimental to birds, since Niort's and common species richness were negatively related to roads and modern flat roof buildings. These habitats are extremely poor in natural food resources (i.e. not produced by humans) and offer few sites to reproduce (Beninde et al. 2015; Gil and Brumm 2014), in contrast to vegetated areas that contain primary sources of food and reproduction sites for multiple bird species. Areas with impervious surface and buildings are colonized by only a few species (i.e. urban exploiters) that are able to take advantage of this artificial environment (Blair 1996; Kark et al. 2007). Nevertheless, the presence of such species depends on the degree of urbanization of the city. For example, modern flat roof buildings offer fewer nesting sites for urban exploiters than older buildings and houses (Moudrá et al. 2018; Tratalos et al. 2007). Artificial habitats are also risky for all birds, because birds can die due to collision with buildings, cars, and other motorized vehicles (Chace and Walsh 2006). Further, roads and modern buildings are often sources of pollution, including chemical, light, and noise pollution. In support of this, we found that the surface area of roads and modern buildings in Niort was positively correlated with noise pollution intensity. Consequently, urban noise was associated with a lower bird species richness. It is known that noise can disrupt avian communication used for mating and parental care (Halfwerk et al. 2011a; Halfwerk et al. 2011b; Leonard and Horn 2012). Noise disturbance can also negatively affect reproductive success, nestling development, and survival (Halfwerk et al. 2011b; Injaian et al. 2018; Kleist et al. 2018; Meillère et al. 2015). Therefore, noisy environments are not suitable for many species, which explains the lower avian biodiversity of the highly urbanized sites in our study. The lack of resources, the life-threatening risk of roads, and the reduced reproductive success in noisy environments are possible reasons for why birds tend to avoid artificial areas and, instead, stay in more beneficial green areas.

Importance of green corridors for avian biodiversity

Our results support the idea that green corridors play a crucial role for avian biodiversity in cities. First, we found that bird species richness was highest in the green sites that were located in the vicinity of the green corridor. This is not particularly surprising because the green corridor in Niort is mainly composed of a river with vegetated banks and, thus, can be a good avian habitat. Banks are mostly composed of trees and bushes that allow birds to hide, feed, and reproduce (Barth et al. 2015; Han et al. 2019; Ibáñez-Álamo et al. 2020; Tryjanowski et al. 2017). The presence of the riparian corridor can thus increase the amount of vegetation available for birds and, therefore, increase avian richness and abundance (Dallimer et al. 2012; Kang et al. 2015). Other studies have also shown higher levels of bird species richness close to rivers (Han et al. 2019; Morelli et al. 2017a; Stagoll et al. 2010). Altogether with our results, this suggests that the presence of a river inside the corridor can increase bird species richness close to the corridor, by offering a source of water and vegetation. Interestingly, we did not find a significant effect of the corridor on Shannon diversity or Simpson's evenness. One explanation is that the riparian corridor increases the number of species, but their abundance remains low. Consequently, diversity and evenness increase more slowly than species richness. Further, the correlation of species richness with diversity and evenness ($p = 0.06$) suggests that green corridors are also beneficial for bird diversity.

Importantly, the combined effect of green sites and the corridor on bird species richness confirms that these are both key elements of the urban landscape for avian biodiversity because they allow birds to move into the city without crossing unfavorable habitats, i.e. highly urbanized areas (Shanahan et al. 2011; Vergnes et al. 2012). In previous studies, the presence of a riparian corridor has been shown to be more efficient in enhancing connectivity for birds than other corridors, such as fencerows or grass strips (Dallimer et al. 2012; Gillies and CCS 2008; Stagoll et al. 2010). The majority of species may be able to move into green spaces because they are located close to the green corridor, which offers a source habitat with rich understory and tall native vegetation (Pennington et al. 2010). In contrast, these species may not be able to move into isolated green spaces, which are located far from the green corridor, because they are surrounded by artificial areas.

Contribution of rare species to urban bird species richness

Avian biodiversity in Niort was determined by 47 species. Among these, 14 species were defined as rare species (according to the Gaston's method; Leroy et al. 2012). These 14 species are rarely found in cities or urbanized environments, and they are classically associated with other types of habitats, such as farmlands and wetlands (Croci et al. 2008; Hume 2009). Therefore, we can consider that these 14 species are urban avoiders due to their very low occurrence in Niort. These urban avoiders may make a large contribution to the avian biodiversity of cities (i.e. 30% in our study). The presence of rare bird species can improve ecosystem functioning, because rare species can provide specific ecosystem services that are not fulfilled by common urban exploiters (Kang et al. 2015; Sekercioglu 2006). Importantly, we found that the presence of rare species was significantly influenced by the green corridor, but not necessarily by the habitat structure of the census site (buildings, vegetation, road, noise; see Online Resource 2). Rare species seem less adapted to urban conditions, probably because they are not typically generalists and are more detrimentally affected by anthropogenic urban activities. As a consequence, they may not be able to colonize the highly urbanized areas (Callaghan et al. 2019b; Moller 2009; Vergnes et al. 2012). For example, the cirl bunting (*Emberiza cirlus*) and yellowhammer (*Emberiza citrinella*) were already classified as urban avoiders (Croci et al. 2008), and we found them mostly in sites that were within the riparian corridor of Niort. Species presence inside the corridor is probably due to the abundant vegetation, which is principally composed of connected old trees and dense shrubs. It has already been shown that bird species richness increases with the age of trees and the cover of shrubs in cities (Kang et al. 2015; Matsuba et al. 2016; Tryjanowski et al. 2017). Also, the presence of both deciduous trees and conifers inside the corridor can enhance bird biodiversity (Huang et al. 2015; Morelli et al. 2017a; Mörtberg and Wallentinus 2000). Because rare species are less present, they may be less competitive for food and water resources than the common species (MacGregor-Fors et al. 2010; Shochat et al. 2010). The presence of a large river can facilitate access to water, and its vegetated banks offer many food resources. Interestingly, some rare species were not observed exclusively in the corridor, but also in other sites located in the vicinity of the corridor. The green corridor may enhance the connectivity between vegetated habitats surrounding the city and green infrastructures inside the city, allowing rare species to disperse into the city, especially in the sites close to the green corridor. In addition, the green corridor and its surroundings are often characterized by significant vegetation cover, which may also explain why a large number of bird species can be found around the green corridor. However, it is difficult to disentangle the relative impact of connectivity and increased vegetation cover because these two variables are closely related (Beninde et al. 2015; Mörtberg and Wallentinus 2000; Shanahan et al. 2011).

Interestingly, we found that total and common bird species richness, Shannon diversity, and Simpson's evenness were higher next to the city edge compared to the center of the city. This result suggests that it is more difficult for birds to colonize the core of the urban matrix, compared to its periphery (MacGregor-Fors and Ortega-Álvarez 2011). Moreover, this edge effect supports the idea that the proximity to less urbanized habitats may promote the colonization of the city center by bird species. Previous studies have shown that the effectiveness of corridors was positively influenced by the composition of the surrounding matrix (Baum et al. 2004; Vergara 2011). Niort is surrounded by farmlands and wild areas that may increase the presence of several bird species. These species may colonize the city edges, but they cannot easily reach the city center because they must cross several ecological barriers, such as roads and highly built areas (Puppim de Oliveira et al. 2011; Ries et al. 2004). Although avian biodiversity is higher close to the city edge, rare species do not seem to benefit from this edge effect (Fig. 3c). In contrast, green corridors seem to allow these rare species to colonize the urban environment, highlighting even more their ecological importance for urban biodiversity (Zúñiga-Vega et al. 2019).

In conclusion, our study confirms that the presence of a large riparian corridor can improve bird biodiversity in cities. Urban bird communities are often dominated by a few common species (Marzluff et al. 2001), and less common species need an appropriate corridor to colonize cities. By using the green corridor, rare species can enter the city, disperse inside the heterogeneous urban environment and settle into the green corridor and/or in green spaces in the vicinity of the corridor. Surrounding habitats also play a role in bird dispersal in cities because species richness increased toward the edge of the city. Corridors may therefore be crucial if they contribute to the ability of individuals from these surrounding habitats to disperse into and colonize the city center. Future studies should now examine the movements of birds between surrounding habitats and the city to better evaluate the importance of green corridors for the accessibility of cities for urban avoiders.

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Authors contributions EB, FB and FA designed the study, conducted the statistical analyses, and drafted the manuscript.

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