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# Landscape and Urban Planning

## How do urban green space designs shape avian communities? Testing the area–heterogeneity trade-off

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Abstract:	<p>In cities, green areas are essential for biodiversity conservation, with land cover heterogeneity being a decisive factor. Yet, as heterogeneity increases for a given green area, the patch size of land covers automatically decreases, as the area available for individual species, especially habitat specialist species. This relationship, known as the area-heterogeneity trade-off, is expected to lead to a unimodal relationship between species richness and land cover heterogeneity, and contrasted effects between species according to their level of urban avoidance.</p> <p>We investigated the potential consequences of this trade-off on birds in green areas selected along an urban intensity gradient in six European cities. Using a European database on bird occurrences in nesting habitats, we defined a continuous gradient of urban avian avoidance.</p> <p>We confirmed the marked area-heterogeneity trade-off in urban green areas but found no effect of land cover heterogeneity on total avian richness at green area level. However, both land cover heterogeneity and patch size were positively associated with richness of urban avoider species, indicating that urban avoiders fared better in green areas with large and heterogeneous patches. Total richness was also higher in green areas surrounded by an urban matrix composed of a variety of land covers.</p> <p>To protect urban bird avoiders, which are most at risk in cities, green area managers</p>

	and urban planners should thus be aware that land cover heterogeneity is not a panacea if patch sizes are too small. To conserve avian richness, we stress the importance of maintaining large vegetated areas as well as heterogeneity in land covers within the urban matrix.
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Title

**How do urban green space designs shape avian communities? Testing the area–heterogeneity trade-off**

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## 1      **1. Introduction**

2      In cities, nature develops in all places but faces multiple pressures due to human activities that are  
3      more intense than in non-urban areas (Muratet & Chiron, 2021). Consequently, urbanisation has  
4      significant impacts on species distribution, ecological interactions and diversity of communities  
5      (Marzluff et al., 2008). At the city level, improving the suitability and permeability of urban  
6      habitats is essential in order to facilitate the movements of living organisms and maintain viable  
7      population sizes and complex ecological networks. In this regard, the meta-analysis of Beninde et  
8      al. (2015) stressed the importance of green space design strategies and identified land cover area  
9      and its heterogeneity as the main predictors of species richness of several taxa. For instance,  
10     species richness responded positively to area, with the strongest effects on birds followed by  
11     insects and plants. Land cover heterogeneity promotes species richness through resource use  
12     differences (i.e. niche partitioning) by increasing the opportunities for different living conditions  
13     and the coexistence of consumer species (Finke & Snyder, 2008). Habitat amount and  
14     heterogeneity (e.g. habitat diversity) have attracted much attention in ecology, as researchers seek  
15     to determine the ecological rules that shape populations and communities and objectively define  
16     the threshold or minimum viable area below which diversity decreases (Drinnan, 2005).

17     While the positive relationship between the heterogeneity or area of land cover and species  
18     richness is widely acknowledged, the effects of heterogeneity and area have rarely been tested  
19     together. However, these two factors are dependent. As heterogeneity increases, in the sense of  
20     diversity of different land-cover types, the total amount of a given land cover decreases within a  
21     landscape (Figs. 1a-b). In addition to the effect of compositional heterogeneity on the total amount  
22     of each land cover type, dividing a land cover patch into several units increases configurational  
23     heterogeneity and reduces the average patch size of land cover (Figs. 1c-d; Fahrig et al., 2011).



24 Ignoring these negative correlations, known as the “area–heterogeneity trade-off” (Allouche et al.,  
25 2012), may lead to mischaracterising the effects of land cover heterogeneity on species richness.

26 In this respect, Kadmon & Allouche (2012) suggested that environmental heterogeneity has a  
27 general unimodal rather than a positive effect on species richness. Using empirical data on birds,  
28 Allouche et al. (2012) validated this hypothesis and provided a comprehensive evaluation of the  
29 mechanisms underlying this pattern. For relatively low levels of heterogeneity, when area is not a  
30 limiting factor, species richness is expected to increase with heterogeneity due to species  
31 colonisation with new species adapted to the newly available niches (Figs. 1e-f). As heterogeneity  
32 continues to increase, richness is expected to decrease when the amount of effective area available  
33 for the individual species decreases, which possibly reduces population sizes and increases the  
34 likelihood of stochastic extinctions (Allouche et al., 2012). We expect that this unimodal  
35 relationship is particularly fitted to environments where the trade-off between habitat area (or mean  
36 patch area) and heterogeneity is accentuated by the limited space left for nature as in cities. In  
37 Europe, only 18% of urban areas are covered by vegetation, thus reducing the possibility for large  
38 habitat patches (Fuller & Gaston, 2009). Small elements like gardens are a major component of  
39 the green area proportion in many cities (Goddard et al., 2010). In addition to the small size of  
40 green spaces, stakeholders such as public managers and private landowners also promote a  
41 plurality of habitat conditions by dividing them into smaller lots covered by lawns, grasslands,  
42 dense or sparse tree cover and shrub layers in addition to aquatic habitats. The diversification of  
43 land cover types can thus split green spaces into very small fragments.

44 Despite the large diversity of green spaces in European cities, the purposes and practices behind  
45 the creation of land cover mosaics are common standards used by most city managers across the  
46 continent (Kohout & Kopp, 2020). These standards aim to provide people with cultural (e.g.,

47 aesthetics), social (e.g., recreational), economic and health benefits (Muratet & Chiron, 2021)  
48 while conserving urban biodiversity (Muratet et al., 2015). Managers of urban green spaces often  
49 assume that environmental heterogeneity increases species diversity (Aronson et al., 2017). It was  
50 therefore proposed that management actions should endeavour to increase the heterogeneity of  
51 habitat conditions to promote local species diversity (Kati et al., 2010). Based on this overview,  
52 decisions that promote greater heterogeneity in cities might thus lead to unintended results,  
53 especially if the overall size of the urban green spaces is small and species abundance is low.

54 The predicted effects of land cover heterogeneity on birds are unlikely to be uniform across  
55 species. As shown by Allouche et al. (2012), the position of the inflection point, i.e. the level of  
56 heterogeneity that maximizes richness in the unimodal relationship, depends on niche width of the  
57 species. Niche width is also termed “niche or ecological specialisation” (Devictor et al., 2010). If  
58 the patch area is not a limiting factor, land cover heterogeneity may increase richness of specialist  
59 species, and of species that specifically benefit from the juxtaposition of complementary habitats,  
60 such as woody structures for nesting or as shelter and open areas for foraging. On the contrary,  
61 generalists (i.e., species with broader niches) can persist in a wide variety of environmental  
62 conditions across space or time, are less sensitive to reduced habitat patch areas and less prone to  
63 local extinctions (Allouche et al., 2012). Richness of specialists are thus expected to increase with  
64 land cover heterogeneity (at constant patch size area), and with habitat patch size (at constant land  
65 cover heterogeneity) at a higher rate than generalists. In birds, habitat specialist species have lower  
66 dispersal abilities and cannot thrive in human-degraded ecosystems (Clavel et al., 2011). They are  
67 less abundant and decline at a greater rate than generalists along the urbanisation gradient (Guetté  
68 et al., 2017) such that avian specialisation is negatively associated with tolerance to urban stressors  
69 (e.g., pollution, fragmentation, low habitat quality) (Callaghan et al., 2020a). Testing the area–



70 heterogeneity trade-off in urban green spaces in terms of avian diversity and according to the  
71 degree of species urban avoidance is thus particularly relevant. To date, this has not been assessed  
72 in cities. Untangling the relative effects of area and heterogeneity on avian fauna is critical if we  
73 are to design urban green areas that can conserve the most urban-sensitive species.

74 In this study, we first investigated whether there is a trade-off between land cover heterogeneity  
75 and mean patch area in urban green spaces. We predicted a negative correlation between these two  
76 variables. We explored this relationship in six European cities from boreal to Mediterranean  
77 climates. Although landscape design, planting and green space management practices are often the  
78 same across cities, we expected some variations due to the geographical context and size of the  
79 cities in question (Alós Ortí et al., 2022). Second, we tested whether this trade-off shapes the avian  
80 communities and results in the expected unimodal relationship between avian species richness and  
81 land cover heterogeneity in urban green spaces. We predicted a higher bird richness at intermediate  
82 than at low and high heterogeneity levels. Finally, we evaluated the proportion of urban avoider  
83 species in cities, and if and how their traits explain the response of bird richness to mean patch  
84 area and land cover heterogeneity. We expected that urban avoider species (i.e., species that  
85 usually breed in natural or semi-natural habitats but not in human settlements or other artificial  
86 environments) would show a stronger positive relationship with mean patch area, and a stronger  
87 positive relationship with land cover heterogeneity than urban-adapted species, all other variables  
88 being equal.

89

## 90 **2. Methods**

### 91 2.1 Study areas



92 We sampled avian communities in six European cities: Almada and Lisbon (Portugal), Paris  
93 (France), Zurich (Switzerland), Poznan (Poland) and Tartu (Estonia). The selected cities represent  
94 a gradient of latitude and longitude to cover most of the climatic conditions in mainland Europe.  
95 To ensure the consistency of the spatial extent between cities, in some cases we used their full  
96 extent (e.g., Tartu) and in others only a section (e.g., Paris). In all cases, we verified that a density  
97 gradient of urban areas was represented by asking coordinators of the study for each city to select  
98 a spatial extent with low and high proportion of impervious areas (Pinho et al., 2021).

99

## 100 2.2 Sampling site selection

101 To avoid heterogeneity between national databases, we used a pan-European land cover  
102 classification based on the European Urban Atlas (2018), which provides maps for urban areas  
103 across Europe (i.e., minimum mapping unit = 0.25 ha, minimum mapping width = 10 m). For  
104 consistency in land use intensity and typology across Europe, we only used the “Urban Green  
105 Areas” category (hereafter abbreviated UGA, Code 14100 in the Mapping Guide v6.2 for the  
106 Urban Atlas) to select the sampled sites. UGAs are public green areas for predominantly  
107 recreational use such as gardens, parks or castle parks, or forests and other green areas extending  
108 from the surroundings into urban areas.

109 Within the study areas, we selected UGAs according to two independent gradients: 1) UGA size  
110 and 2) structural connectivity with green elements (i.e., UGAs and other areas considered as  
111 favourable land covers for birds such as forest and low urban density with <30% impervious  
112 surface). We calculated the degree of connectivity between green areas using the Proximity Index  
113 (PI) in Fragstats within a 5 km radius from every selected UGA. The PI is the area of all nearby

114 green elements (m<sup>2</sup>) within the selected radius weighted by edge to edge distance squared to a  
115 specific UGA (McGarigal et al., 2012).

116 All possible UGAs were classified in six size classes and six PI classes equally splitted along the  
117 two gradients and similarly across cities to allow comparisons, leading to 36 possible  
118 combinations. Within these combinations and keeping a minimum distance of 500 m between  
119 UGAs (except for two sites in Zurich, and two sites in Tartu separated by 260 m and 170 m  
120 respectively), UGAs were selected randomly. Due to UGAs limitations, we used between 15  
121 (Almada) and 35 (Paris) combinations (total of 176 UGAs, see Table 1 for more details).

122

### 123 2.3 Description of land cover at UGA and landscape levels

124 We computed land cover composition and configuration metrics at the local (within UGAs) and  
125 landscape levels, which were potentially drivers of the avian community.

126 At the local level, we produced a land cover map of each UGA using the photo-interpretation of  
127 high-resolution aerial images (i.e., 0.5 m) from 2015 with ESRI ArcMap 10.4. The photo-  
128 interpretation was performed at a scale of 1:600, allowing us to distinguish between the main land  
129 cover types within green areas (Alós Ortí et al., 2022). We classified land cover into 10 categories  
130 known to influence bird diversity: allotments gardens (i.e. parcels containing cultivated areas with  
131 fruits or vegetables, as well as a shed for tools and shelter), artificial surfaces (i.e. houses, roads  
132 and playgrounds), bare land, coniferous trees, broadleaved trees, lawns and grasslands, lakes and  
133 ponds, riparian vegetation, rivers and streams, and shrubs (Bino et al., 2008). In each UGA, we  
134 mapped all patches of land cover. Aerial images did not allow us to precisely classify the extent  
135 of all land cover types due to the overlapping vertical layers. Therefore, our land cover maps



136 provided accurate information about tree canopy (i.e. the upper layer) and the other layers not  
137 covered by trees. Based on this mapping, we measured UGA total area and the heterogeneity of  
138 land cover categories using Shannon's diversity index (Fahrig et al., 2011). The Shannon index is  
139 the most applied metric to capture the variety and the richness of land use/land cover and its  
140 characteristics in a given extent or spatial unit (Zhang et al., 2023). For UGA land cover  
141 configuration, we calculated mean patch area and contagion index, which measures the degree of  
142 aggregation of the same land cover within each UGA (Riitters et al., 1996). This index is computed  
143 based on the frequencies by which different pairs of land covers occur as adjacent pixels on a map.  
144 To describe land cover composition at the landscape level, we used all land cover classes of the  
145 Urban Atlas and calculated the land cover heterogeneity using Shannon's diversity index in a 500  
146 m buffer distance from the edge of the UGAs. This distance is a good compromise to detect the  
147 maximum landscape effect on diversity and composition of urban bird communities (Melles et al.,  
148 2003; Chang et al., 2017; Villaseñor et al., 2021), while minimizing overlap between buffers and  
149 ensuring independence in landscape analysis (pairwise distances among UGAs were larger than  
150 750 m in 99% of cases, Zuckerberg et al., 2020). Because buffer area depends on the UGA size  
151 and its shape, we controlled for the effect of the buffer area around each UGA on landscape  
152 heterogeneity. We used the residuals of the relationship between the land cover heterogeneity and  
153 buffer area in the statistical analyses. For landscape connectivity, we used the PI as calculated  
154 above (i.e., within a 5 km radius from every selected UGA). Except for the PI, all local and  
155 landscape metrics were calculated in R using the "landscapemetrics" package (Hesselbarth et al.,  
156 2019).

157

158 2.4 Bird sampling

159 In 2019, we counted birds using one point count per UGA, located as close as possible to its  
160 centroid on a location where the main land cover types (trees, bush, grassland, water) are present  
161 in a 50 m radius. In this manner, we collected information on potential bird species living in  
162 different types of land covers.

163 Within each country, we hired an experienced birdwatcher to count birds within 4 hours from  
164 daybreak to standardise the time of sampling along latitudes. Each plot was sampled twice to detect  
165 both more residential and more migratory bird species during the breeding season. First counts  
166 started early April (for Almada and Lisbon) and second counts ended late May (for Tartu and  
167 Poznan) with at least 3 weeks between the two counts for each city. We adapted the sampling day  
168 to the local weather conditions to avoid rain, fog and wind. All observations were conducted on  
169 weekdays from Monday to Friday. UGAs surveyed on the same day had the order of sampling  
170 randomised for the second survey to ensure that the time of the day did not influence species  
171 detection.

172 During each visit, the birdwatcher counted and identified all individuals heard or seen for 10 min.  
173 This duration is a minimum but represents a non-negligible investment of time that we considered  
174 as reasonable to detect a large proportion of bird species at sampling point and estimate bird  
175 responses to main local and landscape drivers (Voříšek, 2008). Birds were counted inside a 100 m  
176 radius area around the observer and within UGA's boundaries. Birds flying over the sampling  
177 point (transients) were recorded separately, as they neither arrived or left the sampled area during  
178 the point count nor clearly indicated their use of the area as a breeding territory. However, flying  
179 birds feeding or hunting in the air (i.e., swifts) were noted as observed within the 100 m radius.  
180 Species richness was the total number of species counted within a 100 m radius during the two  
181 visits for each UGA.



182 We used a constant-area sampling (i.e. inside a 100 m radius area) rather than an area-balanced  
183 approach with more sampling points in the largest UGAs for two reasons. First, we aimed at  
184 understanding influences of variables shaping the area - heterogeneity trade-off without the  
185 influence of sampling effort. Second, replicating count points in large green areas is cumbersome,  
186 demanding a lot of field work if we wanted to cover the full green area extent (e.g. one point count  
187 location for every 250 m by 250 m area). To avoid potential bias due to our sampling strategy, we  
188 verified that counting area (3.14 ha) covered the full extent of most UGAs (63% of them were  
189 smaller than this area) or was representative of the UGA land cover heterogeneity. For UGAs  
190 bigger than 3.14 ha, there was a good correlation in land cover heterogeneities between the UGA  
191 and the counting area levels, and a good correlation in mean patch areas between these two levels  
192 too (Pearson's correlation coefficient  $\rho = 0.77$  and  $0.97$  respectively,  $p < 0.01$ ). Bird sampling was  
193 thus conducted in an area representative of the whole UGAs studied.

194 As ambient noise during bird surveys could influence bird detection, we accounted for in statistical  
195 models (see below). During the first 4 minutes of counting birds, the birdwatcher collected noise  
196 data and measured the maximum sound volume in decibels (dB) in the environment for 1 minute  
197 in each of the four cardinal directions using a digital decibel metre (device Preciva®, measuring  
198 range: 30-130 dB; accuracy:  $\pm 1.5$  dB) set on a tripod at the height of 1 metre. We then calculated  
199 the mean "maximum sound volume" (dBmax) as we surveyed each point twice (temporal  
200 replicate). Any potential noise peak bias during the 1-minute sampling period would be smoothed  
201 by the second survey. Finally, we recorded temperature (in °C) and wind (Beaufort scale) to  
202 exclude potential observations collected during bad weather conditions.

203

204 2.5 Defining avian avoidance in urban areas



205 We built a continuous gradient of urban avian avoidance, which is consistent with the breeding  
206 ecology of species, and integrated a variety of habitat requirements for nesting (Keller et al., 2020).  
207 For that purpose, we used the life-history trait database of Storchová & Hořák (2018), which  
208 compiles information about bird occurrences in 15 nesting habitats: deciduous forest, coniferous  
209 forest, woodland, shrub, savanna, tundra, grassland, mountain meadows, reed, swamps, desert,  
210 freshwater, marine, rocks and human settlements. This information was derived from *The Birds of*  
211 *the Western Palearctic* handbook (Cramp, 2006) and covers most bird species breeding in the  
212 Western Palearctic. Habitat occurrences for four species (*Anser anser*, *Bubulcus ibis*, *Egretta*  
213 *garzetta*, *Nycticorax nycticorax*) are missing from Storchová & Hořák (2018). We removed them  
214 from the habitat preference analysis and regression models using this information. We then carried  
215 out principal component analysis (PCA function, R package FactoMineR; Husson et al., 2007)  
216 using information about bird occurrences in each nesting habitat. We evaluated the multivariate  
217 relationships between species coordinates on principal components and habitat variables to define  
218 the avian avoidance of urban areas (see Results).

219 Our approach differs from using expert knowledge to define species preferences to cities. Expert-  
220 based knowledge is valuable, but species ranking along a gradient of urban avoidance may vary  
221 between experts or countries, leading to oversimplified categories (“urban dweller” vs “urban  
222 avoider”). Even though Callaghan & colleagues (2020b) previously estimated urban avoidance for  
223 European birds, we could not use their database because 25 species included in our study were  
224 missing from it (21% of the total number found here).

225

## 226 2.6 Statistical analyses

### 227 2.6.1 Trade-offs between mean patch areas and land cover heterogeneity of UGAs

228 To evaluate the area-heterogeneity trade-offs in our study area, we fitted a linear mixed model with  
229 “UGA land cover heterogeneity” (Shannon’s index) and “UGA total area” (log-transformed) as  
230 predictors of “UGA mean patch area” (log-transformed) (R package lme4; Pinheiro et al., 2021).  
231 In this model, we used the whole dataset, i.e. all cities, and added “city” as a random factor to  
232 account for the nested design of the study (Zuur et al., 2009). To assess the robustness of these  
233 relationships at the city level, we separately repeated the analysis for each city using a linear model  
234 and the same predictors.

235

#### 236 2.6.2 Local and landscape effects on bird richness

237 We built a generalised linear mixed model using a Poisson family (glmer, R package lme4;  
238 Pinheiro et al., 2021) with “UGA land cover heterogeneity” and its squared value as predictors of  
239 avian richness to test for non-linear effect of the area–heterogeneity trade-off. As fixed effects, we  
240 added other variables that might influence birds: “land cover heterogeneity of landscape”  
241 (Shannon’s diversity), “UGA total area” (log-transformed), “UGA mean patch area” (log-  
242 transformed) and “proximity index”. We included as a potentially confounding variable  
243 “maximum sound volume” (dBmax). We did not include the “UGA contagion index” from the list  
244 of predictors as it was significantly correlated with “UGA land cover heterogeneity” (Pearson’s  
245 correlation coefficient  $\rho = -0.72$  with p-value  $< 0.01$ ; Appendix H). We used the whole dataset and  
246 added “city” as a random factor. Additionally, we repeated this analysis for each city separately  
247 using generalised linear models (glm) with the same predictors.

248



249 2.6.3 Influence of urban avoidance on the response of species richness to local and landscape  
250 variables

251 Based on the PCA, we assigned each bird species to a coordinate on the second component (PC2)  
252 representing their level of urban avoidance (Appendix A). We then categorised species into three  
253 terciles corresponding to minimum, intermediate and high values of urban avoidance along PC2.  
254 To define terciles, we didn't equally split the urban avoidance gradient because species number  
255 would have been very unbalanced making statistical analysis problematic. Our splitting minimises  
256 species number differences among terciles which resulted in 37, 45 and 33 species for minimum,  
257 intermediate and high values of urban avoidance respectively.

258

259 For all UGAs, we calculated the avian richness of terciles as the number of species belonging to  
260 each urban avoidance tercile, and used it as the response variable in a glmer using a Poisson family.  
261 As fixed effects, we included "UGA land cover heterogeneity" and its squared value to test for its  
262 non-linear effect, "UGA total area" (log-transformed), "UGA mean patch area" (log-transformed),  
263 "urban avoidance tercile", "proximity index", "land cover heterogeneity of landscape" and  
264 "maximum sound volume". We incorporated the interactive effects between tercile group and  
265 "UGA land cover heterogeneity", and between tercile group and "mean patch area" into the model  
266 to assess the effect of urban avoidance on the response of species richness to UGA variables. We  
267 added "city" as a random factor to account for the nested design of the study. Finally, we computed  
268 a chi-squared ( $\chi^2$ ) test on the response variable (i.e., avian richness of terciles) to assess variability  
269 in the distribution of tercile avian richness between cities.

270 Prior to fitting the models described above, we standardised the explanatory variables by  
271 subtracting the mean and dividing by the standard deviation. We assessed statistical significance

272 using the ‘Anova’ function (type II, with  $\chi^2$  and Z statistics for the Poisson and Gaussian families,  
273 respectively) and performed Tukey HSD post-hoc tests (‘TukeyHSD’ function) to compare avian  
274 richness between cities and terciles.

275 To check for multicollinearity between explanatory variables, we computed variance inflation  
276 factors (VIF) using *check\_collinearity* function (R package performance). To alleviate moderate  
277 level of multicollinearity (VIF < 4) between some explanatory variables (Zuur et al., 2009), we  
278 then applied a hierarchical partitioning procedure (R packages ‘hier.part’ for glm and ‘partR2’ for  
279 glmer) to obtain independent contribution of each explanatory variables based on semi-partial  $R^2$   
280 and quantified its uncertainty using parametric bootstrapping (Walsh & McNally, 2008; Stoffel et  
281 al., 2021). For all models, we statistically verified that the residuals met the assumptions of  
282 homoscedasticity and normality using DHARMA package (Hartig, 2021). For Poisson models,  
283 absence of residuals’ overdispersion was checked (“testDispersion” function). We also graphically  
284 confirmed the spatial independence of the residuals by computing a spline correlogram using the  
285 ‘spline.correlog’ function (package ncf; Bjørnstad, 2019). Graphs were generated using “ggplot2”  
286 package in R (Wickham, 2019; version 3.3.3). All analyses were performed in R version 4.1.2 (R  
287 Core Team, 2021).

288

### 289 **3. Results**

290 In total, we recorded 119 nesting bird species (7523 individuals) in the 176 green areas studied  
291 across the six European cities (see the list of species in Appendix B). Mean bird richness per UGA  
292 was 14.7 species (between 4 and 28, Table 1).

293

### 294 3.1 Relationships between mean patch area, UGA land cover heterogeneity and avian richness

295 Results from our linear models (Appendix C) confirmed a significant area-heterogeneity trade-off  
296 in urban green areas, as mean patch area in UGAs was negatively associated with land cover  
297 heterogeneity (Appendix I). Additionally, mean patch area was positively associated with UGAs'  
298 total area, as expected. These relationships were consistent across cities.

299 Species richness was positively correlated with UGA total area and land cover heterogeneity at the  
300 landscape level (Figs. 2b-c). Contrary to our prediction and after controlling for effects of these  
301 two latter variables we found no effect of UGA land cover heterogeneity on avian species richness  
302 (neither linear nor unimodal) in a model combining all cities (Appendix D, Figs. 2a). At city level,  
303 we found a unimodal relationship between land cover heterogeneity and avian richness for Zurich  
304 only (Appendix E).

305

306

### 307 3.2 Continuum of urban avoidance trait in birds

308 Based on the trait database of Storchová & Hořák (2018), we found that the birds encountered in  
309 UGAs have nesting habitats encompassing all categories found in Europe from marine and coastal  
310 habitats to swamps and forests, with the exception of deserts. The most frequent habitats occupied  
311 by the observed bird species were deciduous forests (56 sp.), coniferous forests (41 sp.) and human  
312 settlements (35 sp.). The vast majority of species occupied different habitat types (2.6 on average),  
313 although 17 species (14%) were attributed to a single habitat. Among them, two species nest only  
314 on human settlements (*Streptopelia decaocto* and *Alopochen aegyptiaca*), making them strict  
315 urban dwellers (Fischer et al., 2015).



316 The PCA for the nesting habitat trait revealed three principal components, which explained 20.0%,  
317 14.2% and 11.1% of the total variance, respectively (Figs. 3a-b, Appendix F). The first axis (PC1)  
318 separated forest and woodland species from marine and freshwater species (“forest-grassland and  
319 aquatic species” gradient). The second axis (PC2) separated species of human settlements and  
320 rocks from those living in reeds, swamps, shrubs and tundra, thus representing a gradient of “avian  
321 avoidance of urban areas”. Finally, the third axis (PC3) did not show any clear pattern; it will not  
322 be discussed further.

323 To assess the robustness of PC2 as an index of urban avoidance, we correlated it with a continuous  
324 measure of urban tolerance (i.e., “urban score”) calculated based on the eBird observations of bird  
325 occurrences along a gradient of urbanisation in Europe (Callaghan et al., 2020b). This score was  
326 calculated as the distributional response of species to VIIRS night-time lights, a proxy of human  
327 population density and urbanization. Although some species were lacking from the urban score  
328 (21% of our species list), the two indices were negatively correlated (Pearson’s correlation  
329 coefficient  $\rho = -0.45$  with  $p\text{-value} < 0.001$ ), thus validating the use of PC2 as an urban avoidance  
330 index. Our measure extended the calculation of urban avoidance to 25 other species in European  
331 cities.

332

### 333 3.3 Avoider species and their variation among cities

334 Based on PC2 coordinates (Fig. 3b), we grouped species into three terciles. Tercile 1 (PC2: -3.2 to  
335 -0.69, 37 species, low urban avoidance) consisted of urban dweller species such as *Columbia livia*,  
336 *Streptopelia decaocto* and *Apus apus* that nest on man-made structures, and urban utiliser species  
337 such as *Corvus corone* and *Columba palumbus* that are so-called generalist species. Tercile 2 (PC2:  
338 -0.69 to 0.11, 45 species, medium urban avoidance) grouped avoider species such as *Dryocopus*

339 *martius* and *Buteo buteo* that usually nest outside developed urban areas in forest patches but can  
340 self-sustain populations in large contiguous UGAs. This tercile also included a few urban utilisers  
341 like *Turdus merula* and *Anas platyrhynchos*. Tercile 3 (PC2: 0.11 to 5.65, 33 species, high  
342 avoidance) was composed of aquatic (e.g., *Remiz pendulinus*, *Cettia cetti*, *Acrocephalus*  
343 *schoenobaenus*) as well as shrub and grassland species (e.g., *Lullula arborea*, *Hippolais icterina*),  
344 which very rarely occur in urban areas. Although such species are generally absent from developed  
345 areas, they may persist in networks of natural areas embedded in an urban matrix (Fischer et al.,  
346 2015).

347 The number of species in the three terciles varied among cities ( $\chi^2= 39.18$ ,  $df = 10$ ,  $p\text{-value}<0.001$ ).

348 The proportion of species belonging to the high avoidance group (Tercile 3) was higher in Poznan  
349 and Tartu (28% of species) than in Zurich, Almada, Paris and Lisbon (between 10% and 18%, Fig.  
350 4, Appendix G).

351

352 3.4 Influence of urban avoidance on the response of species richness to local and landscape  
353 variables

354 We found significantly contrasting responses of species richness to mean patch area of UGA  
355 depending on the level of urban avoidance, shifting from negative for species associated with  
356 human settlements (Tercile 1, low avoidance) to positive for urban avoider species (Terciles 2 and  
357 3 for medium and high avoidance groups respectively, Fig. 5a, Table 2). We found similar  
358 relationships regarding the species richness response to land cover heterogeneity of UGA  
359 depending on the level of urban avoidance of birds. Relationships gradually shifted from negative  
360 to positive between species associated with human settlements (Tercile 1) and urban avoider  
361 species (Terciles 2 and 3) (Fig. 5b, Table 2). Variance contribution of UGA land cover



362 heterogeneity (including its interactive effect with urban avoidance level) to species richness  
363 variation ( $R^2=0.031$ , Table 2) was however lower than contribution of UGA mean patch area  
364 ( $R^2=0.056$ , Table 2).

365

## 366 **4. Discussion**

### 367 4.1 Area–heterogeneity trade-off and their effect on avian richness

368 Our results highlight that the mean patch area and land cover heterogeneity of UGAs are not  
369 independent factors: as heterogeneity increases, land cover patch size decreases. This pattern is the  
370 consequence of dividing UGA area into different land cover types (i.e., heterogeneity of  
371 composition) and the same land cover into small fragments (i.e., heterogeneity of configuration or  
372 fragmentation). This relationship was consistent across cities and confirms that despite the  
373 “manipulated nature” of UGAs, their design is governed by the same rules as in less human-  
374 dominated environments (Parris, 2018). The area–heterogeneity trade-offs thus apply to urban  
375 landscapes, which underscores the need to study patch area and land cover heterogeneity in the  
376 same framework of analysis if we want to disentangle their roles in avian diversity.

377 Contrary to our expectations, we found neither positive nor unimodal relationships between land  
378 cover heterogeneity and avian species richness within UGAs, as proposed by Allouche et al.  
379 (2012). Despite the different approaches used for measuring the heterogeneity of local conditions  
380 in UGAs (e.g., through land cover richness, vegetation structure or its complexity, presence of  
381 microhabitats), empirical studies generally observed a positive correlation between heterogeneity  
382 and species richness (Husté et al., 2006; Nielsen et al., 2014; González-Oreja et al., 2012). This  
383 relationship was illustrated for various taxonomic groups such as plants, birds, mammals and

384 reptiles (Cornelis & Hermy, 2004; Garden et al., 200 ; Matthies et al., 2017). In these studies, part  
385 of the species-heterogeneity relationships can be attributed to larger parks that tend to harbour a  
386 greater number of habitat units (e.g., lawn, forest, pond, etc.) and hence greater species richness  
387 than smaller ones (Cornelis & Hermy, 2004), but this relationship was also found in small parks  
388 (between 0.1 and 2 ha in Pachuca city, Mexico, Carbó-Ramírez & Zuria 2011). Controlling the  
389 effect of land cover heterogeneity by UGA area (total or mean patch size) in our study should thus  
390 not entirely explain the gap between our results and previous studies.

391 The species-heterogeneity relationship is an essential element of niche-based theories of species  
392 diversity and a key concept of the unimodal relationship presented by Allouche et al. (2012):  
393 environmental heterogeneity should provide suitable conditions for a larger number of species with  
394 different ecological requirements, thereby increasing the local species pool (Chase & Leibold,  
395 2003). No relationship with heterogeneity may result from the reduced land cover diversity in the  
396 studied UGAs, which hampered our ability to detect changes in avian communities. This is  
397 unlikely because our sampling clearly evidenced variability in the land cover types (Table 1). The  
398 absence of a relationship might also arise from the relatively limited occurrence of key habitats  
399 such as aquatic environments. The occurrence of waterbodies such as lakes, ponds, river streams  
400 and riparian habitats has plummeted in urban ecosystems due to significant degradation from  
401 drainage and changes in the hydrological regimes of cities (Moggridge et al., 2014). In our  
402 sampling, these environments were underrepresented compared with terrestrial ones. However,  
403 34% of sampled species (n=40) were associated with one or several aquatic habitats, thus  
404 indicating that these species were not absent from our sampling.

405 Finally, birds may only occupy a few patches among those accessible for nesting in UGAs, thus  
406 making the relationship between bird richness and land cover heterogeneity inaccurate at the UGA



407 level. For instance, ground nesting birds rarely reproduce in open urban habitats like lawns and  
408 grasslands because of multiple threats, which could affect the behaviour, reproduction and survival  
409 of chicks and adults (e.g., higher disturbance caused by pedestrians, domestic animals, or  
410 management actions like grass cutting, (Fernandez-Juricic & Jokimäki, 2001)). In urban  
411 woodlands, cleared understory vegetation (no shrub or herbaceous vegetation layers, and dead  
412 wood being removed) may increase disturbances and predation risks and limit food availability  
413 (Crocì et al., 2008).

414 Avian richness was positively influenced by the total area of UGAs. Larger UGAs increase the  
415 effective area available for individual species, thereby increasing population sizes and decreasing  
416 the likelihood of stochastic extinctions (Allouche et al., 2012). Our results confirmed the species-  
417 area relationship: a well-known pattern already observed in birds, mammals and plants within  
418 UGAs and in more natural ecosystems (Nielsen et al., 2014; Matthies et al., 2017). Interestingly,  
419 avian richness also increased with land cover heterogeneity in the neighbouring landscape. The  
420 land cover heterogeneity of the adjacent matrix is related to the diversity of terrestrial and aquatic  
421 natural habitats. Birds nesting in these habitats may spill over into UGAs and use them as foraging,  
422 nesting or refuge sites (Mayorga et al., 2020).

423

424 4.2 Urban avoider species richness is greater in large and diversified green patches of land covers

425 The share of urban avoider species (terciles 2 and 3) in terms of species richness was greater in  
426 urban green areas with large land cover patches than in small ones. Richness of urban avoiders can  
427 simply be explained by habitat preferences and distribution of selected habitats among small and  
428 large green patches.. Also, urban avoiders are less able to persist in small habitat patches (high  
429 edge-to-area ratio), because they prefer the interior of large patches, similar to many specialists of



430 forest and aquatic ecosystems (Fernandez-Juricic, 2001). Within-patch habitat quality is unlikely  
431 to be constant as UGA size and heterogeneity change. On the contrary, the number of urban  
432 adapted species (tercile 1, urban dwellers and utilisers) decreased with patch size within UGAs.  
433 Urban dwellers can persist in urban environments independently of the natural areas, while urban  
434 utilisers can exploit resources supplied by human activities (Fischer et al., 2015). The latter can be  
435 widely distributed and locally abundant in cities (Ducatez et al., 2018). Being mostly generalist,  
436 they can thrive in fragmented environments, because they are able to nest and feed in various  
437 environments.

438 Competitive interactions between urban adapted and avoider species may also explain these  
439 relationships. Urban adapted species may gradually disappear in large natural patches to avoid  
440 increasing competition with urban avoiders, which are specialist birds (Staute et al., 2021). This  
441 process could partly explain the segregation of habitat specialist and generalist birds between large  
442 and small patches. In small and fragmented patches, urban adapted birds can be widespread and  
443 behaviourally dominant species (Ducatez et al., 2018). They can also exclude rarer and more  
444 subordinate species such as urban avoiders through competitive interference (Martin & Bonier,  
445 2018).

446 Although we did not find any effect of land cover heterogeneity of UGAs on total avian richness,  
447 we evidenced its positive effect on the richness of urban avoider species. Because these latter are  
448 often habitat specialists, land cover heterogeneity can provide the suitable conditions for more  
449 species with different ecological requirements, thereby increasing their local species pool (Chase  
450 & Leibold, 2003). Since land cover heterogeneity is negatively correlated with mean patch area of  
451 UGAs, effect of land cover heterogeneity on urban avoider species cannot be analysed apart from

452 the effect of mean patch size. We thus revealed a trade-off on species richness depending on  
453 species urban tolerance.

454

#### 455 4.3 Relevance of green space design for bird conservation

456 We reported a relatively rich bird diversity (21% of European breeding bird species, Keller et al.,  
457 2020), thus making UGAs relevant areas for bird conservation. Most of these areas correspond to  
458 parks, renowned as urban biodiversity hotspots (Nielsen et al., 2014). It was therefore crucial to  
459 understand how designing UGAs for nurturing a diversity of bird species. Achieving this target is  
460 the result of a compromise between land cover surface area and its heterogeneity.

461 Although a recent analysis on the importance of natural areas recognised the value of small spaces  
462 for biodiversity conservation (Riva & Fahrig, 2022), we highlight the necessity to put effort into  
463 protecting large UGAs composed of big enough land cover patches to conserve bird richness.  
464 Compared to small patches, large areas provide better protection for urban avoiders, which are  
465 most at risk globally (Clavel et al., 2011). Even though small green areas such as woodlots and  
466 public or private gardens are widespread and sometimes the only natural areas in cities, large areas  
467 are scarce and regularly exposed to urban development pressure (Fuller & Gaston, 2009).

468 Land cover diversification of UGAs (e.g., mixing woodlots, grasslands, waterbodies, and so on.)  
469 may increase the potential number of ecological niches and hence species richness of local  
470 assemblages (Callaghan et al., 2019). Restoring or protecting different land cover types is  
471 achievable in large UGAs where space is not a limiting resource compared to smaller ones. In  
472 small UGAs however, land cover diversification should not be regarded as a panacea by urban  
473 planners (Kati et al., 2010) because it could lead to a drastic reduction in the average amount of a



474 given habitat and its effective area available for specialist birds or birds that exploit complementary  
475 habitats. This may unintendedly reduce the occurrence of the most endangered species in cities.  
476 For birds, a minimum area of 4.4 ha and of 53.3 ha were described to prevent the loss of urban  
477 adapters and of area-sensitive species like urban avoiders (Beninde et al., 2015). We thus  
478 recommend limiting land cover heterogeneity on small UGAs to maintain green patches as large  
479 as possible.

480 To optimize biodiversity at city level, activities of design and management should be coordinated  
481 all across a city. Actions should diversify ecological conditions across green areas and not just  
482 within. In small areas, maximizing the coverage of a specific habitat type but different across  
483 UGAs would maintain urban avoiders populations in local species assemblages and enhance beta-  
484 diversity. Actions should target ecological context from which UGAs are originate to preserve  
485 their uniqueness as city tend to homogenize local conditions (Groffman et al., 2014). Although  
486 this could work for biodiversity, designing UGAs dominated by a few land cover types in small  
487 UGAs could be negatively perceived by users if it does not take into consideration preference of  
488 people for some green area characteristics (e.g. presence of open areas, playgrounds, flowerbeds,  
489 waterbodies, tree cover, see Palliwoda and Priess, 2021 and Madureira et al., 2018). A key  
490 challenge for UGA design is thus combining human needs with ecological requirements for  
491 preserving and enhancing avian communities especially green area sensitive species.

492 Finally, our study pointed out the importance of maintaining a variety of land cover types in the  
493 urban matrix surrounding green areas, which appears to be as important as within UGA  
494 heterogeneity for conserving local bird assemblages. The ongoing urban densification process  
495 observed in some European cities (Li et al., 2022) can thus pose a threat by reducing land cover  
496 diversity (e.g. through the loss of private gardens or rare habitats) and richness of bird species in



497 UGAs. Conservation strategies should thus promote actions at the city level to conserve land cover  
498 heterogeneity and high quality habitats closed to public green areas.

499

## 500 **5. Conclusions**

501 We evidenced the marked land cover area-heterogeneity trade-off in urban green areas. We showed  
502 the predominant role of green area size on avian richness. Urban avoiders thrive in urban green  
503 areas with large and heterogeneous patches but are at risk in smaller ones unless they exhibit large  
504 habitat patches. We suggest the importance of coordinating design and management actions at the  
505 city levels across green areas to optimise bird conservation depending on UGA size and their  
506 heterogeneity level. We also highlight the need to confront ecological theories with empirical data  
507 across different bioclimatic zones to better understand urban ecosystems and advise stakeholders  
508 with robust and ecologically informed knowledge.

509 Our study opens the door to future research questions. We intentionally used a trait to quantify  
510 species preference to urban habitats and indirectly to the notion of habitat specialisation, which  
511 lies at the heart of niche theory. To go further, future research should investigate the species  
512 colonisation/extinction processes in land cover patches. For this purpose, long-term studies are  
513 required on persistence across small patches versus large ones (or across homogeneous versus  
514 heterogeneous). Also, the role of species interaction in the distribution of urban generalists and  
515 specialists (avoiders) along a urban gradient remains to be explored. Whether the increase in  
516 generalists is due to the relaxed interspecific competition from specialist species is unknown.  
517 Although our study assessed the trade-off in different biogeographical contexts, whether the area-  
518 heterogeneity relationship hold true in more specific environments (e.g. aquatic or terrestrial) has  
519 not yet been explored.

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## List of tables

**Table 1:** Summary table of the urban green areas (UGAs) and landscape areas in the six cities investigated in this study as well as the avian species richness expressed as mean, minimum and maximum values. Land cover heterogeneity of UGAs and landscapes corresponds to the Shannon diversity index of habitat types respectively within UGAs (i.e., ten land cover categories) and within a 500-metre buffer around the UGAs (i.e., land use categories of the Urban Atlas). The contagion index measures the degree of aggregation of the same land cover within each UGA. dBmax is the maximum number of decibels in the environment (dBmax) during bird counts in each UGA. The proximity index measures the degree of green area isolation and is the sum of the area of all nearby green spaces divided by the square of the distance to the focal green area. Climate data were collected for the variables of temperature (Mean temp.) and precipitation (Annual prec.) between 1991 and 2021 and are issued from the European Centre for Medium-Range Weather Forecasts (ECMWF, source [www.ecmwf.int](http://www.ecmwf.int), access 23/06/2022). All coordinate data for the cities are taken from the OpenStreetMap project (source <https://www.openstreetmap.fr>, access 23/06/2022).

**Table 2:** Results of regression model analysing the influence of urban avoidance (tercile groups) on the response of species richness to local variables of UGAs and landscape (500 m buffer around each urban green area, UGA) across the six cities. Our model controlled for maximum noise (dBmax) and included 'city' as random effect to account for possible consistent differences among cities. (UGA land cover heterogeneity)<sup>2</sup> is the squared term of UGA land cover heterogeneity to test for a non-linear relationship. We reported the slope estimate, its standard error (Std. Error), degree of freedom (df), the p-value (model without the interaction effect), and semi-partial R<sup>2</sup> (part R<sup>2</sup>) values that provide an estimate of the variance explained by a fixed effect independent of other predictors. Total variance explained by the model was 0.692 (Marginal R<sup>2</sup> value). Significant variables are highlighted in bold in the table (\*p<0.05, \*\*p<0.01, \*\*\*p<0.001). Statistical tendencies (0.050<p<0.010) are followed by a full stop (.).



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City	Number of UGAs	Urban green area mean (min;max)					Landscape (500 m) mean (min;max)		City climate		City coordinates		Species richness mean (min;max)	
		Area (ha)	Mean patch area (ha)	Land cover heterogeneity	Number of habitat types	Contagion index	dBmax (decibels)	Land cover heterogeneity	Proximity index	Mean temp. (°C)	Annual prec. (mm)	Longitude (deg.)		Latitude (deg.)
Almada	15	6.7 (0.4;43.2)	0.1 (0.02;0.36)	1.2 (0.4;1.8)	5.3 (2;10)	59.8 (48.5;68.7)	64.9 (60.1;71.1)	1.6 (1.2;2.0)	3.1 (0.2;10.0)	16.5	591	38°40'00"N	9°9'00"W	14.5 (9;22)
Lisbon	31	5.3 (0.4;31.4)	0.2 (0.03;0.70)	1.1 (0.1;1.7)	5.0 (2;8)	61.1 (49.8;88.3)	66.9 (61.6;81.9)	1.7 (1.1;2.0)	2.8 (0.4;9.1)	16.7	591	38°43'N	9°08'W	14.6 (4;22)
Paris	35	3.2 (0.2;18.5)	0.1 (0.02;0.42)	0.9 (0.4;1.7)	4.6 (2;7)	63.4 (43.4;83.7)	67.9 (52.9;119.0)	1.4 (0.7;2.0)	3.4 (0.5;9.5)	11.7	720	48°51'24"N	2°21'07"E	12.6 (6;19)
Poznan	32	7.8 (0.4;108.7)	0.2 (0.03;2.41)	0.9 (0.3;1.3)	4.3 (2;8)	63.0 (44.9;88.4)	68.9 (59.7;72.8)	1.6 (0.8;2.1)	3.8 (0.7;9.4)	9.7	649	52°24'00"N	16°55'00"E	18.3 (10;28)
Tartu	32	5.3 (0.3;32.0)	0.4 (0.03;3.48)	0.8 (0.0;1.4)	4.6 (1;7)	68.7 (50.1;100)	69.9 (49.5;64.2)	1.7 (1.2;2.0)	2.9 (0.6;6.4)	6.4	727	58°22'44"N	26°43'12"E	14.6 (8;23)
Zurich	31	3.8 (0.2;28.2)	0.1 (0.02;0.14)	1.1 (0.2;1.4)	4.8 (3;7)	60.5 (48.9;86.0)	70.9 (54.4;70.2)	1.8 (1.5;2.3)	4.1 (1.5;10.2)	9.7	1460	47°22'40"N	8°32'28"E	13.8 (6;18)

Table 2: Results of regression model analysing the influence of urban avoidance (tercile groups) on the response of species richness to local variables of UGAs and landscape (500 m buffer around each urban green area, UGA) across the six cities. Our model controlled for maximum noise (dBmax) and included ‘city’ as random effect to account for possible consistent differences among cities. (UGA land cover heterogeneity)<sup>2</sup> is the squared term of UGA land cover heterogeneity to test for a non-linear relationship. We reported the slope estimate, its standard error (Std. Error), degree of freedom (df), the p-value (model without the interaction effect), and semi-partial R<sup>2</sup> (part R<sup>2</sup>) values that provide an estimate of the variance explained by a fixed effect independent of other predictors. Total variance explained by the model was 0.692 (Marginal R<sup>2</sup> value). Significant variables are highlighted in bold in the table (\*p<0.05, \*\*p<0.01, \*\*\*p<0.001). Statistical tendencies (0.050<p<0.010) are followed by a full stop (.).

Predictor of species richness	Estimate	Std. Error	Chisq-value	df	p-value	part R <sup>2</sup>
(Intercept)	1.980	0.123	40.240	1	<b>&lt;0.001***</b>	
Mean patch area (log)	0.064	0.045	2.070	1	0.150	<0.001
UGA total area (log)	0.103	0.036	8.385	1	<b>0.004**</b>	0.004
UGA land cover heterogeneity	0.021	0.031	0.043	1	0.510	<0.001
(UGA land cover heterogeneity) <sup>2</sup>	-0.012	0.015	0.732	1	0.392	<0.001
Proximity index	0.003	0.021	0.018	1	0.893	<0.001
Landscape land cover heterogeneity	0.056	0.024	5.519	1	<b>0.019*</b>	<b>0.005</b>
dBmax	-0.050	0.028	3.346	1	0.067.	0.005
Urban avoidance			527.052	2	<b>&lt;0.001***</b>	<0.001
Tercile 1	1.980	0.123				
Tercile 2	-0.338	0.042				
Tercile 3	-1.424	0.062				
UGA land cover heterogeneity: Urban avoidance			6.390	2	<b>0.041*</b>	<b>0.031</b>
UGA land cover heterogeneity (tercile 1)	-0.020	0.040				
UGA land cover heterogeneity (tercile 2)	0.060	0.046				

	UGA land cover heterogeneity (tercile 3)	0.166	0.067			
Mean patch area (log): Urban avoidance				19.925	2	<0.001***
	Mean patch area (log) (tercile 1)	-0.045	0.049			<b>0.056</b>
	Mean patch area (log) (tercile 2)	0.182	0.049			
	Mean patch area (log) (tercile 3)	0.242	0.070			



**Figure 1:** Area–heterogeneity trade-offs in urban ecosystems.

When the urban green area (UGA) is limited (urban parks are perfect examples of such non-extensible zones), the area–heterogeneity trade-off (a) describes the decrease in the area of various land covers expected with an increase in land cover heterogeneity (i.e., compositional heterogeneity) (Allouche et al., 2012). For example, starting from a green space area ‘A’ with two equally distributed land covers (black and dark grey squares;  $A/2$  each), increasing land cover heterogeneity to four land cover types decreases the area of each one ( $A/4$  in this example). (b) In our sample of 176 UGAs from six European cities (see their distribution on the inserted map; Lisbon and Almada overlap at this scale), we can empirically confirm the expected relationship displayed in (a). Note that the y-axis in (b) is the area of land covers of a given UGA standardised by its total area, which accounts for variability in the sampled UGAs (i.e., the relationship in (a) is expected at a constant area). (c) Theoretically, while compositional heterogeneity is independent from configurational heterogeneity [6], both co-occur in European UGAs. Thus, the reduction in patch area (i.e., measure of configurational heterogeneity) for all the types of land cover present here occurs when land cover heterogeneity (i.e., compositional heterogeneity) increases. (d) This is verified by the relationship displayed in (c) in the studied urban green areas. Note that the y-axis in (d) is the mean patch size of a given UGA divided by its total area to account for variability in our UGAs (i.e., the relationship in (c) is expected at constant area). (e) Land cover heterogeneity allows for the colonisation of new species adapted to the newly available niches. Concurrently, the decreasing area of each land cover type (see (a-b)) can push species to local extinction, and species requiring the largest effective area of a given land cover are at the highest risk (Allouche et al., 2012 ; Ben-Hur & Kadmon, 2020). (f) The area–heterogeneity trade-off thus leads to the hypothesis that species richness has a unimodal response to land cover heterogeneity: when reaching the level of heterogeneity at which extinction and colonisation are equal, further land cover diversification decreases species richness. The exact types of relationships depicted here (a, c, d, e) can differ depending on the studied ecosystem and species (Ben-Hur & Kadmon, 2020), as illustrated by the differences between panels (a) vs (b) and (c) vs (d). While the area–heterogeneity trade-off and its implications are still under debate (Carnicer et al., 2013), here we investigate whether the area–heterogeneity trade-off holds true in UGAs, leading to a unimodal response of species richness in avian communities to land cover heterogeneity.

**Figure 2:** Effects of urban green area (UGA) and landscape (500 m buffer around each UGA) variables on species richness of avian communities for all cities (a). We computed the estimates and confidence interval (CI) based on the regression models presented in Appendix D. (UGA land cover heterogeneity)<sup>2</sup> is the squared term of UGA land cover heterogeneity. dBmax is the maximum sound volume during bird counting. We provide estimated mean relationships between species richness and total area of UGAs (b ;  $P=0.004$ ) and landscape land cover heterogeneity of UGAs (c ;  $P=0.020$ ). We used different dot shapes for each city: Pa, Ta, Lx, Po, Al and Zu stand for the cities of Paris, Tartu, Lisbon, Poznan, Almada and Zurich, respectively.

**Figure 3:** Principal component analysis with (a) variables and (b) individuals (i.e., species coded as the first three letters of the genus and species; see Appendix A for a summary of the species names) with regard to nesting bird habitat preferences. This analysis positioned the species along a gradient of urban avoidance on PC2 from low avoidance (low value) to high avoidance (high value). The blue colour gradient indicates the contribution of variables to PC1 and PC2 (a), and the different colours in (b) indicates the species according to terciles 1 (low urban avoidance; green), 2 (medium urban avoidance; orange) and 3 (high urban avoidance; purple).

**Figure 4:** Avian species richness for the different levels of avian urban avoidance (terciles) in the six cities. For each city, we pooled the bird species belonging to terciles 1 (low avoidance; green), 2 (medium avoidance; orange) and 3 (high avoidance; purple). We ordered the cities according to the total number of species from the least to the most. We provided the proportion of species per tercile in white.

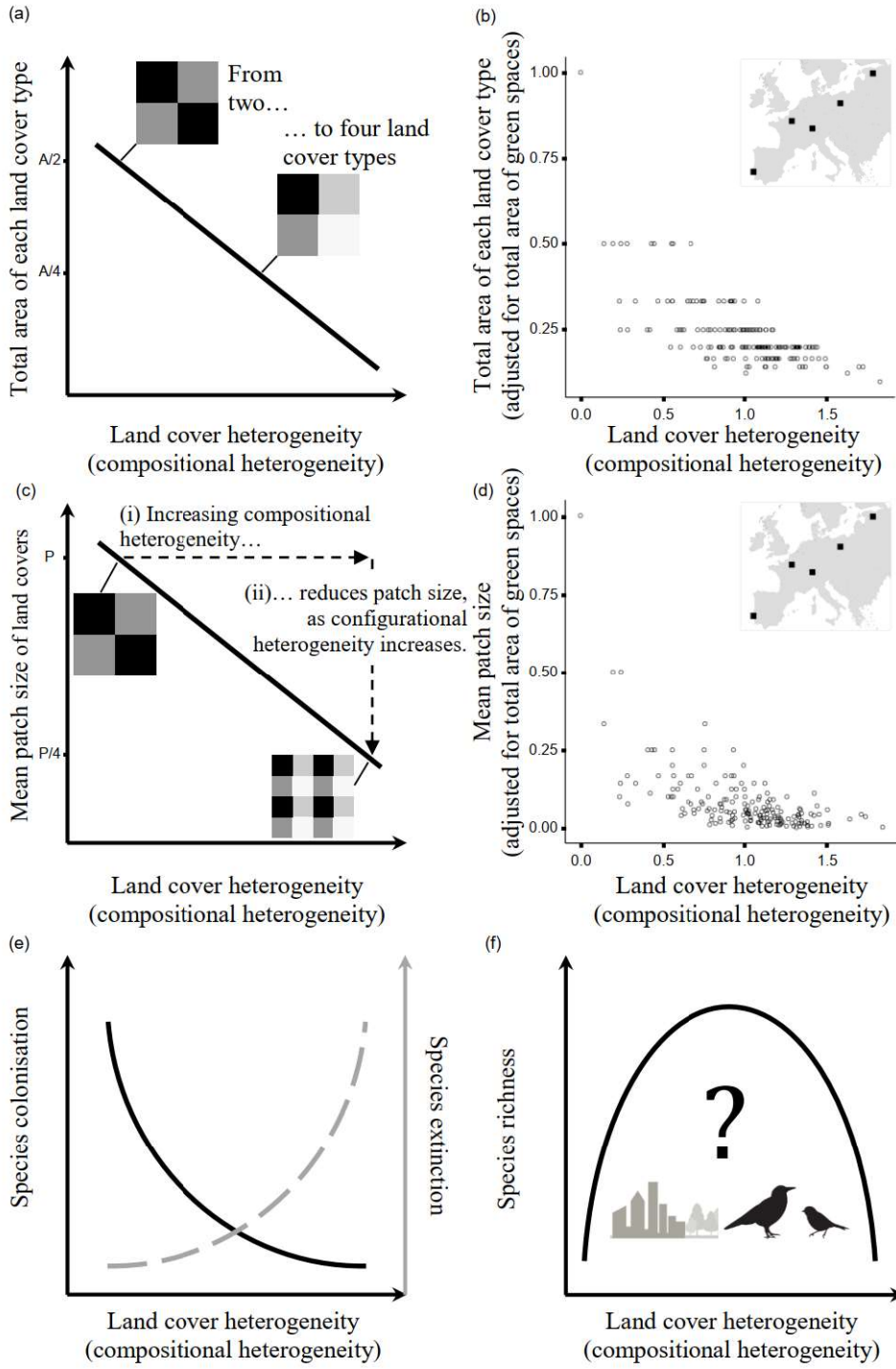
**Figure 5:** Responses of species richness to the mean patch area (a) and land cover heterogeneity of UGAs (b) according to the level of avian urban avoidance: low urban avoidance (green, tercile 1), medium avoidance (orange, tercile 2) and purple (high avoidance, tercile 3). Grey shaded bands indicate are 95% confidence intervals estimated from the generalized linear mixed model (Table 2).



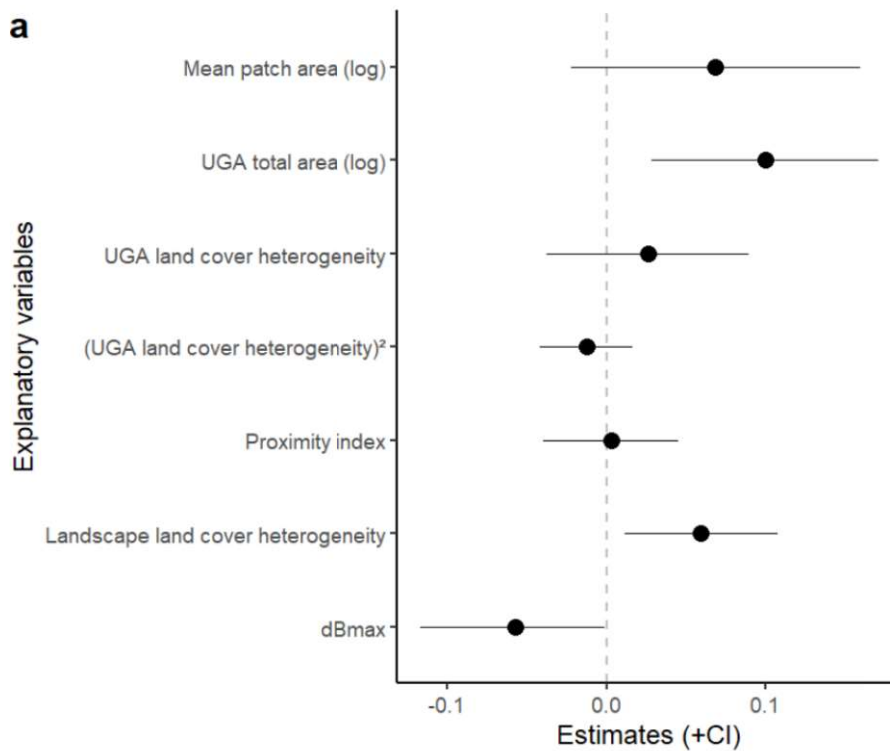
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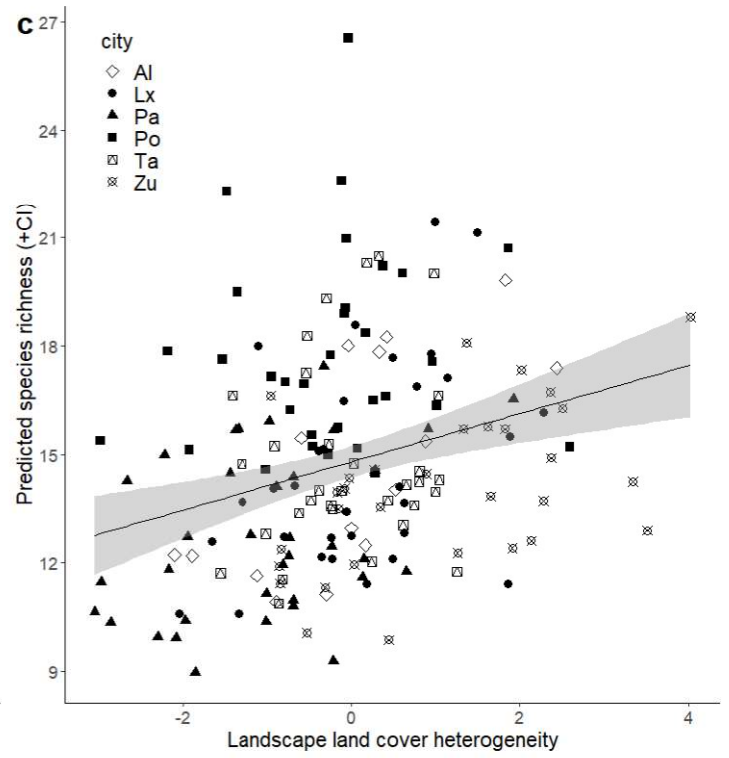
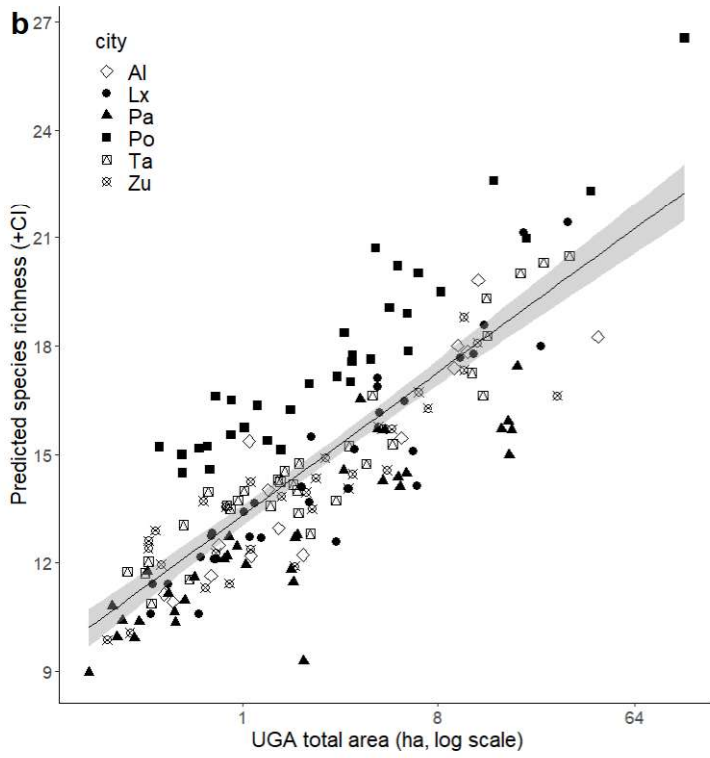
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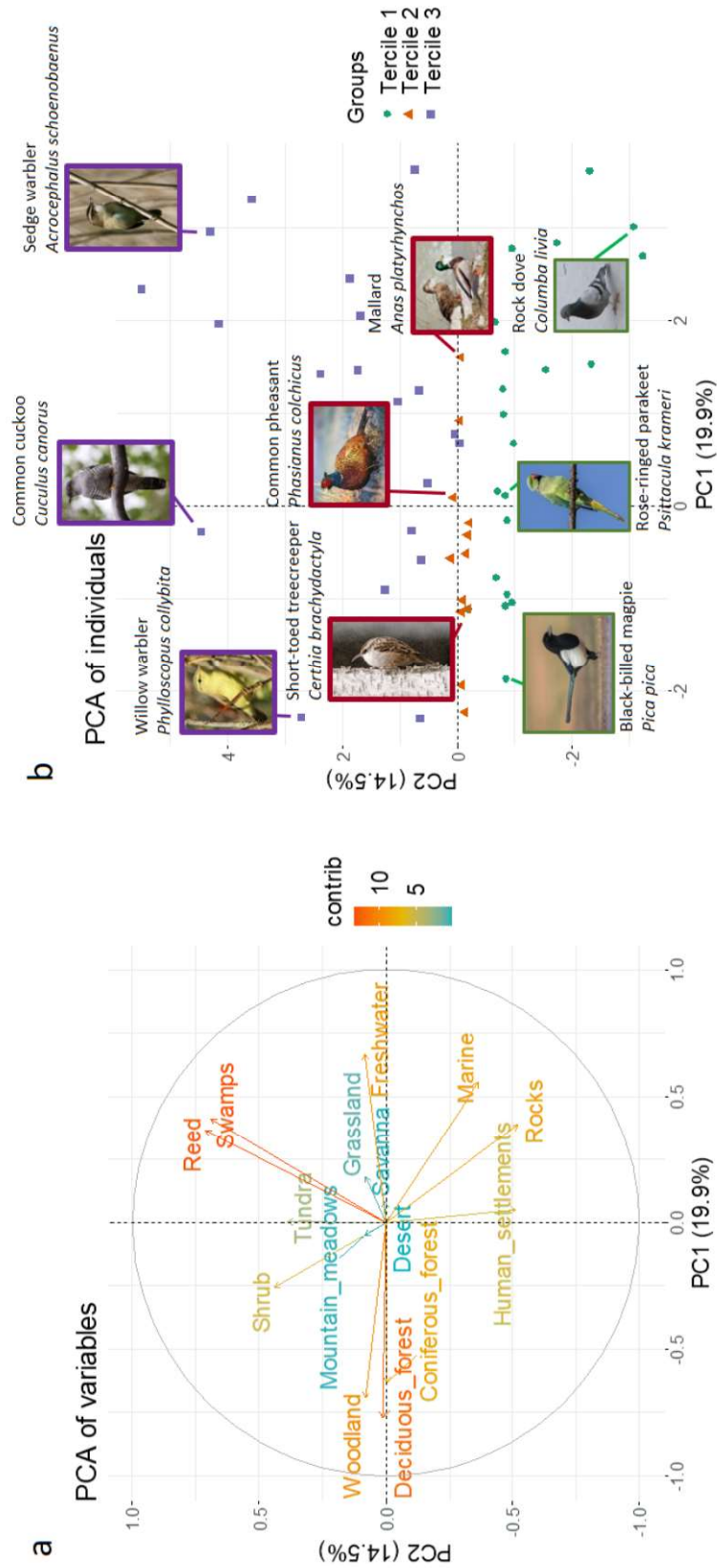
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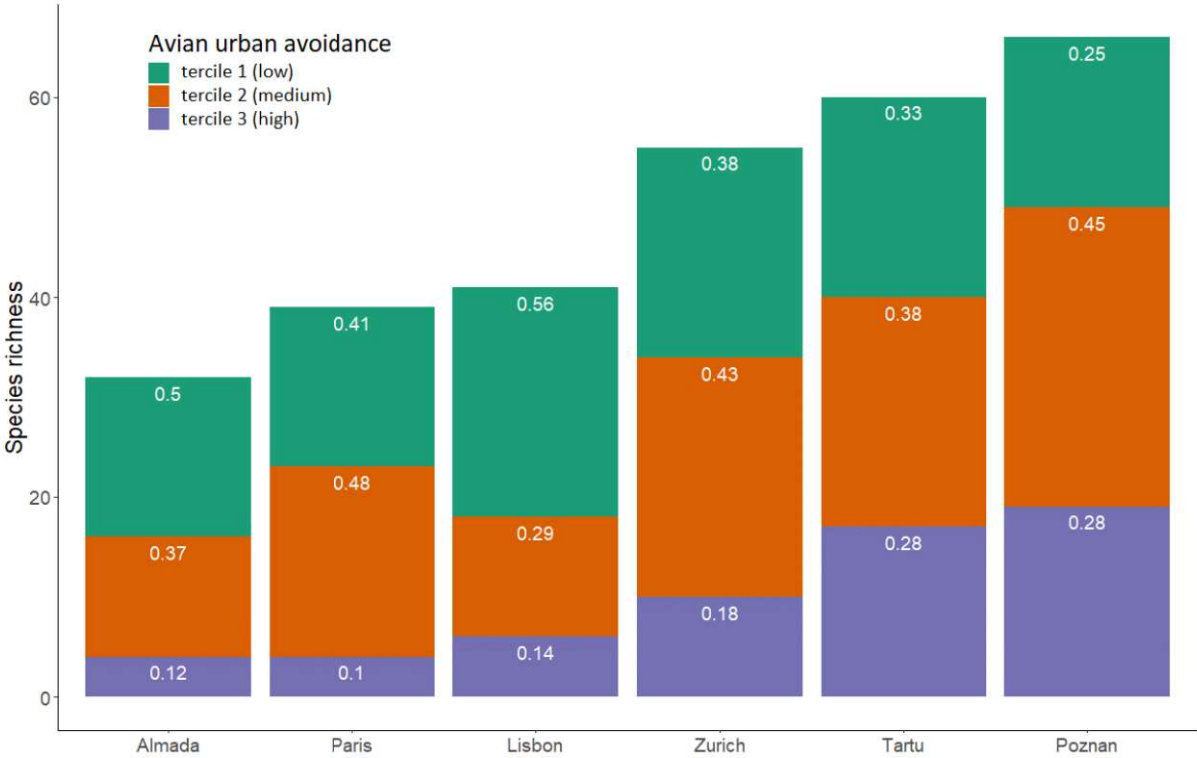




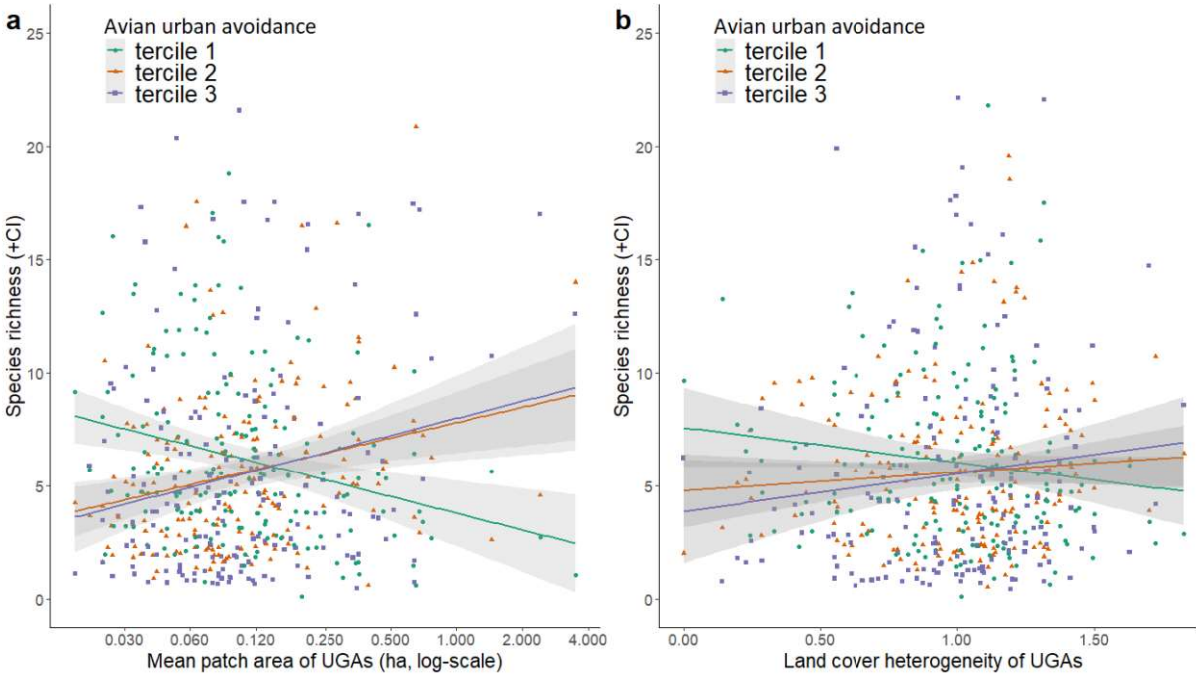
**Figure 3:** Principal component analysis with (a) variables and (b) individuals. This analysis positioned the species along a gradient of urban avoidance on PC2 from low avoidance (low value) to high avoidance (high value). The blue-red colour gradient indicates the contribution of variables to PC1 and PC2 (a), and the different colours in (b) indicates the species according to terciles 1 (low urban avoidance; green), 2 (medium urban avoidance; orange) and 3 (high urban avoidance; purple). Each symbol in (b) represents one or several species (n = 115 species ; habitat occurrences for four species were missing from Storchová & Hořák (2018) and were not plotted). To illustrate gradients, we positioned three species per tercile (English and Latin names). See Appendix B for a summary of the species names with regard to urban avoidance values and tercile group. Photo credits: R. Knight (Common cuckoo), W. van der Ham (Willow warbler), L. Lukasiak (Common pheasant), N. Wulf (Rock dove), R. Bartz (Mallard), C.J. Sharp (Rose-ringed parakeet), K. Billington (Sedge Warbler), J. Bleak (Short-toed treecreeper), D. Delso (Black-billed magpie).



**Figure 4:** Avian species richness for the different levels of avian urban avoidance (terciles) in the six cities. For each city, we pooled the bird species belonging to terciles 1 (low avoidance; green), 2 (medium avoidance; orange) and 3 (high avoidance; purple). We ordered the cities according to the total number of species from the least to the most. We provided the proportion of species per tercile in white.



**Figure 5:** Responses of species richness to the mean patch area (a) and land cover heterogeneity (b) according to the level of avian urban avoidance: low urban avoidance (green, tercile 1), medium avoidance (orange, tercile 2) and purple (high avoidance, tercile 3). Grey shaded bands indicate 95% confidence intervals estimated from the generalized linear mixed model (Table 2).







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**Appendix A:** Correlation coefficients between bird nesting habitats and the first three principal components (PCs).

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**Appendix G:** Tukey HSD (Honestly Significant Difference) post-hoc tests.

**Appendix H:** Correlogram plot of the predictors for all cities pooled together.

**Appendix I:** Relationship between mean patch area and land cover heterogeneity (Shannon's index of land cover types) of the studied urban green areas.

**Appendix A:** Correlation coefficients between bird nesting habitats and the first three principal components (PCs). Data on bird occurrences in 15 nesting habitats in Europe were compiled by Storchová & Hořák (2018). Occurrence data derive from *The Birds of the Western Palearctic* handbook (Cramp, 2006). p-value: ns: non-significant, \*p<0.05, \*\*p<0.01, \*\*\*p<0.001.

Habitats / Principal Components (% of variance)	PC 1 (20.1%)	PC 2 (14.2%)	PC 3 (11.1%)
Grassland	0.22*	ns	0.67***
Shrub	-0.23**	0.42***	0.29**
Rocks	0.33***	-0.52***	ns
Reeds	0.35***	0.70***	ns
Swamps	0.42***	0.66***	ns
Marine	0.50***	-0.34***	-0.30**
Coniferous forest	-0.65***	ns	-0.34***
Freshwater	0.67***	ns	-0.35***
Woodland	-0.70***	ns	0.29**
Deciduous forest	-0.79***	ns	-0.24**
Human settlements	ns	-0.50***	0.22*
Mountain meadows	ns	ns	0.31***
Savanna	ns	ns	0.60***
Tundra	ns	0.40***	ns



**Appendix B:** List of the 119 bird species recorded in six European cities (within a total of 176 urban green areas) along with their urban avoidance value (PC2, this study), tercile group (1: low urban avoidance, 2: medium urban avoidance, 3: high urban avoidance), species occurrence (% of sites occupied) and number of individuals counted per city. NA: information not available.

Species (latin name)	Species code	Urban avoidance index (PC2)	Tercile group	Occurrence (%)	Number of individuals counted					
					Almada	Lisbon	Paris	Poznan	Tartu	Zurich
<i>Acanthis cannabina</i>	acacan	0.15	3	6.7	0	0	0	18	0	0
<i>Accipiter nisus</i>	accnis	0.09	2	1	0	0	0	1	0	0
<i>Acrocephalus arundinaceus</i>	acraru	3.64	3	1.5	0	0	0	3	0	0
<i>Acridotheres cristatellus</i>	accri	-0.25	2	1.5	5	0	0	0	0	0
<i>Acrocephalus dumetorum</i>	acrdu	0.73	3	1.5	0	0	0	0	2	0
<i>Acrocephalus palustris</i>	acpal	1.64	3	2.1	0	0	0	3	1	0
<i>Acrocephalus schoenobaenus</i>	acrsch	4.36	3	2.1	0	0	0	1	2	0
<i>Acrocephalus scirpaceus</i>	acrsci	2.01	3	3.1	0	0	1	4	0	2
<i>Aegithalos caudatus</i>	aegcau	0.73	3	5.1	0	4	3	1	0	7
<i>Alopochen aegyptiaca</i>	aloaeg	-0.78	1	2.1	0	6	0	0	0	0
<i>Anas platyrhynchos</i>	anapla	0.01	2	16.4	0	15	11	26	12	15
<i>Anas strepera</i>	anastr	-0.04	2	1	0	0	0	2	0	0
<i>Anser anser</i>	ansans	NA	NA	1	0	12	0	0	0	0
<i>Apus apus</i>	apuapu	-2.27	1	36.9	14	15	57	83	15	53
<i>Apus melba</i>	apumel	-2.27	1	2.1	0	0	0	0	0	11
<i>Apus pallidus</i>	apupal	-3.15	1	8.2	15	110	0	0	0	0
<i>Ardea cinerea</i>	ardcin	0.01	2	2.1	0	0	1	0	0	2
<i>Aythya fuligula</i>	aytful	0.01	2	1	0	0	0	1	0	0
<i>Branta canadensis</i>	bracan	-0.78	1	1.5	0	0	2	1	0	0
<i>Bubulcus ibis</i>	bubibi	NA	NA	1.5	0	5	0	0	0	0
<i>Buteo buteo</i>	butbut	0.09	2	3.1	2	2	0	0	0	1
<i>Carduelis carduelis</i>	carcar	-0.78	1	39.5	28	46	4	18	23	40
<i>Carduelis chloris</i>	carchl	0.03	2	52.3	42	45	8	0	35	14
<i>Carduelis spinus</i>	carspi	-0.02	2	3.6	0	0	0	0	0	1
<i>Cecropis daurica</i>	cecdau	-1.48	1	1	3	0	0	0	0	0
<i>Certhia brachydactyla</i>	cerbra	0.09	2	36.4	10	29	27	14	0	17
<i>Certhia familiaris</i>	cerfam	-0.02	2	2.6	0	0	0	0	4	0
<i>Cettia cetti</i>	cetcet	4.15	3	1	1	0	0	0	0	0
<i>Chroicocephalus ridibundus</i>	chrrid	0.76	3	3.1	0	13	0	0	0	46

<i>Cisticola juncidis</i>	cisjun	1.07	3	3.1	3	3	0	0	0	0
<i>Coccothraustes coccothraustes</i>	coccoc	-0.09	2	13.8	0	0	0	7	29	1
<i>Columba livia</i>	colliv	-3.20	1	53.8	274	435	117	106	29	28
<i>Columba oenas</i>	coloen	0.09	2	2.1	0	0	5	0	0	0
<i>Columba palumbus</i>	colpal	-0.70	1	72.3	11	50	147	101	30	67
<i>Corvus corone</i>	corcor	-0.88	1	66.7	21	7	55	35	80	76
<i>Corvus frugilegus</i>	corfru	-0.70	1	6.7	0	0	0	18	19	0
<i>Corvus monedula</i>	cormon	-0.88	1	21	0	0	3	55	36	4
<i>Cuculus canorus</i>	cuccan	4.39	3	2.6	0	0	0	5	0	0
<i>Cyanistes caeruleus</i>	cyacae	-0.78	1	68.2	15	45	93	0	36	61
<i>Delichon urbicum</i>	delurb	-2.27	1	13.3	28	21	0	18	0	1
<i>Dendrocopos major</i>	denmaj	-0.80	1	13.3	1	3	4	11	6	5
<i>Dendrocopos medius</i>	denmed	0.01	2	4.6	0	0	0	1	7	0
<i>Dendrocopos minor</i>	denmin	0.01	2	1.5	0	0	0	2	0	0
<i>Dryocopus martius</i>	drymar	-0.02	2	1	0	0	0	2	0	0
<i>Egretta garzetta</i>	egrgar	NA	NA	1	0	1	0	0	0	0
<i>Emberiza calandra</i>	embcac	-0.25	2	1	0	1	0	0	0	0
<i>Emberiza citrinella</i>	embcit	0.58	3	1	0	0	0	1	0	0
<i>Emberiza schoeniclus</i>	embsch	5.65	3	1	0	0	0	1	0	0
<i>Erithacus rubecula</i>	erirub	0.81	3	43.6	9	29	42	3	20	23
<i>Estrilda astrild</i>	estast	1.80	3	1	0	2	0	0	0	0
<i>Falco tinnunculus</i>	faltin	-1.35	1	6.2	3	4	0	4	0	2
<i>Ficedula albicollis</i>	ficalb	-0.09	2	1	0	0	0	0	1	0
<i>Ficedula hypoleuca</i>	fichyp	0.09	2	9.7	0	0	0	4	16	0
<i>Ficedula parva</i>	ficpar	-0.02	2	1	0	0	0	0	1	0
<i>Fringilla coelebs</i>	fricoe	-0.80	1	59	0	6	38	47	66	89
<i>Fulica atra</i>	fulatr	0.01	2	2.1	0	0	2	2	0	7
<i>Gallinula chloropus</i>	galchl	0.11	3	3.1	0	0	8	0	0	0
<i>Garrulus glandarius</i>	gargla	-0.02	2	17.9	7	20	10	6	1	5
<i>Hippolais icterina</i>	hipict	0.73	3	9.2	0	0	0	5	11	1
<i>Hirundo rustica</i>	hirrus	-1.03	1	14.4	31	28	0	0	1	2
<i>Jynx torquilla</i>	jyntor	0.01	2	3.1	0	0	0	0	5	0
<i>Larus argentatus</i>	lararg	-3.15	1	9.2	0	0	2	0	25	0
<i>Larus canus</i>	larcac	-0.87	1	2.6	0	0	0	0	5	0
<i>Larus fuscus</i>	larfus	-1.66	1	2.1	1	4	0	0	0	0
<i>Larus michahellis</i>	larmic	-2.16	1	7.2	6	12	0	0	0	1
<i>Locustella naevia</i>	locnae	2.11	3	1	0	0	0	0	0	1
<i>Lophophanes cristatus</i>	lopcri	-0.02	2	3.6	6	0	0	0	0	1
<i>Lullula arborea</i>	lularb	0.58	3	1	0	0	0	1	0	0
<i>Luscinia luscinia</i>	luslus	0.63	3	4.1	0	0	0	2	6	0



<i>Luscinia megarhynchos</i>	lusmeg	0.63	3	5.6	0	0	0	12	0	0
<i>Mergus merganser</i>	mermer	0.11	3	1	0	0	0	0	0	3
<i>Milvus migrans</i>	milmig	0.99	3	2.1	0	0	0	0	0	3
<i>Milvus milvus</i>	milmil	-0.36	2	2.1	0	0	0	0	0	4
<i>Motacilla alba</i>	motalb	-0.83	1	26.7	7	29	0	0	24	10
<i>Motacilla cinerea</i>	motcin	0.73	3	1	0	0	0	0	0	1
<i>Muscicapa striata</i>	musstr	-0.70	1	5.1	0	0	0	0	4	7
<i>Nycticorax nycticorax</i>	nycnyc	NA	NA	1	0	1	0	0	0	0
<i>Oriolus oriolus</i>	oriori	0.01	2	3.6	0	0	0	5	1	0
<i>Parus major</i>	parmaj	-0.70	1	78.5	7	25	103	54	50	83
<i>Passer domesticus</i>	pasdom	-0.16	2	57.9	104	181	84	97	30	58
<i>Passer montanus</i>	pasmon	0.73	3	21	0	0	0	44	59	1
<i>Periparus ater</i>	perate	-0.12	2	11.8	6	18	0	0	0	0
<i>Phalacrocorax carbo</i>	phacar	-0.87	1	2.6	0	0	1	0	0	3
<i>Phasianus colchicus</i>	phacol	-0.14	2	1.5	0	0	0	2	0	0
<i>Phoenicurus ochruros</i>	phooch	-2.27	1	22.6	7	16	3	4	0	31
<i>Phoenicurus phoenicurus</i>	phopho	0.01	2	12.3	0	0	0	9	18	1
<i>Phylloscopus collybita</i>	phycol	-0.02	2	26.2	0	0	15	10	16	33
<i>Phylloscopus sibilatrix</i>	physib	-0.02	2	4.1	0	0	0	0	9	0
<i>Phylloscopus trochilus</i>	phytro	3.03	3	14.9	0	0	0	9	8	18
<i>Picus canus</i>	piccan	0.01	2	1	0	0	0	1	0	0
<i>Pica pica</i>	picpic	-0.70	1	34.4	0	0	42	52	4	16
<i>Picus viridis</i>	picvir	-0.02	2	8.2	0	0	7	7	0	2
<i>Podiceps cristatus</i>	podcri	0.01	2	1	0	0	0	0	0	1
<i>Podiceps ruficollis</i>	podruf	0.01	2	1	0	0	0	2	0	0
<i>Poecile palustris</i>	poepal	-0.09	2	2.1	0	0	2	2	0	1
<i>Prunella modularis</i>	prumod	0.81	3	13.3	0	0	27	0	2	0
<i>Psittacula krameri</i>	psikra	-1.20	1	21.5	0	58	53	0	0	0
<i>Pyrrhula pyrrhula</i>	pyrpyr	-2.01	1	3.6	0	0	0	0	7	0
<i>Recurvirostra avosetta</i>	recavo	-0.87	1	1	0	10	0	0	0	0
<i>Regulus ignicapilla</i>	regign	0.09	2	10.3	1	6	4	1	0	10
<i>Regulus regulus</i>	regreg	-0.12	2	5.1	0	0	7	0	2	1
<i>Remiz pendulinus</i>	rempen	3.64	3	1	0	0	0	0	1	0
<i>Serinus serinus</i>	serser	-0.80	1	39.5	50	115	0	22	1	10
<i>Sitta europaea</i>	siteur	-0.02	2	21.5	0	0	10	10	13	17
<i>Sterna hirundo</i>	stehir	-0.87	1	2.6	0	0	0	0	4	0
<i>Streptopelia decaocto</i>	strdec	-0.98	1	37.4	62	39	2	38	0	12
<i>Sturnus unicolor</i>	stuuni	-0.93	1	22.1	46	128	0	0	0	0
<i>Sturnus vulgaris</i>	stuvul	-0.83	1	49.7	0	0	53	102	43	39
<i>Sylvia atricapilla</i>	sylatr	-0.02	2	58.5	13	36	40	25	7	94
<i>Sylvia borin</i>	sylbor	0.73	3	4.6	0	0	0	4	4	0



<i>Sylvia communis</i>	sylcom	0.63	3	3.1	0	0	0	2	3	0
<i>Sylvia curruca</i>	sylcur	0.63	3	15.9	0	0	0	22	10	0
<i>Sylvia melanocephala</i>	sylmel	0.52	3	13.8	18	18	0	0	0	0
<i>Thectocercus acuticaudatus</i>	theacu	-1.20	1	2.1	0	6	0	0	0	0
<i>Troglodytes troglodytes</i>	trotro	0.09	2	28.7	15	33	44	2	1	3
<i>Turdus iliacus</i>	turili	0.81	3	2.6	0	0	0	0	4	0
<i>Turdus merula</i>	turner	0.03	2	84.1	84	229	73	62	28	95
<i>Turdus philomelos</i>	turphi	0.03	2	16.4	0	0	6	22	7	6
<i>Turdus pilaris</i>	turpil	0.09	2	29.2	0	0	0	87	77	0

**Appendix C:** Results of the regression models between mean patch area, land cover heterogeneity and area of UGAs. We reported the slope estimate, standard error (Std. Error) and degree of freedom (df) for each explanatory variable. Significant variables are highlighted in bold in the table (\*p<0.05, \*\*p<0.01, \*\*\*p<0.001).

Level <sup>a</sup>	Mean patch area predictor (log)	Estimate	Std. error	F-value	df	p-value
All cities (n=176, 0.666)	UGA land cover heterogeneity	-0.498	0.037	183.160	1	<b>&lt;0.001***</b>
	Area of UGAs (log)	0.666	0.035	356.920	1	<b>&lt;0.001***</b>
Almada (n=15, 0.740)	UGA land cover heterogeneity	-0.612	0.123	24.769	1	<b>&lt;0.001***</b>
	Area of UGAs (log)	0.719	0.129	31.012	1	<b>&lt;0.001***</b>
Lisbon (n=31, 0.736)	UGA land cover heterogeneity	-0.300	0.083	13.008	1	<b>&lt;0.001***</b>
	Area of UGAs (log)	0.817	0.089	84.749	1	<b>&lt;0.001***</b>
Paris (n=35, 0.781)	UGA land cover heterogeneity	-0.427	0.063	46.398	1	<b>&lt;0.001***</b>
	Area of UGAs (log)	0.487	0.052	88.890	1	<b>&lt;0.001***</b>
Poznan (n=32, 0.792)	UGA land cover heterogeneity	-0.617	0.089	47.890	1	<b>&lt;0.001***</b>
	Area of UGAs (log)	0.578	0.075	59.415	1	<b>&lt;0.001***</b>
Tartu (n=32, 0.903)	UGA land cover heterogeneity	-0.739	0.065	130.760	1	<b>&lt;0.001***</b>
	Area of UGAs (log)	0.884	0.066	178.470	1	<b>&lt;0.001***</b>
Zurich (n=31, 0.363)	UGA land cover heterogeneity	-0.277	0.092	9.010	1	<b>&lt;0.01**</b>
	Area of UGAs (log)	0.383	0.090	17.917	1	<b>&lt;0.001***</b>

<sup>a</sup>Number of UGAs and adjusted R<sup>2</sup> value

**Appendix D:** Results of the regression model analysing the effects of landscape (500 m buffer around each urban green area, UGA) and UGA variables on species richness of avian communities using dataset from all cities (176 UGAs with complete land cover information). Relationships were controlled for the maximum sound volume level (dBmax) and included ‘city’ as a random effect to account for possible consistent differences among cities (generalised linear mixed model). “(UGA land cover heterogeneity)<sup>2</sup>” is the squared term of UGA land cover heterogeneity to test for a non-linear relationship. We reported the slope estimate, standard error (Std. Error) and degree of freedom (df) for each explanatory variable. We added semi-partial R<sup>2</sup> (part R<sup>2</sup>) values that provide an estimate of the variance explained by a fixed effect independent of other predictors. Significant variables are highlighted in bold in the table (\*p<0.05, \*\*p<0.01, \*\*\*p<0.001). Marginally significant statistical tendencies (0.050<p<0.010) are followed by a full stop (.). Non-significant two-way interactions or quadratic terms (i.e. UGA land cover heterogeneity<sup>2</sup>) were removed from the models in order to better estimate single effects of predictors.

Level <sup>a</sup>	Predictor of species richness	Estimate	Std. Error	Chisq-value	df	p-value	part R <sup>2</sup>
All cities (n=176, 0.297)	dBmax	-0.047	0.028	2.944	1	0.086.	0.025
	UGA total area (log)	0.103	0.036	8.289	1	<b>0.004**</b>	0.018
	Mean patch area (log)	0.068	0.045	2.347	1	0.126	0.008
	Proximity index	0.005	0.021	0.049	1	0.825	0.000
	Landscape land cover heterogeneity	0.055	0.024	5.400	1	<b>0.020*</b>	0.031
	UGA land cover heterogeneity	0.024	0.032	0.562	1	0.454	0.002
	(UGA land cover heterogeneity) <sup>2</sup>	-0.014	0.015	0.853	1	0.356	0.004

<sup>a</sup>Number of UGAs and marginal R<sup>2</sup> value



**Appendix E:** Results of full regression models analysing the effects of landscape (500 m buffer around each urban green area, UGA) and UGA variables on species richness of avian communities in the six studied cities. Relationships were controlled for the maximum noise level (dBmax) (generalised linear model). Almada was omitted because of the small sample size. (UGA land cover heterogeneity)<sup>2</sup> is the squared term of UGA land cover heterogeneity to test for a non-linear relationship. We reported the slope estimate, standard error (Std. Error) and degree of freedom (df) for each explanatory variable. Significant variables are highlighted in bold in the table (\*p<0.05, \*\*p<0.01, \*\*\*p<0.001). Marginally significant statistical tendencies (0.050<p<0.10) are followed by a full stop (.). We also reported semi-partial R<sup>2</sup> (part R<sup>2</sup>) values that provide an estimate of the variance explained by a fixed effect independent of other predictors.

Level <sup>a</sup>	Predictor of species richness	Estimate	Std. Error	Chisq-value	df	p-value	part R <sup>2</sup>
	dBmax	-0.250	0.103	6.217	1	<b>0.013*</b>	0.027
	UGA total area (log)	0.333	0.115	8.171	1	<b>0.004**</b>	0.041
	Mean patch area (log)	-0.193	0.123	2.440	1	0.118	0.015
	Proximity index	0.029	0.047	0.370	1	0.543	0.001
Lisbon (n=31, 0.756)	Landscape land cover heterogeneity	-0.011	0.063	0.033	1	0.857	0.001
	UGA land cover heterogeneity	-0.329	0.225	2.142	1	0.143	0.006
	(UGA land cover heterogeneity) <sup>2</sup>	0.020	0.035	0.330	1	0.565	0.000
Paris (n=35, 0.677)	dBmax	-0.025	0.038	0.440	1	0.507	0.003
	UGA total area (log)	0.159	0.091	3.070	1	0.080.	0.034
	Mean patch area (log)	0.031	0.164	0.037	1	0.848	0.014
	Proximity index	0.064	0.061	1.067	1	0.302	0.001

	Landscape land cover heterogeneity	0.057	0.061	0.851	1	0.356	0.010
	UGA land cover heterogeneity	0.167	0.283	0.350	1	0.554	0.005
	(UGA land cover heterogeneity) <sup>2</sup>	0.021	0.053	0.156	1	0.693	0.001
<hr/>							
Poznan (n=32, 0.624)	dBmax	-0.015	0.132	0.013	1	0.909	0.000
	UGA total area (log)	0.053	0.075	0.496	1	0.481	0.030
	Mean patch area (log)	0.210	0.107	3.842	1	<b>0.050*</b>	0.030
	Proximity index	-0.020	0.052	0.149	1	0.699	0.001
	Landscape land cover heterogeneity	0.090	0.071	1.640	1	0.200	0.004
	UGA land cover heterogeneity	0.432	0.308	1.952	1	0.162	0.006
	(UGA land cover heterogeneity) <sup>2</sup>	-0.010	0.055	0.032	1	0.858	0.002
<hr/>							
Tartu (n=32, 0.536)	dBmax	-0.087	0.089	0.952	1	0.329	0.009
	UGA total area (log)	0.151	0.139	1.178	1	0.278	0.015
	Mean patch area (log)	-0.043	0.149	0.083	1	0.773	0.010
	Proximity index	-0.060	0.077	0.614	1	0.434	0.004

	Landscape land cover heterogeneity	0.106	0.092	1.340	1	0.247	0.004
	UGA land cover heterogeneity	-0.356	0.392	0.822	1	0.365	0.002
	(UGA land cover heterogeneity) <sup>2</sup>	-0.039	0.050	0.617	1	0.432	0.002
<hr/>							
Zurich (n=31, 0.692)	dBmax	-0.027	0.093	0.083	1	0.774	0.001
	UGA total area (log)	0.086	0.084	1.060	1	0.303	0.02
	Mean patch area (log)	0.056	0.139	0.165	1	0.684	0.006
	Proximity index	0.047	0.056	0.692	1	0.406	0.004
	Landscape land cover heterogeneity	0.049	0.049	0.975	1	0.323	0.010
	UGA land cover heterogeneity	0.006	0.272	0.001	1	0.982	0.005
	(UGA land cover heterogeneity) <sup>2</sup>	-0.119	0.057	4.555	1	<b>0.033*</b>	0.022
<hr/>							

<sup>a</sup>Number of UGAs and marginal R<sup>2</sup> value



**Appendix F:** Correlation coefficients between bird nesting habitats and the first three principal components (PCs). Data on bird occurrences in 15 nesting habitats in Europe were compiled by Storchová and Hořák (2018). Occurrence data derive from *The Birds of the Western Palearctic* handbook (Cramp, 2006). p-value: ns: non-significant, \*p<0.05, \*\*p<0.01, \*\*\*p<0.001.

Habitats / Principal Components (% of variance)	PC 1 (20.1%)	PC 2 (14.2%)	PC 3 (11.1%)
Grassland	0.22*	ns	0.67***
Shrub	-0.23**	0.42***	0.29**
Rocks	0.33***	-0.52***	ns
Reeds	0.35***	0.70***	ns
Swamps	0.42***	0.66***	ns
Marine	0.50***	-0.34***	-0.30**
Coniferous forest	-0.65***	ns	-0.34***
Freshwater	0.67***	ns	-0.35***
Woodland	-0.70***	ns	0.29**
Deciduous forest	-0.79***	ns	-0.24**
Human settlements	ns	-0.50***	0.22*
Mountain meadows	ns	ns	0.31***
Savanna	ns	ns	0.60***
Tundra	ns	0.40***	ns

**Appendix G:** Tukey HSD (Honestly Significant Difference) post-hoc tests comparing the avian richness between tercile groups (1 or low urban avoidance, 2 or medium urban avoidance and 3 or high urban avoidance) and cities. We ranked the results according to the p-value.

Comparison (tercile group:city)	Difference	Lower	Upper	p-value adjusted
1:Lisbon-3:Almada	6.731	4.482	8.981	0.000
1:Paris-3:Almada	5.781	3.574	7.988	0.000
1:Paris-3:Lisbon	5.921	4.157	7.685	0.000
1:Poznan-2:Lisbon	3.395	1.593	5.197	0.000
1:Poznan-2:Paris	4.579	2.829	6.328	0.000
1:Poznan-3:Almada	7.417	5.179	9.655	0.000
1:Poznan-3:Lisbon	7.556	5.754	9.359	0.000
1:Poznan-3:Paris	7.436	5.687	9.185	0.000
1:Tartu-3:Almada	5.409	3.159	7.658	0.000
1:Tartu-3:Lisbon	5.548	3.732	7.365	0.000
1:Tartu-3:Paris	5.428	3.664	7.191	0.000
1:Tartu-3:Poznan	3.804	2.002	5.607	0.000
1:Zurich-3:Almada	5.989	3.740	8.239	0.000
1:Zurich-3:Lisbon	6.129	4.313	7.946	0.000
1:Zurich-3:Paris	6.008	4.244	7.772	0.000
1:Zurich-3:Poznan	4.385	2.583	6.187	0.000

1:Zurich-3:Tartu	4.710	2.893	6.526	0.000
2:Paris-1:Lisbon	-3.893	-5.657	-2.129	0.000
2:Poznan-3:Almada	5.354	3.116	7.592	0.000
2:Poznan-3:Lisbon	5.494	3.692	7.296	0.000
2:Poznan-3:Paris	5.373	3.624	7.122	0.000
2:Tartu-3:Almada	4.312	2.062	6.561	0.000
2:Tartu-3:Lisbon	4.452	2.635	6.268	0.000
2:Tartu-3:Paris	4.331	2.567	6.095	0.000
2:Zurich-1:Poznan	-3.524	-5.326	-1.722	0.000
2:Zurich-3:Lisbon	4.032	2.216	5.849	0.000
2:Zurich-3:Paris	3.912	2.148	5.675	0.000
3:Almada-1:Almada	-6.133	-8.745	-3.522	0.000
3:Lisbon-1:Almada	-6.273	-8.522	-4.024	0.000
3:Lisbon-1:Lisbon	-6.871	-8.687	-5.054	0.000
3:Lisbon-2:Almada	-4.473	-6.722	-2.224	0.000
3:Lisbon-2:Lisbon	-4.161	-5.978	-2.345	0.000
3:Paris-1:Almada	-6.152	-8.359	-3.945	0.000
3:Paris-1:Lisbon	-6.750	-8.514	-4.986	0.000



3:Paris-1:Paris	-5.800	-7.510	-4.090	0.000
3:Paris-2:Almada	-4.352	-6.559	-2.145	0.000
3:Paris-2:Lisbon	-4.041	-5.804	-2.277	0.000
3:Poznan-1:Almada	-4.529	-6.767	-2.291	0.000
3:Poznan-1:Lisbon	-5.127	-6.929	-3.325	0.000
3:Poznan-1:Paris	-4.177	-5.926	-2.428	0.000
3:Poznan-1:Poznan	-5.813	-7.600	-4.025	0.000
3:Poznan-2:Poznan	-3.750	-5.538	-1.962	0.000
3:Tartu-1:Almada	-4.854	-7.103	-2.604	0.000
3:Tartu-1:Lisbon	-5.452	-7.268	-3.635	0.000
3:Tartu-1:Paris	-4.501	-6.265	-2.738	0.000
3:Tartu-1:Poznan	-6.137	-7.939	-4.335	0.000
3:Tartu-1:Tartu	-4.129	-5.946	-2.313	0.000
3:Tartu-2:Poznan	-4.075	-5.877	-2.272	0.000
3:Zurich-1:Almada	-6.144	-8.393	-3.895	0.000
3:Zurich-1:Lisbon	-6.742	-8.558	-4.925	0.000
3:Zurich-1:Paris	-5.792	-7.556	-4.028	0.000
3:Zurich-1:Poznan	-7.427	-9.230	-5.625	0.000

3:Zurich-1:Tartu	-5.419	-7.236	-3.603	0.000
3:Zurich-1:Zurich	-6.000	-7.817	-4.183	0.000
3:Zurich-2:Almada	-4.344	-6.593	-2.095	0.000
3:Zurich-2:Lisbon	-4.032	-5.849	-2.216	0.000
3:Zurich-2:Poznan	-5.365	-7.167	-3.563	0.000
3:Zurich-2:Tartu	-4.323	-6.139	-2.506	0.000
3:Zurich-2:Zurich	-3.903	-5.720	-2.087	0.000
1:Zurich-2:Paris	3.151	1.387	4.915	0.000
2:Lisbon-3:Almada	4.022	1.772	6.271	0.000
2:Tartu-1:Poznan	-3.105	-4.907	-1.303	0.000
2:Zurich-3:Almada	3.892	1.643	6.142	0.000
2:Paris-1:Paris	-2.943	-4.652	-1.233	0.000
2:Paris-3:Lisbon	2.978	1.214	4.742	0.000
3:Paris-2:Paris	-2.857	-4.567	-1.148	0.000
3:Tartu-2:Tartu	-3.032	-4.849	-1.216	0.000
3:Almada-2:Almada	-4.333	-6.945	-1.722	0.000
3:Zurich-2:Paris	-2.849	-4.613	-1.085	0.000
2:Zurich-1:Lisbon	-2.839	-4.655	-1.022	0.000

3:Tartu-2:Lisbon	-2.742	-4.558	-0.925	0.000
2:Tartu-3:Poznan	2.708	0.905	4.510	0.000
2:Paris-1:Almada	-3.295	-5.502	-1.088	0.000
2:Lisbon-1:Lisbon	-2.710	-4.526	-0.893	0.000
1:Tartu-2:Paris	2.571	0.807	4.334	0.000
2:Poznan-2:Paris	2.516	0.767	4.265	0.000
2:Zurich-3:Tartu	2.613	0.796	4.429	0.000
1:Poznan-2:Almada	3.083	0.845	5.321	0.000
3:Tartu-2:Almada	-3.054	-5.303	-0.804	0.000
3:Poznan-2:Lisbon	-2.417	-4.220	-0.615	0.000
2:Tartu-1:Lisbon	-2.419	-4.236	-0.603	0.001
2:Paris-3:Almada	2.838	0.631	5.045	0.001
2:Zurich-3:Poznan	2.288	0.486	4.091	0.001
3:Poznan-2:Almada	-2.729	-4.967	-0.491	0.003
2:Zurich-1:Zurich	-2.097	-3.913	-0.280	0.007
2:Poznan-1:Poznan	-2.063	-3.850	-0.275	0.008
1:Tartu-1:Poznan	-2.008	-3.810	-0.206	0.013
1:Zurich-2:Lisbon	1.968	0.151	3.784	0.019



2:Zurich-1:Paris	-1.888	-3.652	-0.125	0.022
1:Lisbon-2:Almada	2.398	0.149	4.647	0.023
1:Paris-2:Lisbon	1.759	-0.004	3.523	0.051
2:Zurich-1:Almada	-2.241	-4.490	0.008	0.052
3:Poznan-3:Lisbon	1.744	-0.058	3.546	0.071
2:Lisbon-1:Almada	-2.112	-4.361	0.138	0.095
1:Poznan-1:Paris	1.636	-0.113	3.385	0.099
3:Poznan-3:Paris	1.623	-0.126	3.372	0.106
1:Zurich-2:Tartu	1.677	-0.139	3.494	0.111
3:Zurich-3:Poznan	-1.615	-3.417	0.187	0.143
3:Tartu-2:Paris	-1.559	-3.322	0.205	0.160
2:Tartu-2:Paris	1.474	-0.290	3.238	0.240
2:Zurich-1:Tartu	-1.516	-3.333	0.300	0.241
2:Tartu-1:Paris	-1.469	-3.233	0.295	0.245
2:Zurich-2:Poznan	-1.462	-3.264	0.341	0.289
2:Tartu-1:Almada	-1.822	-4.071	0.428	0.291
1:Zurich-1:Poznan	-1.427	-3.230	0.375	0.331
3:Tartu-3:Lisbon	1.419	-0.397	3.236	0.355

2:Poznan-1:Lisbon	-1.377	-3.179	0.425	0.398
1:Tartu-2:Lisbon	1.387	-0.429	3.204	0.399
2:Poznan-2:Lisbon	1.333	-0.470	3.135	0.461
3:Tartu-3:Paris	1.299	-0.465	3.062	0.469
1:Zurich-2:Almada	1.656	-0.593	3.905	0.469
1:Tartu-1:Lisbon	-1.323	-3.139	0.494	0.491
3:Poznan-3:Almada	1.604	-0.634	3.842	0.521
3:Zurich-3:Tartu	-1.290	-3.107	0.526	0.538
3:Poznan-2:Paris	-1.234	-2.983	0.515	0.551
2:Almada-1:Almada	-1.800	-4.411	0.811	0.595
2:Paris-2:Almada	-1.495	-3.702	0.712	0.627
2:Paris-2:Lisbon	-1.183	-2.947	0.580	0.644
1:Paris-2:Almada	1.448	-0.759	3.655	0.683
2:Tartu-1:Tartu	-1.097	-2.913	0.720	0.805
2:Zurich-2:Paris	1.054	-0.709	2.818	0.817
2:Tartu-2:Poznan	-1.042	-2.845	0.760	0.854
1:Poznan-1:Almada	1.283	-0.955	3.521	0.863
3:Tartu-3:Almada	1.280	-0.970	3.529	0.871

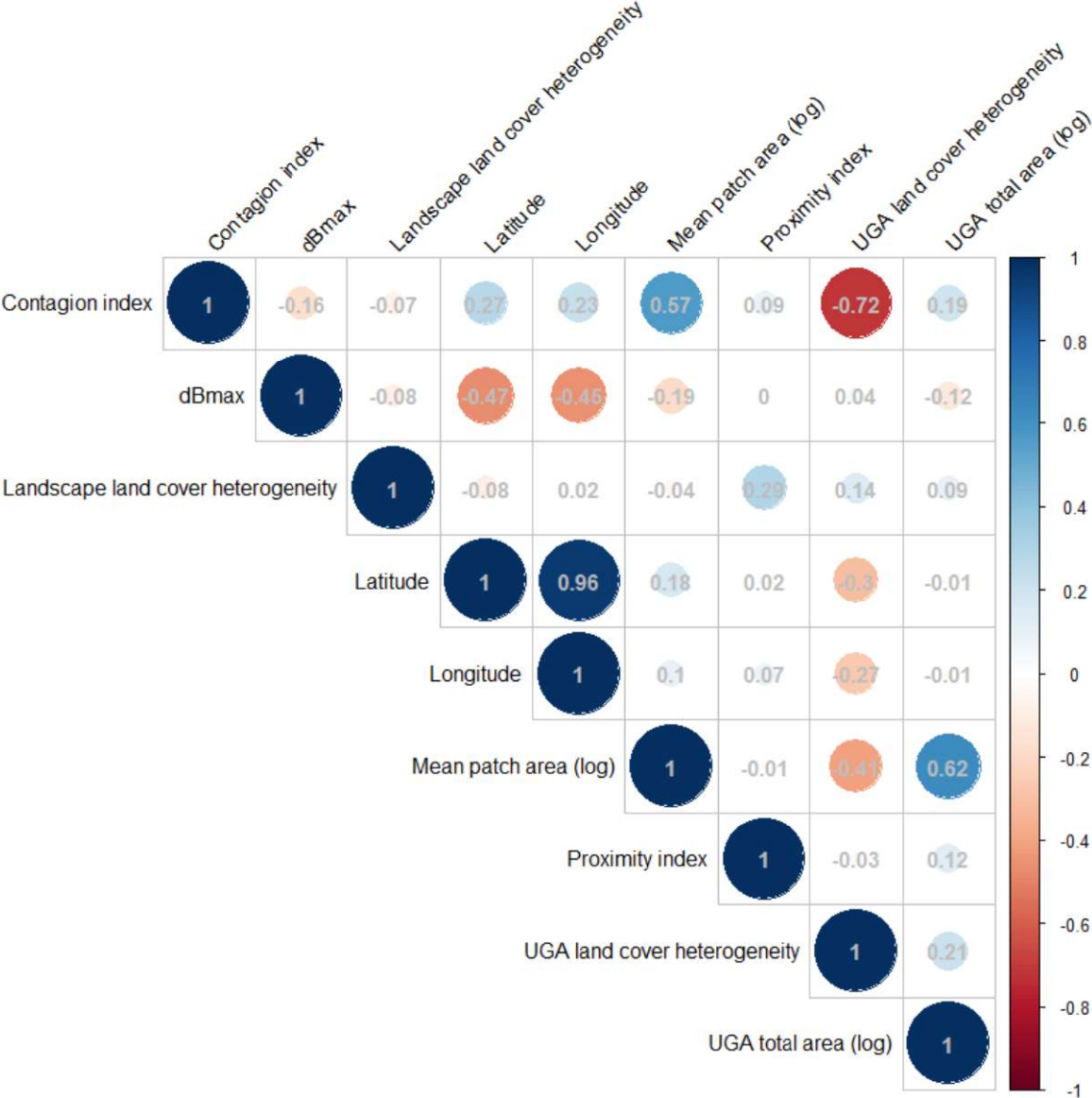
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2:Poznan-2:Almada	1.021	-1.217	3.259	0.981
1:Zurich-1:Lisbon	-0.742	-2.558	1.075	0.994
1:Poznan-1:Lisbon	0.685	-1.117	2.488	0.997
1:Zurich-2:Poznan	0.635	-1.167	2.437	0.999
2:Poznan-1:Almada	-0.779	-3.017	1.459	0.999
1:Tartu-1:Almada	-0.725	-2.974	1.525	1.000
1:Zurich-1:Tartu	0.581	-1.236	2.397	1.000
1:Lisbon-1:Almada	0.598	-1.651	2.847	1.000
2:Poznan-1:Paris	-0.427	-2.176	1.322	1.000
2:Zurich-2:Tartu	-0.419	-2.236	1.397	1.000
1:Tartu-1:Paris	-0.372	-2.136	1.391	1.000
2:Zurich-2:Almada	-0.441	-2.690	1.808	1.000
3:Tartu-3:Poznan	-0.325	-2.127	1.478	1.000
1:Paris-1:Almada	-0.352	-2.559	1.855	1.000
1:Tartu-2:Poznan	0.054	-1.748	1.857	1.000
1:Zurich-1:Almada	-0.144	-2.393	2.105	1.000



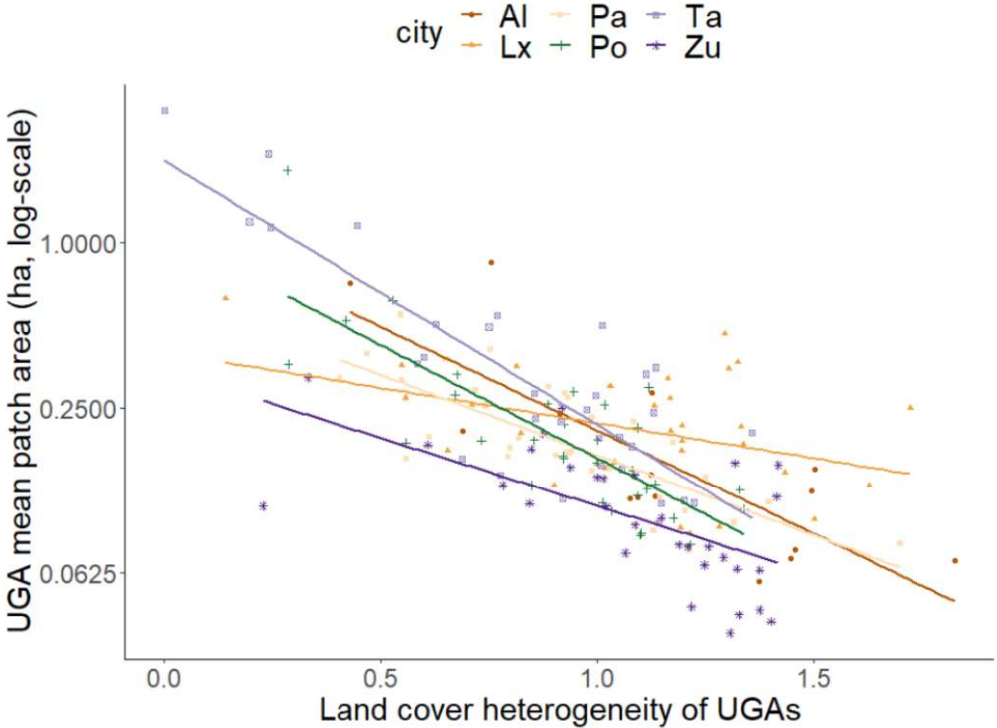
1:Zurich-1:Paris	0.208	-1.556	1.972	1.000
2:Lisbon-2:Almada	-0.312	-2.561	1.938	1.000
2:Tartu-2:Almada	-0.022	-2.271	2.228	1.000
2:Tartu-2:Lisbon	0.290	-1.526	2.107	1.000
2:Zurich-2:Lisbon	-0.129	-1.946	1.687	1.000
3:Lisbon-3:Almada	-0.140	-2.389	2.110	1.000
3:Paris-3:Almada	-0.019	-2.226	2.188	1.000
3:Paris-3:Lisbon	0.121	-1.643	1.885	1.000
3:Zurich-3:Almada	-0.011	-2.260	2.239	1.000
3:Zurich-3:Lisbon	0.129	-1.687	1.946	1.000
3:Zurich-3:Paris	0.008	-1.756	1.772	1.000

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**Appendix H:** Correlogram plot of the predictors for all cities pooled together. The colour and intensity of the circles are proportional to the correlation coefficients in grey. Except for latitude, only the contagion index, which measures the degree of aggregation of the same land cover within each UGA, was above the high correlation threshold ( $\rho > 0.7$  with p-value  $< 0.01$ ) (Zuur et al., 2009). We thus removed this latter variable as it was highly correlated with UGA land cover heterogeneity.



**Appendix I:** Relationship between mean patch area and land cover heterogeneity (Shannon's index of land cover types) of the studied urban green areas (n=176 UGAs). The different slopes represent the relationship for each city. Al, Pa, Ta, Lx, Po and Zu stand for the cities of Almada, Paris, Tartu, Lisbon, Poznan and Zurich, respectively. Model results are presented in Table S3.





**Data accessibility**

Data are available on request

**Conflict of interest declaration**

The authors declare that they have no known competing financial interests or personal relationships that have or could be perceived to have influenced the work reported in this article.

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