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## Effects of urbanization on taxonomic, functional and phylogenetic avian diversity in Europe

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1 **Effects of urbanization on taxonomic, functional and phylogenetic avian diversity in**

2 **Europe**

3

4 *Running head: Avian diversity in European cities*

5

6 Word count: 4951

## 7 **Abstract**

8 Europe is an urbanized continent characterized by a long history of human-wildlife  
9 interactions. This study aimed to assess the effects of specific elements of urbanization  
10 and urban pollution on complementary avian diversity metrics, to provide new insights on  
11 the conservation of urban birds.

12 Our study recorded 133 bird species in 1624 point counts uniformly distributed in  
13 seventeen different European cities. Our results thus covered a large spatial scale,  
14 confirming both effects of geographical and local attributes of the cities on avian diversity.  
15 However, we found contrasting effects for the different diversity components analyzed.  
16 Overall, taxonomic diversity (bird species richness), phylogenetic diversity and relatedness  
17 were significantly and negatively associated with latitude, while functional dispersion of  
18 communities showed no association whatsoever. At the local level (within the city), we  
19 found that urban greenery (grass, bush, and trees) is positively correlated with the number  
20 of breeding bird species, while the building cover showed a detrimental effect. Functional  
21 dispersion was the less affected diversity metric, while grass and trees and water (rivers or  
22 urban streams) positively affected the phylogenetic diversity of avian communities. Finally,  
23 the phylogenetic relatedness of species increased with all the main indicators of  
24 urbanization (building surface, floors, pedestrian's density and level of light pollution) and  
25 was only mitigated by the presence of bushes.

26 We argue that maintaining adequate levels of avian diversity within the urban settlements  
27 can help to increase the potential resilience of urban ecosystems exposed to the stress  
28 provoked by rapid and continuous changes. We listed some characteristics of the cities  
29 providing positive and negative effects on each facet of urban avian diversity.

30 **Keywords:** biotic homogenization; bird diversity; conservation; functional diversity; light

31 pollution; noise pollution; urban green

32

## 33 INTRODUCTION

34 The development of human settlements and global urbanization increase habitat loss and  
35 fragmentation (Schmiegelow and Mönkkönen, 2002; Sklenicka, 2016; Spellerberg, 1998),  
36 negatively affecting the biodiversity at different levels of organization (Crooks et al., 2004;  
37 Morelli et al., 2017; Wilson et al., 2016). The urban areas are among the fastest growing  
38 land-use types across the globe (McDonald, 2008). It is expected that the number of  
39 people living in cities and peri-urban areas will continue increasing to reach approximately  
40 68% of the world population in 2050 (United Nations, 2019). Additionally, these types of  
41 areas are characterized by very dynamic socio-ecological systems (Folke et al., 2002),  
42 constituting an important challenge for ecological communities surrounding or even  
43 occupying such areas.

44 The expansion of urban areas alters both biotic and abiotic ecosystem properties, thereby  
45 leading to biodiversity loss around the world Federico Morelli. Nonetheless, biodiversity  
46 can be partitioned into many facets or components, each one describing a different  
47 characteristic of the species assemblages (Meynard et al., 2011; Verde Arregoitia et al.,  
48 2013). Recently, studies highlighted the importance of considering different facets of  
49 communities for better characterizing their conservation status, especially in urban areas  
50 (Devictor et al., 2010; Lees and Moura, 2017; Morelli et al., 2017). Taxonomic diversity,  
51 simply measured as the number of species in a given assemblage (Magurran, 2004), is  
52 often used to describe the species assemblages. On the other hand, functional diversity is  
53 an essential aspect linking species assemblage with ecosystem functioning and  
54 environmental constraints (Mouchet et al., 2010). For example, functional diversity can  
55 indicate the variety of roles that different organisms play in the ecosystem and assembly  
56 rules are driven by functional traits (Petchey and Gaston, 2006). Last but not least,

57 phylogenetic diversity, which quantifies the evolutionary diversity in communities,  
58 describing the evolutionary heritage or relatedness of all species in a given community  
59 (Faith and Baker, 2007; Laity et al., 2015; Tucker et al., 2016), is increasingly considered  
60 to be a great tool in community ecology and nature conservation (Tucker et al., 2019;  
61 Winter et al., 2013). In the specific case of the effects of urbanization on overall  
62 biodiversity, is particularly relevant to highlight that strategies based only on taxonomic  
63 diversity could be inadequate to consider the ecological role and then the contribution of  
64 each species to the community (Safi et al., 2013).

65 Birds are among the group of species most deeply impacted by the urbanization process  
66 (Devictor et al., 2008; McKinney and Lockwood, 1999). The effects of urbanization on  
67 biodiversity are several, but scientists agree that they are mainly negative (Aronson et al.,  
68 2014; Grimm et al., 2008; Ibáñez-Álamo et al., 2016; McKinney, 2002). Previous studies  
69 have dealt with changes in avian community composition related to functional traits,  
70 leading to reductions of functional spaces effectively occupied (Jokimäki et al., 2014; Pauw  
71 and Louw, 2012), to changes in urban tolerance (Callaghan et al., 2020) and to declines in  
72 the number of specialist species. These effects are commonly attributed to a process  
73 known as 'biotic homogenization' (Clergeau et al., 2006; Devictor et al., 2008; Ferenc et  
74 al., 2014b). However, the effects of urbanization on birds' phylogenetic diversity still  
75 continue to be uncertain (Ibáñez-Álamo et al., 2016; Morelli et al., 2016), even though  
76 certain clades are known to be more vulnerable than others to anthropogenic pressures  
77 (Thuiller et al., 2011). Several structures in urban areas can represent different challenges  
78 and opportunities for bird species, depending on how adaptable birds are to coexist with  
79 humans (Tryjanowski et al., 2021). The amount and characteristics of urban greenery can  
80 determine the capacity of urban areas to support fauna and then be useful for managers  
81 and urban planners to mitigate some of the negative effects of urbanization on biodiversity

82 (Escobar-Ibáñez et al., 2020; Villaseñor et al., 2021). Nevertheless, a cautionary principle  
83 is needed since the total vegetation abundance could be an inadequate proxy for  
84 measuring the urban greenery benefits supporting biodiversity (Berland et al., 2020).  
85 Some other anthropogenic structures can also attract bird species to the urban areas,  
86 offering suitable sites for perching, nesting, and foraging (Morelli et al., 2014; Palacio,  
87 2020; Reynolds et al., 2019). In fact, farmlands, villages and cities provide habitat and food  
88 resources for urban exploiters or adapters bird species (Evans et al., 2009b, 2009a;  
89 Reynolds et al., 2017; Tryjanowski et al., 2021, 2015).

90 Additionally, the levels of light and/or noise pollution of the cities could be associated with  
91 urban birds' distribution because they attract or prevent their presence. There is solid  
92 scientific evidence about the negative effect of artificial light at night (ALAN) on many  
93 species, including amphibians, birds, mammals, insects and even plants (Bennie et al.,  
94 2015; Robert et al., 2015). During the last few decades, ALAN increased to such an extent  
95 that it pollutes the environment, representing a serious biodiversity threat (Dominoni et al.,  
96 2016; F. Hölker et al., 2010; Franz Hölker et al., 2010; Kempenaers et al., 2010; Owens et  
97 al., 2020). The documented effects of ALAN on bird species are related with alterations of  
98 the natural daily, monthly and seasonal light and dark rhythms, capacities of individuals  
99 related to navigate using night sky view, and also with changes in natural circadian  
100 rhythms, behavioral alterations as well as interferences with migration activities in many  
101 species (Adams et al., 2019; Dominoni, 2015). Furthermore, noise pollution also affects  
102 the behavior and fitness of bird species, compromising their reproductive success (Díaz et  
103 al., 2011; Francis et al., 2012; Ortega, 2012). Noise pollution is a byproduct of the  
104 urbanization process, related to the density of human settlements, transport services and  
105 industrial activities. The recent rise in noise levels in cities and urban areas is marked in  
106 both magnitude and extent, with an estimated 30% of the European population exposed to

107 noise levels from road traffic greater than 55dB (decibels) at night  
108 (<http://www.euro.who.int/en/health-topics/environment-and-health/noise/data-and->  
109 statistics), that is significantly above the threshold of 40dB recommended by the World  
110 Health Organization. However, despite the potential impact of this novel and widespread  
111 environmental force across the globe, only little is known about how this ecologically novel  
112 acoustic condition affects natural communities (Francis et al., 2012).

113 A better understanding of the impact of urban characteristics on the mitigation of  
114 biodiversity loss can help develop strategies for wildlife management in urban ecosystems  
115 (Miller and Hobbs, 2002; Villaseñor et al., 2021). In the last decades several studies  
116 focusing on the main effects of urbanization on biodiversity distribution and maintenance  
117 (Beninde et al., 2015; Escobar-Ibáñez et al., 2020; Pautasso et al., 2011; Sushinsky et al.,  
118 2013), as well as in terms of biotic or evolutionary homogenization (Crooks et al., 2004;  
119 Morelli et al., 2016; Sol et al., 2017) were published. However, a more accurate  
120 assessment of how and which urban characteristics affect different facets of avian diversity  
121 is still needed.

122 The main aim of this study is to assess the impact of specific elements of urbanization and  
123 urban pollution on complementary avian diversity metrics to provide new insights on the  
124 conservation of urban birds in European cities. More specifically, we tested whether  
125 geographical patterns as latitude, urban characteristics such as land use composition,  
126 building structure and vegetation arrangements, plus light and noise pollution affect  
127 taxonomic, functional, and phylogenetic diversity of breeding bird populations in European  
128 cities.

129



## 130 **METHODS**

### 131 **Study area and bird data collection**

132 Fieldwork was performed in 17 different cities located along a continent-wide latitudinal  
133 gradient in 10 European countries (Fig. 1). The approach involving different urbanized  
134 areas is particularly indicated for investigating general patterns at a large spatial scale  
135 (Ibáñez-Álamo et al., 2016; Morelli et al., 2016).

136 Data on bird species were collected using the standardized point counts method (Bibby et  
137 al., 1992; Voříšek et al., 2010) randomly selected within each city without any prior  
138 knowledge of whether sites are characterized by rich or poor avian communities, carried  
139 out during the 2018 breeding season. The surveys were locally adjusted to the start of the  
140 breeding season based on the local experts' knowledge (e.g., early April in southern Spain  
141 or late May in northern Finland) to minimize potential issues related to differences in the  
142 detectability of bird species (Kéry et al., 2005). All point counts were positioned in  
143 urbanized areas not closer than 500 m from the city border to avoid sampling transitional  
144 suburban areas and separated by at least 150 m from the nearest point count. A total of  
145 1624 point counts were visited with around 100-point counts in each city, with only a few  
146 exceptions (Pesaro: 56, Zielona Góra: 60, Rovaniemi: 83 and Prague: 120). All point  
147 counts were visited after the sunrise for 4 hours only during favorable weather conditions  
148 for a total of 5 minutes of observations. The location of each point was recorded with a  
149 GPS. Data on bird species were collected only by local expert ornithologists to reduce  
150 detection issues due to skill differences among observers. All birds seen or heard within  
151 50m distance from the observer were recorded, except nocturnal species that were not  
152 included in counts because they require a different strategy of surveying.

153 **Urban characteristics, light pollution, and noise pollution**

154 All urban study areas surveyed had multi-storey buildings, single-family houses, roads,  
155 and parks. Our classification of environments as urban (proportion of built-up area >50%,  
156 building density >10/ha and residential human density >10/ha) followed Marzluff *et al.*  
157 (2001), and it has been used in previous studies of urban avian ecology (Clergeau *et al.*,  
158 2006; Loss *et al.*, 2009; Møller *et al.*, 2015; Morelli *et al.*, 2016). In each point count, we  
159 collected data on relative vegetation cover and land use composition within a distance of  
160 50m from the observer (Díaz *et al.*, 2013). Land use/cover categories were classified into 5  
161 types: building (which includes residential building, built with infrastructure and processing  
162 areas and roads), grass, water bodies, bushes (which includes plants from gardens), and  
163 trees (isolated trees, tree lines and patches). All this information is based on *in situ*  
164 estimations performed by the observers. Additionally, we also calculated the average  
165 number of floors of the buildings around the observer, the number of pedestrians walking  
166 during the 5-minutes point count, and the number of bird feeders and nest-boxes directly  
167 visible around 50m from the observer's position.

168 Information for each point about light pollution was extracted from web  
169 <https://www.lightpollutionmap.info>. We used precalculated values from VIIRS satellite of  
170 the year 2018. The values extracted correspond to the Radiance  $10^{-9} \text{ W / cm}^2 \cdot \text{sr}$ , where  
171 W = Watts and sr = steradian.

172 We developed noise pollution models with the 'openoise' tool for QGIS  
173 (<https://plugins.qgis.org/plugins/opeNoise>). This plugin allows one to compute the mean  
174 noise level in 2D space (e.g., around the point count) generated by point sources or by  
175 road sources at fixed receiver points and buildings. We used a noise source based on  
176 Urban Atlas land use categories (see Tab. S3 for more details) and Open Street Map

177 (OSM) buildings as an advanced input for noise reduction and diffraction. We calculated  
178 noise spreading in a 250m range from each source point or line. The results obtained are  
179 the model-based noise values in dB units (mean, range and standard deviation) in a range  
180 of 50m around the point counts.

### 181 **Community and diversity metrics**

182 The bird community at each point count was defined as the total number of bird species  
183 recorded during the visit. Species richness was expressed as the total number of bird  
184 species recorded in each point count (Magurran, 2004). To describe the functional  
185 diversity of the bird species assemblages, we used the functional dispersion (FDis), an  
186 index estimated as the mean distance of all species in the assemblage to the weighted  
187 centroid of the community in trait space (Cappelatti et al., 2020; Laliberté and Legendre,  
188 2010). The functional dispersion was calculated using 18 avian traits provided by Wilman  
189 et al. (2014), focusing on diet and foraging stratum of species. The species trait table  
190 consists of 10 variables that describe the preferences on diet or food types and eight  
191 variables describing the preferences on the substrate from which food is taken. All  
192 variables express the composition of diet or foraging substrate using percentages of ten  
193 major food items (invertebrates, vertebrates (endotherm), vertebrates (ectotherm),  
194 vertebrates (fish), vertebrates (unknown), scavenger, frugivore, nectarivore, granivore,  
195 folivore), and percentages of eight major foraging strata (i.e., below surf, around surf,  
196 ground, understory, mid-high, canopy, aerial, pelagic) (Wilman et al., 2014). For  
197 determining the diet or foraging stratum of each bird species, the proportions were scored  
198 from secondary literature based on word order in sentences describing the diet. Thus, the  
199 trait data are based on semi-quantitative information assessing the relative importance of  
200 each item for the whole life history, characterizing a large portion of the “Eltonian” niches

201 of species (see more details about the traits in Wilman et al. (2014)). A similar data type  
202 was used in a recent study focusing on bird trophic niche (Pigot et al., 2020). The  
203 functional dispersion in each point count was calculated using the 'FD' package for R  
204 (Laliberté et al., 2015).

205 Finally, we calculated phylogenetic diversity (PD) (Faith, 1992) and phylogenetic species  
206 variability (PSVs) or phylogenetic relatedness (Helmus et al., 2007) for each species  
207 assemblage. The PSVs indicate the degree of average phylogenetic relatedness of  
208 species in a given community. To estimate PD and PSVs we built a phylogenetic tree  
209 using the relationships among the species in each point count, based on genetic data from  
210 all bird species (Jetz et al., 2012) provided in 'BirdTree' ([www.birdtree.org](http://www.birdtree.org)), by considering  
211 a consensus tree obtained with the function 'consensus' on 100 random trees, with the  
212 'ape' v5.3 package for R (Paradis et al., 2004). Both metrics were estimated using the  
213 'Picante' v1.7 package for R (Kembel et al., 2010).

## 214 **Statistical analyses**

215 To investigate potential associations between the distribution of each one of the four avian  
216 community and diversity metrics (i.e., species richness, functional dispersion, phylogenetic  
217 diversity and phylogenetic relatedness) and the latitude of the cities investigated, we used  
218 generalized linear models (McCullagh and Nelder, 1989), considering the type of  
219 distribution of each response variable (Box and Cox, 1964). When the response variable is  
220 assumed or suspected to be correlated with the total number of species in the community  
221 (e.g., phylogenetic diversity, Fig. S1), bird species richness (BSR) was added as a  
222 predictor into the modeling procedure. The goodness of fit of each model was estimated  
223 as the ratio between residual and null deviance of the data indicated in the models'  
224 outputs.

225 Generalized Linear Mixed Models (GLMMs) were used to study the changes in bird  
226 community and diversity metrics concerning land use/cover composition around each point  
227 count, the abundance of bushes and trees, number of floors of buildings, number of  
228 pedestrians, nest-boxes and bird feeders, level of light and noise pollution, modeled as  
229 fixed effects. All predictors were re-scaled and centered with the 'scale' function in R, to  
230 avoid convergence warnings during the modeling procedure. No multicollinearity issue was  
231 found among the selected predictors, after exploring it through a correlation matrix and  
232 visual correlograms in R. City was included as a random effect to account for possible  
233 consistent differences among cities. Models were fitted using the package 'lme4' for R  
234 (Bates et al., 2014). The goodness of fit of models was assessed by the mean of the  $R^2$ .  
235 The  $R^2$  measure used in this study was an extension of the statistic from Edwards et al.  
236 (2008) using penalized quasi-likelihood (PQL) estimation (Jaeger et al., 2017). It was  
237 computed by using the package 'r2glmm' for R (Jaeger, 2017).

238 All statistical tests were performed using R software version 3.6.0 (R Development Core  
239 Team, 2019).

240

## 241 RESULTS

### 242 Composition, functional and phylogenetic diversity of bird communities in

#### 243 European cities

244 A total of 133 bird species (Table S2) was recorded at 1624 point counts uniformly  
245 distributed in seventeen European cities (Fig. 1). The top-ten bird species with the highest  
246 frequency of occurrence across the cities were *Passer domesticus* (60%), *Turdus merula*  
247 (43%), *Apus apus* (42%), *Parus major* (37%), *Columba palumbus* (34%), *Columba livia*  
248 (34%), *Streptopelia decaocto* (33%), *Pica pica* (33%), *Chloris chloris* (26%), and *Corvus*  
249 *monedula* (21%) (Table S2).

250 The highest mean values of species richness were found in Poitiers (France), Granada  
251 (Spain), Athens (Greece) and Zielona Góra (Poland). In contrast, the lowest mean values  
252 were found in Jyväskylä (Finland), Budapest (Hungary) and Turku (Finland) (Fig. 1, Table  
253 1). The highest mean values of functional dispersion were located in Tartu (Estonia) and  
254 Groningen (Netherlands), while the lowest values corresponded with Turku (Finland) and  
255 Ioannina (Greece) (Fig. 1, Table 1). Regarding the phylogenetic profile of urban bird  
256 assemblages, we found the highest phylogenetic diversity in Poitiers and Granada cities,  
257 while the lowest values were recorded in Rovaniemi and Jyväskylä (both in Finland) (Fig.  
258 1, Table 1). The phylogenetic species variability among urban bird communities was  
259 highest in Madrid (Spain) and Groningen (Netherlands), and lowest in Rovaniemi and  
260 Jyväskylä (both in Finland) (Fig. 1, Table 1).

#### 261 Effects of latitude and local attributes of the cities on avian diversity

262 Overall, the bird species richness was negatively associated with latitude (Fig. 2, Table  
263 S4). In contrast, functional dispersion of urban birds' communities was not significantly

264 correlated with latitude but was positively associated with the number of species in the  
265 community (Fig. 2, Table S4). Finally, we found that both phylogenetic diversity and  
266 phylogenetic relatedness declined with increasing latitude (Fig. 2, Table S4).

267 The outputs of the modeling procedure showed that taxonomic diversity of urban bird  
268 communities significantly decreases as the building cover increases. In contrast, it  
269 significantly increases when the vegetation cover (i.e., grass, bushes and trees) increases  
270 (Table 2, Fig. 3). On the other hand, the functional dispersion of communities was  
271 significantly and negatively correlated with tree cover, and positively correlated with the  
272 level of light pollution in the cities (Table 2, Fig. 3). Phylogenetic diversity was significantly  
273 and negatively associated with the building coverage, while positively associated with  
274 grass, trees and water cover. Finally, the phylogenetic relatedness of European urban bird  
275 communities significantly increased when water and building cover increased and the  
276 increasing number of building floors, number of pedestrians, and the level of light pollution  
277 (Table 2, Fig. 3). Bush cover was the only variable significantly and negatively associated  
278 with the overall phylogenetic relatedness of urban bird communities (Table 2, Fig. 3).

279 The level of noise pollution, as well as other characteristics of the city such as the number  
280 of bird feeders and nest boxes, were not significantly associated with any of the four avian  
281 diversity and community metrics used in our study (Table 2).

## 282 **DISCUSSION**

283 Urban bird species are expected to be affected by the potential negative effects of the  
284 increasing urbanization process (Aronson et al., 2014; Beninde et al., 2015). In this study,  
285 we provide an extensive and detailed assessment of avian communities within seventeen  
286 different European cities and the relative effects caused by different characteristics of the  
287 cities on each component of the avian diversity. This information is important because not  
288 all components of avian diversity are affected in the same way by urban development  
289 (Ibáñez-Álamo et al., 2019). Our findings offer a framework to focus the main effects of  
290 urban greenery, building density and structure, and the potential impact of noise and light  
291 pollution on bird species assemblages, which could be used in urban planning to increase  
292 the resilience of the urban-nature matrix.

293 We followed a multidimensional approach on the characterization of avian communities,  
294 recognizing that the complexity of ecological systems is better described when focusing on  
295 different facets of avian diversity. Our results constitute a continental-scale assessment of  
296 the phenomena of urbanization impacts on wildlife, and offer valuable information  
297 considering the urgent need for a reconciliation between urban development and  
298 biodiversity conservation (United Nations, 2016).

299 At a large geographical scale, we found that northern European cities are characterized by  
300 avian communities with fewer species. This pattern mirrors a well-recognized ecological  
301 pattern also seen on wild communities: A negative association between species richness  
302 and the latitudinal gradient (Gaston, 2007; Jarzyna et al., 2021). However, other studies  
303 also reported contrasting results for urban birds, showing species richness increasing  
304 towards higher latitudes (Ferenc et al., 2014b). The same negative association was found  
305 in our study for both phylogenetic diversity and relatedness. This could be partially



306 explained by the correlation between species richness and phylogenetic diversity, but not  
307 in the case of phylogenetic relatedness (see Fig. S1). Our results indicate that urban bird  
308 species are less related to each other at northern than at southern latitudes. Interestingly,  
309 the functional dispersion of avian communities within the cities was unrelated to the  
310 latitude of the urban settlements. The functional dispersion of a given community could  
311 change along environmental stress gradients (Valdivia et al., 2017). Such changes are  
312 independent of the overall number of species in the communities (Laliberté and Legendre,  
313 2010).

314 When focusing on the main environmental descriptors of the European cities, we found  
315 that the coverage of green areas at all levels (e.g., soil level as grass and structure level  
316 as bushes and trees) increased the taxonomic diversity of avian communities. In contrast,  
317 increasing the building cover decreased the total number of birds in the species  
318 assemblages. This result confirms numerous previous studies focused on American  
319 (Chapman and Reich, 2007; Melles et al., 2003), Australian (Threlfall et al., 2016),  
320 Chinese (Huang et al., 2015) and European cities (Dale, 2017; Ferenc et al., 2014a;  
321 Morelli et al., 2018). All the other descriptors were not significantly associated with  
322 taxonomic diversity. For example, in our study, the abundance of bird feeders and nest  
323 boxes that was supposed to attract a larger number of species (Tryjanowski et al., 2015),  
324 was not significantly associated with any change in the overall taxonomic diversity. We  
325 expected an effect of bird feeders since urban areas are usually assumed as characterized  
326 by lower availability of natural food resources (Tryjanowski et al., 2015). The potential  
327 effect of the abundance of nest boxes on avian communities is related to the fact that  
328 several birds' cavity-nesters may take advantage of the presence of such artificial support  
329 in urban areas (Jokimäki, 1999; Luniak, 1992). The absence of the effects of bird feeders  
330 and nest boxes in our study may result from our focus on diversity (i.e., the number and

331 identity of species), whereas adding these limiting resources most likely have the largest  
332 impact on species abundances (i.e., the number of individuals within species). Additionally,  
333 we suppose that the role of such elements might be more important during the winter  
334 season (Jokimäki and Kaisanlahti-Jokimäki, 2012).

335 The different elements (land use, building characteristics, pedestrian's density or level of  
336 pollutants) showed different effects on the functional dispersion of avian communities  
337 within the cities. Overall, functional diversity expresses the diversity of functional traits,  
338 which are those components of an organism's phenotype that influence its response to  
339 environmental stress and its effects on ecosystem properties (Hooper et al., 2005; Petchey  
340 and Gaston, 2006). In our study, the effects of urban characteristics on functional  
341 dispersion were less evident than for other community and diversity metrics. Only tree  
342 cover negatively affected the degree of functional dispersion of birds' assemblages. We  
343 speculate that such an association could be due to an overrepresentation of forest birds in  
344 areas covered by large patches of trees, which decrease the overall dispersion of  
345 functional characteristics of the species in the community. However, forest birds could also  
346 be a source of functional heterogeneity, since it is well known that such species often  
347 partition the forest habitat using different foraging substrates, heights and strategies  
348 (Hanzelka and Reif, 2016; Lara et al., 2015). Additionally, we found a positive correlation  
349 between this functional diversity measure and the level of light pollution in the city.

350 However, this correlation could be partially explained by the fact that the highest level of  
351 light pollution in the Finnish city of Jyväskylä, which was also characterized by the highest  
352 values of functional dispersion on urban bird's communities. Another potential explanation  
353 could be related to the presence of several insectivorous species (e.g., *Apus apus*, *Apus*  
354 *melba*, *Delichon urbicum* and *Hirundo rustica*) attracted to foraging activities in areas at  
355 high artificial illumination. The presence of such species, in combination with other seed

356 eaters, and omnivorous birds, could increase the overall gradient of the functional space  
357 used by the species assemblage.

358 Finally, focusing on the phylogenetic print of urban avian communities, we found that some  
359 characteristics of cities, such as the grass coverage, the presence of trees and water  
360 streams, overall increased the level of phylogenetic diversity of the communities. We can  
361 speculate that water bodies could provide habitat for -related birds, typically from different  
362 families than more terrestrial birds (e.g., ducks, geese, shorebirds, gulls). Also, tree  
363 patches within the urban matrix could provide a similar effect, attracting woodpeckers and  
364 even raptors. On the contrary, the density and coverage of buildings significantly  
365 decreased the phylogenetic diversity of the communities. This outcome is important,  
366 constituting a complementary information to previous studies that highlighted how the  
367 urbanization is also filtering negatively the more evolutionary unique bird species (Ibáñez-  
368 Álamo et al., 2016; Morelli et al., 2016; Sol et al., 2017). An accurate plan of urban  
369 greenery, increasing the density and surface of tree or grass patches and water bodies in  
370 some parts of the cities, could help mitigate this negative effect.

371 The last measure evaluated in this study, the phylogenetic species variability or  
372 phylogenetic relatedness of species (Helmus et al., 2007), explains how many species in a  
373 given community are close in an evolutionary point of view. Closely related species  
374 produce a higher phylogenetic relatedness. Interestingly, in all European cities, increasing  
375 the building density, the number of building's floors, the density of pedestrians and the  
376 level of light pollution (all indicators often used to define the degree of anthropization) we  
377 found avian communities composed of birds largely close related from a phylogenetic point  
378 of view. This type of phylogenetic homogenization could describe the structure and  
379 assembly of urban bird communities. We can expect, also following Darwin's hypothesis,

380 that in communities with more closely related species, the level of competition should be  
381 higher (Godoy et al., 2014). Darwin speculated that niche overlap between more closely  
382 related species would hinder their coexistence (Darwin, 1859), and there is evidence that  
383 interspecific competition with urbanized species are preventing less urbanized, closely  
384 related species from colonizing cities (Møller and Díaz, 2018). However, despite that the  
385 evolutionary relatedness could be related to interspecific competition and niche  
386 differences, it could also relate to average fitness differences among species (Godoy et al.,  
387 2014). Anyway, we demonstrated that higher urbanization increases the phylogenetic  
388 relatedness of urban avian communities in Europe. Also, the overall surface of water  
389 bodies or streams in the cities increased the phylogenetic relatedness of species, clearly  
390 because they attract many waterbirds (e.g., *Anas platyrhynchos*, *Anser anser*, etc.) that  
391 are closely related.

392 The only characteristic of the cities favouring less phylogenetically correlated  
393 assemblages, and so a potential tool for urban planning, was the surface of vegetation  
394 cover at the level of shrubs and bushes. Such characteristics are mainly associated to  
395 urban parks and private gardens.

396 In summary, our findings could be used by local and regional governments as  
397 recommendations or guidelines for smart eco-urban planning to incorporate green spaces  
398 and urban greening characteristics into urban planning frameworks, maximizing, when  
399 possible, the avian diversity by considering taxonomic, functional and phylogenetic  
400 dimensions. Specifically, measures such as the creation of small or medium-sized green  
401 areas, composed of trees, bushes or also patches with grass in the densest areas of the  
402 cities, can increase the number of bird species by providing additional niches to be  
403 occupied (Capotorti et al., 2015; Stagoll et al., 2012). Large patches of grass and trees can

404 also favor bird communities with higher phylogenetic diversity. At the same time,  
405 ornamental plants of urban gardens and bushes in the parks can help to create avian  
406 communities less phylogenetically correlated, so characterized by a greater variance in  
407 competitive outcomes and niche use. Overall, maintaining adequate levels of avian  
408 diversity within the urban settlements can help to increase the potential resilience of urban  
409 ecosystems (Elmqvist et al., 2003), a result particularly desired if facing land use and  
410 climate change scenarios.

411

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749

750 **Tables**

751 Table 1. List of the 17 European cities focused on this study, their geographic positions, and values of four investigated avian diversity  
 752 and community metrics (bird species richness (BSR), functional dispersion (FDis), phylogenetic diversity (PD) and phylogenetic  
 753 relatedness (PSVs), expressed as mean and standard deviation (sd).

<b>City</b>	<b>Latitude (mean)</b>	<b>Longitude (mean)</b>	<b>BSR (mean)</b>	<b>BSR (sd)</b>	<b>FDis (mean)</b>	<b>FDis (sd)</b>	<b>PD (mean)</b>	<b>PD (sd)</b>	<b>PSVs (mean)</b>	<b>PSVs (sd)</b>
Granada	37.18263	-3.60464	11.69	4.25	3.5728	0.3399	532.0035	127.7200	0.5480	0.0521
Athens	38.00247	23.78773	9.87	3.77	3.4532	0.5524	489.0876	157.7740	0.5232	0.1068
Ioannina	39.66552	20.85271	5.90	3.18	3.0768	0.6223	342.6522	99.1850	0.5077	0.1066
Toledo	39.86640	-4.03093	7.16	3.14	3.2665	0.7369	385.9180	111.3631	0.5557	0.1023
Madrid	40.44375	-3.70107	5.69	2.70	3.6521	0.6765	372.2879	110.1230	0.6272	0.0819
Pesaro	43.90731	12.90906	6.82	2.72	3.7639	0.4902	409.8594	103.2583	0.5755	0.0869
Poitiers	46.57901	0.344370	12.29	3.12	3.6558	0.2433	565.4686	89.2671	0.5352	0.0456
Budapest	47.50018	19.07067	3.68	1.79	3.1172	0.4751	252.3442	75.8790	0.5452	0.1463
Paris	48.69750	2.185081	6.52	1.95	3.2104	0.5175	392.6384	104.0314	0.5311	0.1126

Prague	50.08755	14.44182	7.52	3.35	3.3311	0.5468	389.1877	117.2042	0.5408	0.1120
Zielona Góra	51.92365	15.49755	9.12	3.27	3.4564	0.4433	464.1151	104.3993	0.5677	0.0621
Poznan	52.41576	16.90839	6.51	2.48	3.4412	0.6199	357.4698	88.2566	0.5244	0.1232
Groningen	53.21866	6.559404	6.19	2.61	3.8182	0.6404	392.9685	130.2227	0.5997	0.0880
Tartu	58.37412	26.72117	7.79	2.72	4.0188	0.6640	430.0078	100.4562	0.5371	0.0922
Turku	60.45367	22.28490	3.86	2.00	3.0229	0.7280	258.7926	68.8306	0.4731	0.1516
Jyväskylä	62.24728	25.75270	3.29	1.51	2.9310	0.8055	220.1992	47.7424	0.4186	0.1378
Rovaniemi	66.30277	25.42584	4.18	1.92	2.9640	0.5638	249.8230	58.5599	0.4355	0.1382

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755 Table 2. Results of generalized linear mixed models (GLMM), accounting for variation in  
756 bird community and diversity metrics (bird species richness, functional dispersion,  
757 phylogenetic diversity, and relatedness) in relation to land use / cover composition around  
758 each point count, abundance of bushes and trees, number of floors of buildings,  
759 abundance of pedestrians, nest-boxes and bird feeders, and level of light and noise  
760 pollution, modeled as fixed effects. City was included as a random effect to account for  
761 possible consistent differences among cities. The full model is based on 1211-point counts  
762 with complete information. Abbreviations: Std. Error, standard error. Significant variables  
763 are highlighted in bold in the table. The R<sup>2</sup> of models was 0.341 for BSR, 0.031 for FDis,  
764 0.113 for PD and 0.197 for PSVs.

<b>Model target: Bird species richness</b>				
Variables	Estimate	Std. Error	z value	p-value
(Intercept)	1.91474	0.08848	21.639	< 2e-16
<b>Grass</b>	<b>0.07278</b>	<b>0.01882</b>	<b>3.868</b>	<b>0.00011</b>
<b>Bush</b>	<b>0.04606</b>	<b>0.01412</b>	<b>3.263</b>	<b>0.00110</b>
<b>Tree</b>	<b>0.04936</b>	<b>0.01445</b>	<b>3.417</b>	<b>0.00063</b>
<b>Built</b>	<b>-0.08563</b>	<b>0.02086</b>	<b>-4.105</b>	<b>4.0E-05</b>
Water	0.01133	0.00899	1.26	0.20774
Light pollution	-0.03839	0.02358	-1.629	0.10341
Noise pollution	-0.00320	0.01126	-0.284	0.77648
Pedestrians	-0.00821	0.01240	-0.662	0.50789
Building floors	-0.00701	0.01560	-0.45	0.65293
Bird feeders	0.00531	0.00974	0.545	0.58547
Nest boxes	-0.01757	0.01324	-1.327	0.18466

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**Model target: Functional dispersion**

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Variables	Estimate	Std. Error	t value	p-value
(Intercept)	3.45436	0.10184	33.921	<0.00001
Grass	-0.00825	0.02881	-0.286	0.77472
Bush	0.03818	0.02100	1.819	0.06897
<b>Tree</b>	<b>-0.04766</b>	<b>0.02198</b>	<b>-2.169</b>	<b>0.03010</b>
Built	-0.01505	0.03096	-0.486	0.62691
<b>Light pollution</b>	<b>0.11208</b>	<b>0.02934</b>	<b>3.82</b>	<b>0.00013</b>
Water	0.01692	0.01450	1.167	0.24335
Noise pollution	0.00407	0.01739	0.234	0.81515
Pedestrians	0.01793	0.01641	1.093	0.27439
Building floors	0.01611	0.02108	0.764	0.44488
Bird feeders	0.00399	0.01482	0.269	0.78805
Nest boxes	0.02224	0.01712	1.299	0.19383

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**Model target: Phylogenetic diversity**

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Variables	Estimate	Std. Error	t value	p-value
(Intercept)	390.16640	26.75840	14.581	<0.00001
<b>Grass</b>	<b>18.61930</b>	<b>5.27790</b>	<b>3.528</b>	<b>0.00042</b>
Bush	7.10220	3.69710	1.921	0.05473
<b>Tree</b>	<b>17.85350</b>	<b>3.87450</b>	<b>4.608</b>	<b>4.1E-06</b>
<b>Built</b>	<b>-13.14680</b>	<b>5.80860</b>	<b>-2.263</b>	<b>0.02361</b>
<b>Water</b>	<b>9.59370</b>	<b>2.55060</b>	<b>3.761</b>	<b>0.00017</b>
Light pollution	6.37070	5.22080	1.22	0.22237
Noise pollution	-5.16680	3.07100	-1.682	0.09248
Pedestrians	-0.33440	2.88890	-0.116	0.90786



Building floors	-2.19700	3.71700	-0.591	0.55448
Bird feeders	3.00870	2.60810	1.154	0.24866
Nest boxes	-2.47160	3.01000	-0.821	0.41157

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**Model target: Phylogenetic relatedness**

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Variables	Estimate	Std. Error	t value	p-value
(Intercept)	0.52989	0.01864	28.435	<0.00001
Grass	-0.00686	0.00486	-1.411	0.15816
<b>Bush</b>	<b>-0.00767</b>	<b>0.00341</b>	<b>-2.25</b>	<b>0.02447</b>
Tree	0.00260	0.00357	0.728	0.46687
<b>Built</b>	<b>0.02244</b>	<b>0.00536</b>	<b>4.191</b>	<b>2.7E-05</b>
<b>Water</b>	<b>0.00824</b>	<b>0.00235</b>	<b>3.5</b>	<b>0.00047</b>
<b>Light pollution</b>	<b>0.03046</b>	<b>0.00479</b>	<b>6.362</b>	<b>1.9E-10</b>
Noise pollution	-0.00300	0.00283	-1.058	0.29009
<b>Pedestrians</b>	<b>0.00955</b>	<b>0.00267</b>	<b>3.583</b>	<b>0.00034</b>
<b>Building floors</b>	<b>0.00693</b>	<b>0.00343</b>	<b>2.023</b>	<b>0.04310</b>
Bird feeders	0.00101	0.00241	0.42	0.67431
Nest boxes	0.00294	0.00278	1.059	0.28967

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766

767 **Figure captions**

768 Figure 1. The seventeen European cities focused on this study, with values of species  
769 richness (BSR), functional dispersion (FDis), phylogenetic diversity (PD) and phylogenetic  
770 relatedness (PSVs) calculated for the avian communities. For graphical purposes, all  
771 variables were standardized from 0 (the minimum value) to 1 (the maximum value). The  
772 background layer represents the artificial light at night (ALAN) for Europe. The image was  
773 produced by mosaicking Defense Meteorological Satellite Program (DMSP) Operational  
774 Linescan System (OLS) satellite images (source: ESRI, NASA - Visible Earth).

775

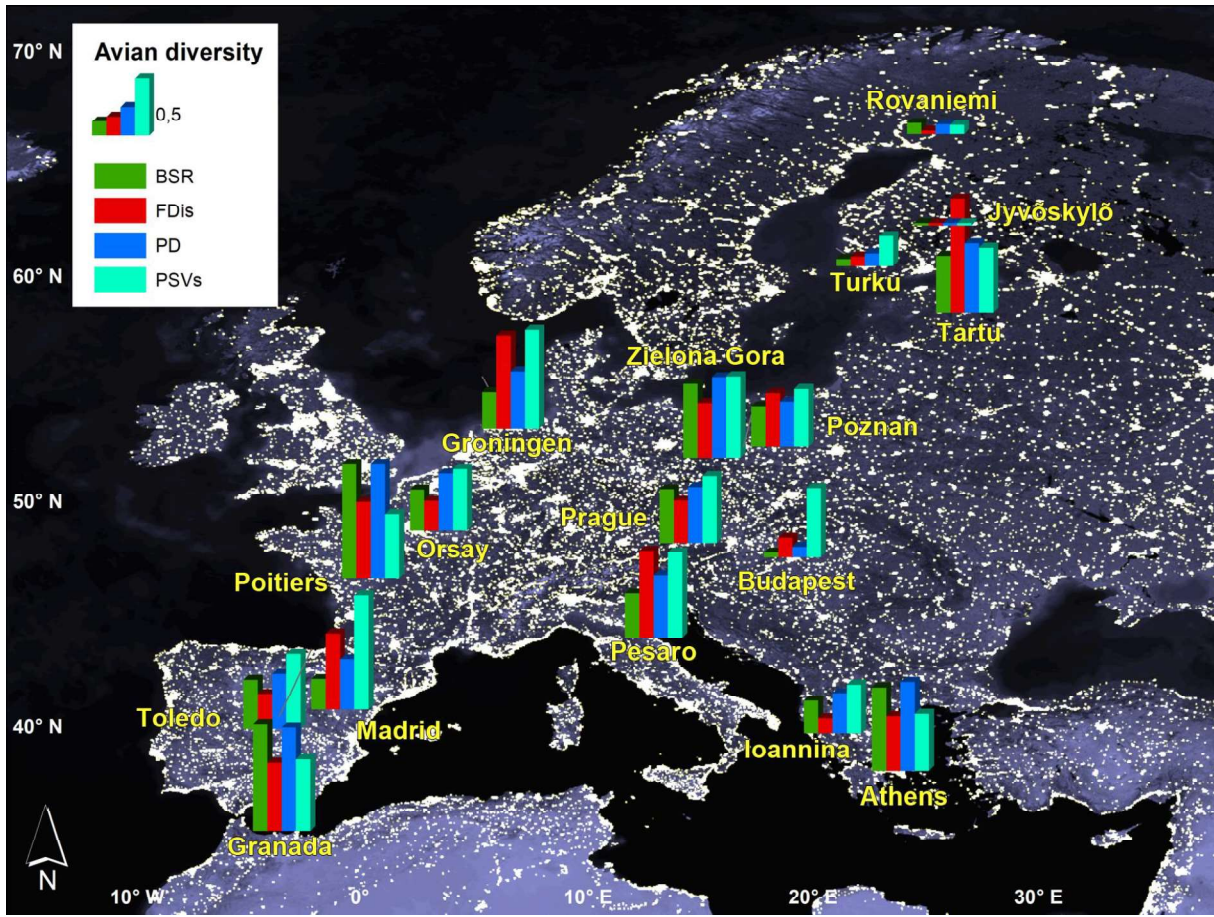
776 Figure 2. Associations between values of (A) species richness (BSR), (B) functional  
777 dispersion (FDis), (C) phylogenetic diversity (PD) and (D) phylogenetic relatedness (PSVs)  
778 calculated for urban avian communities and latitude. The black line is the linear regression,  
779 while the marginal boxplots describe the distribution of data. The figure also shows the  
780 estimates and significance of linear regression models.

781

782 Figure 3. Schematic presentation of main associations between values of species richness  
783 (BSR), functional dispersion (FDis), phylogenetic diversity (PD) and phylogenetic  
784 relatedness (PSVs) calculated for urban avian communities and different characteristics of  
785 the cities. Positive associations are indicated in green colour, while negative ones are  
786 highlighted in red colour. These results reflect the outputs of the modelling procedure,  
787 shown in detail in Table 2.

788

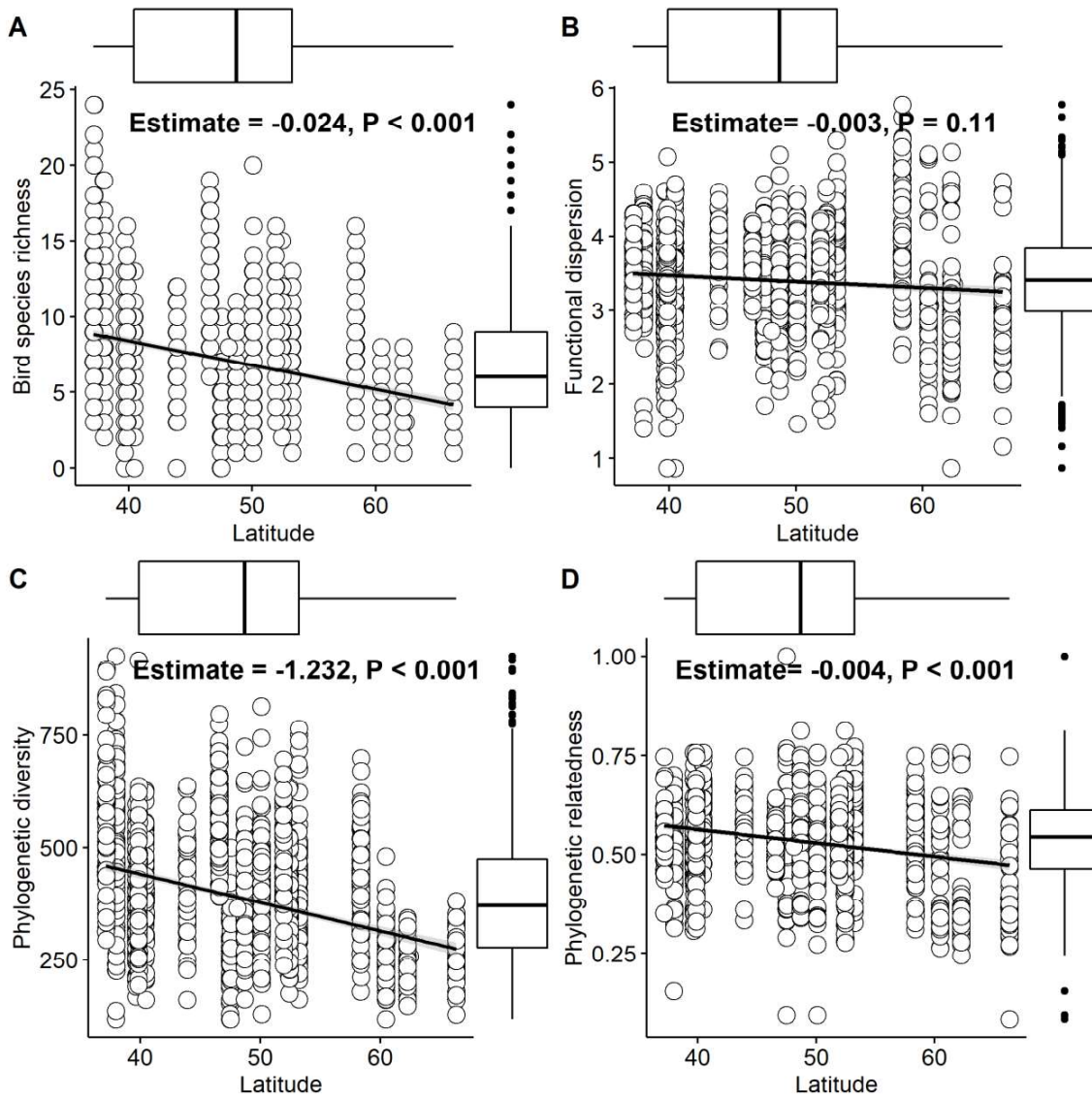
789 Fig. 1



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792 Fig. 2



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795 Fig. 3



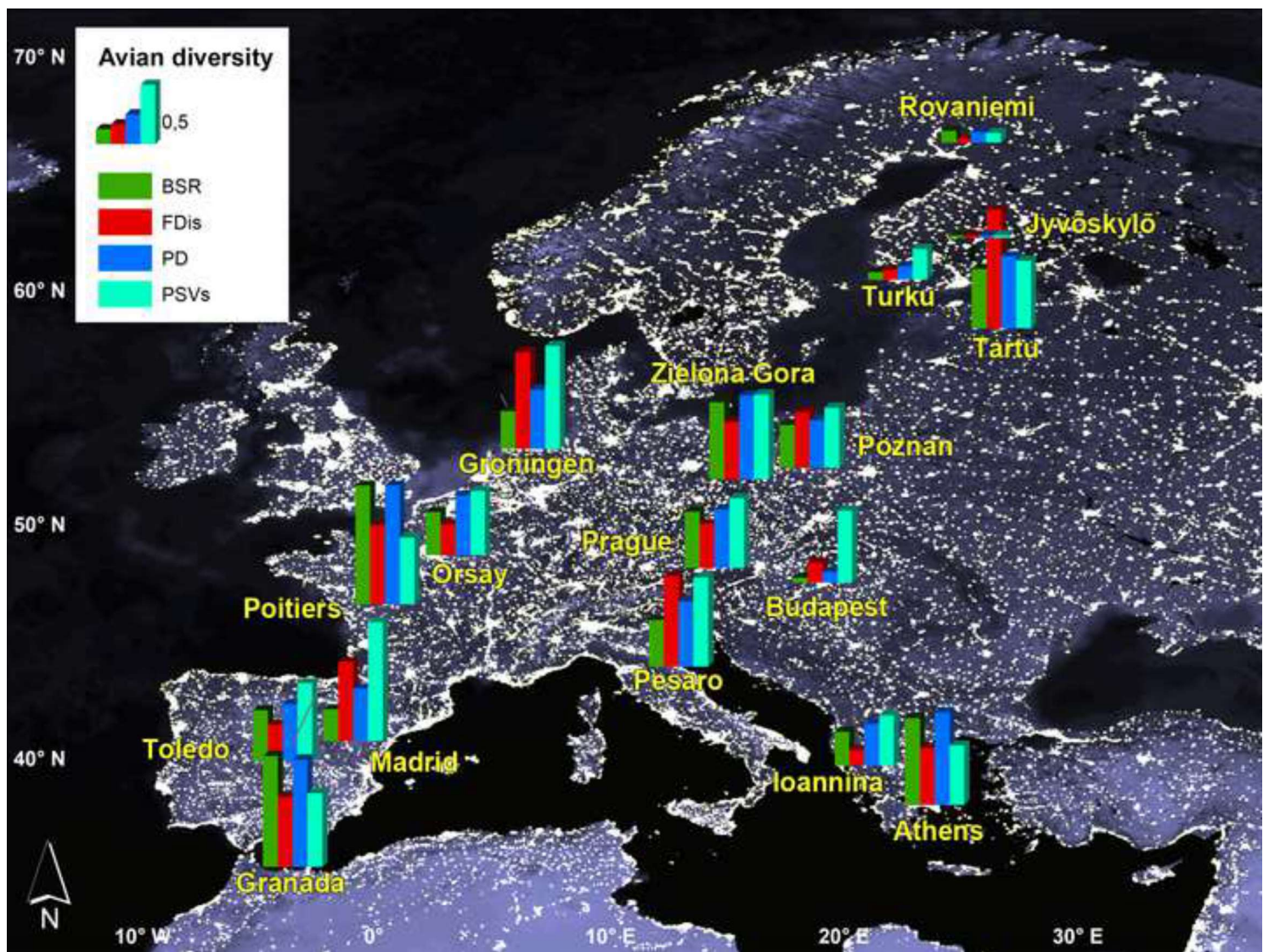
Variables	Taxonomic diversity	Functional dispersion	Phylogenetic diversity	Phylogenetic relatedness
Building	(-)		(-)	(+)
Grass	(+)		(+)	
Bare soil				
Water			(+)	(+)
Bush	(+)			(-)
Trees	(+)	(-)	(+)	
Pedestrians				(+)
Building #floors				(+)
Light pollution		(+)		(+)
Noise pollution				

796



Figure 1

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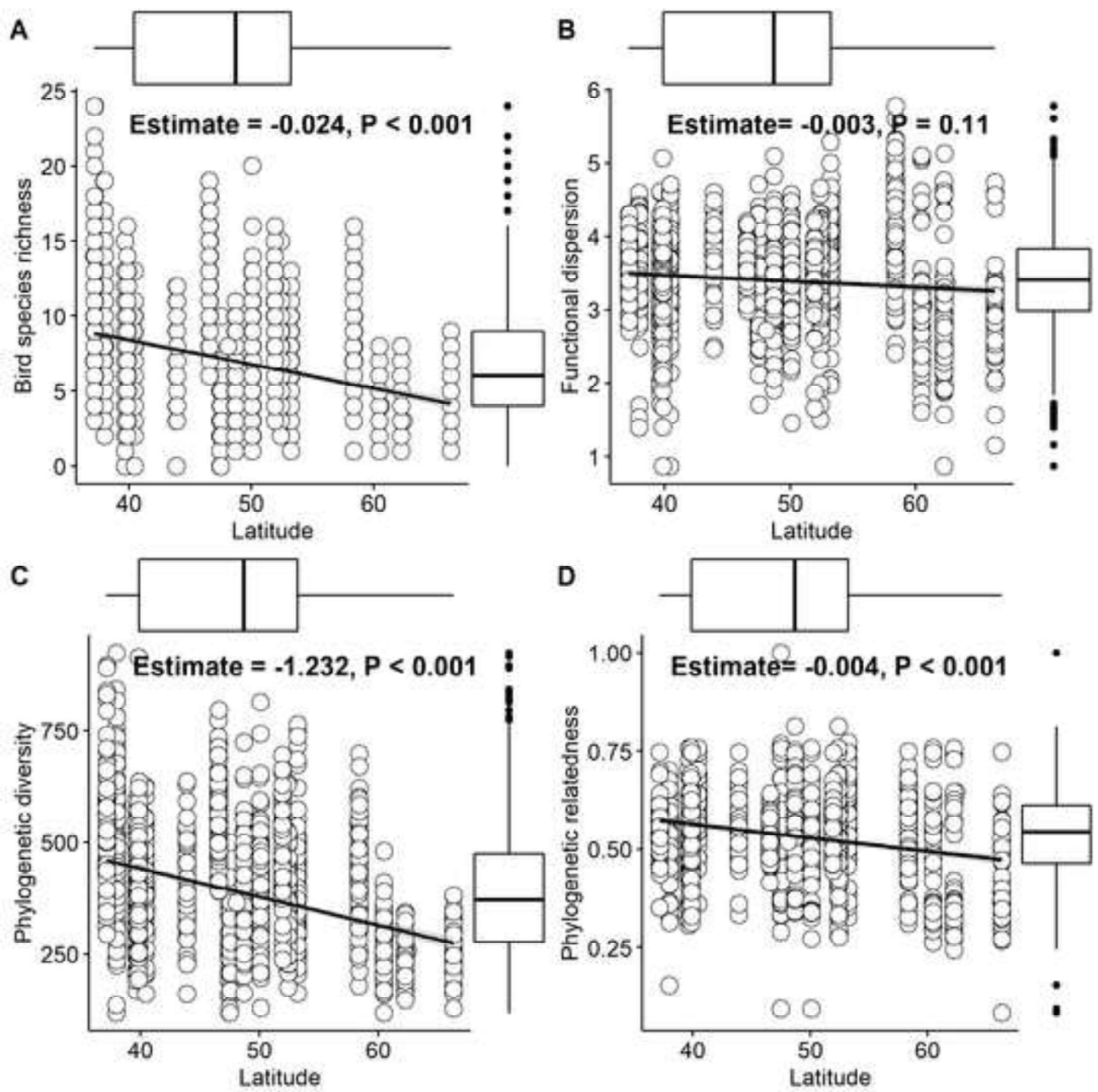


Figure 3

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Variables	Taxonomic diversity	Functional dispersion	Phylogenetic diversity	Phylogenetic relatedness
Building	(-)		(-)	(+)
Grass	(+)		(+)	
Bare soil				
Water			(+)	(+)
Bush	(+)			(-)
Trees	(+)	(-)	(+)	
Pedestrians				(+)
Building #floors				(+)
Light pollution		(+)		(+)
Noise pollution				





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