1   **Biodiversity within the city: Effects of land sharing and land sparing urban**

2   **development on avian diversity**

3

4   Juan Diego Ibáñez-Álamo[1], Federico Morelli[2], Yanina Benedetti[2], Enrique Rubio[1], Jukka

5   Jokimäki[3], Tomás Pérez-Contreras[1], Philipp Sprau[4], Jukka Suhonen[5], Piotr Tryjanowski[6],

6   Marja-Liisa Kaisanlahti-Jokimäki[3], Anders Pape Møller[7] and Mario Díaz[8]

7

8   [1] Department of Zoology, University of Granada, Granada, Spain.

9   [2] Czech University of Life Sciences Prague, Faculty of Environmental Sciences, Department

10   of Applied Geoinformatics and Spatial Planning, Kamýcká 129, CZ-165 00 Prague 6, Czech

11   Republic

12   [3] Nature Inventory and EIA-services, Arctic Centre, University of Lapland, P. O. Box 122,

13   FI-96101 Rovaniemi, Finland

14   [4] Department of Biology, Ludwig-Maximilians-University Munich, Munich, Germany

15   [5] Department of Biology, University of Turku, Turku, Finland

16   [6] Institute of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71C, PL-60-

17   625 Poznań, Poland

18   [7] Ecologie Systématique Evolution, Université Paris-Sud, CNRS, AgroParisTech, Université

19   Paris-Saclay, F-91405 Orsay Cedex, France

20   [8] Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales

21   (BGC-MNCN-CSIC), E-28006 Madrid, Spain

Corresponding author: J.D. Ibáñez-Álamo (e-mail: jia@ugr.es; phone: +34 958243243)

26

Abstract

Urbanization, one of the most extreme human-induced environmental changes, is negatively affecting biodiversity worldwide, strongly suggesting that we should reconcile urban development with conservation. Urbanization can follow two extreme types of development within a continuum: land sharing (buildings mixed with dispersed green space) or land sparing (buildings interspersed with green patches that concentrate biodiversity-supporting vegetation). Recent local-scale studies indicate that biodiversity is typically favored by land sparing. We investigated which of these two types of urbanization is associated with a higher taxonomic (i.e. species richness), functional, and phylogenetic diversity of birds. To do so, we collected information on breeding and wintering bird assemblages in 45 land-sharing and 45 land-sparing areas in nine European cities, which provide the first attempt to explore this question using a large geographical scale and temporal replication. We found that land-sharing urban areas were significantly associated with a higher taxonomic and functional diversity of birds during winter, but not during the breeding season (with only a marginally significant effect for functional diversity). We found no association between the type of urban development and phylogenetic diversity. Our findings indicate that not all components of avian diversity are similarly affected by these two means of urban planning and highlight the importance of integrating the temporal perspective into this kind of studies. Our results also offer useful information to the current debate about the trade-off between biodiversity conservation and human well-being in the context of land

sharing and sparing urban practices. In addition, we found that certain small-scale urban landscape characteristics (i.e. few impervious surfaces, high water or tree cover) and human practices (i.e. bird feeders or plants with berries) can help maintaining more diverse urban bird assemblages. We provide specific suggestions for both policymakers and citizens that hopefully will help to create more biodiversity-friendly cities in the future.

1. Introduction

Urban areas are growing disproportionally faster than any other form of land cover on our planet (United Nations, 2015) with future predictions estimating a global increase by 200% by 2030 to accommodate the increasing urban human population (Fragkias et al., 2013). This human-induced landscape change, known as urbanization, is one of the most extreme anthropogenic impacts on the Earth's ecosystems (Foley et al., 2005; Groom et al., 2006). Urban land-cover is associated with important changes in natural habitat structure and ecosystem functioning (Grimm et al., 2008; Gaston, 2010; Forman, 2014), but also with a significant global reduction in biodiversity (Ibáñez-Álamo et al., 2017; McKinney, 2008; Newbold et al., 2015) that is expected to increase even more in the near future (Seto et al., 2012). Therefore, there is an urgent need to reconcile urban development with biodiversity conservation as recently recognized by the United Nations in its World Cities Report (United Nations, 2016).

Urban areas can be developed in many different ways, but generally fall into a land-sharing or land-sparing model of development (Lin and Fuller, 2013). Land-sharing urban areas are typically associated with extensive urban development and sprawl (e.g. single family houses) and they are characterized by low-density housing and human populations as well as with small and fragmented green areas usually in the form of backyards and street vegetation. On the other hand, land-sparing urban areas are typically associated with urban

intensification (e.g. multi-story buildings) and they are characterized by high-density human populations and housing interspersed by large green patches (i.e. forest remnants or, more frequently, large urban parks) (Lin and Fuller, 2013; Soga et al., 2014). This dichotomy is somewhat arbitrary, as it emphasizes the endpoints of a continuum rather than its gradual nature (Finch et al., 2019; Kremen, 2015), but this framework is of critical importance in the context of urban ecosystem conservation (Lin and Fuller, 2013; Norton et al., 2016; Stott et al., 2015). Consequently, this topic has recently received increasing attention by the scientific community (e.g. Sushinsky et al., 2013; Soga et al., 2014, 2015; Collas et al., 2017; Villaseñor et al., 2017) although habitat fragmentation has been known to be important for biodiversity also within urban areas for a longer time (Fahrig, 2003; Fernández-Juricic and Jokimäki, 2001). The first study to apply the land-sharing/sparing framework into an urban context investigated their effect on biodiversity in the city of Brisbane (Australia) and found that the land-sparing type of development outperformed its land-sharing alternative, retaining richer urban bird assemblages during the breeding season (Sushinsky et al., 2013). Additional local studies modeling the response of other taxa (i.e. trees and mammals) to future urban scenarios also found evidence indicating larger benefits associated with the land-sparing strategy (Caryl et al., 2016; Collas et al., 2017; Villaseñor et al., 2017). Furthermore, Soga et al. (2014) determined that in the city of Tokyo land sparing rather than land sharing allowed a higher population size of ground beetles and butterflies when intensity of urbanization was high. However, this relationship changed under a lower level of urbanization, showing that ground beetles were favored by land sparing but butterflies by land sharing. These pioneering studies have provided useful information regarding the debate about how to develop more biodiversity-friendly cities in the future, but they are local studies temporally restricted (e.g. breeding season) that prevent generalization of results. In order to advance this debate, we

96   urgently need spatially and temporally replicated analyses (Lin and Fuller, 2013; Stott et al.,

97   2015; Sushinsky et al., 2013).

98   Moreover, biodiversity refers to variation at all levels of biological organization and

99   includes three main elements (genetic, ecological and organismal diversity) (Gaston and

100 Spicer, 2004). Species richness is the most commonly used measure of biodiversity, but it has

101 important restrictions to capture certain components of biodiversity such as those associated

102 with evolutionary history or morphological variation (Gaston and Spicer, 2004; Magurran,

103 2004; Magurran and McGill, 2011). Recent trends in biodiversity studies strongly

104 recommend the use of multiple measures to investigate several components of biodiversity

105 simultaneously because they might be affected differently by the same process (Devictor et

106 al., 2010; Hanspach et al., 2015; Lee and Martin, 2017; Morelli et al., 2017a, 2017b). In

107 addition to measures of taxonomic diversity (e.g. species richness), these studies suggest

108 using indicators of functional and phylogenetic diversity that offer information on the

109 different functional traits/roles and evolutionary history of the species of a community.

110 However, despite recent recommendations in nature conservation optimization encouraging

111 the use of these additional diversity measures (Monnet et al., 2014; Winter et al., 2012),

112 previous studies investigating the land-sparing/sharing debate focused exclusively on

113 taxonomic diversity (e.g. Sushinsky et al., 2013; Soga et al., 2014; Villaseñor et al., 2017).

114 The study of these three components of biodiversity is even more important in the urban

115 context given the different association that they show with urbanization at the global scale,

116 with cities holding overall significantly lower taxonomic and phylogenetic diversity (e.g.

117 McKinney, 2008; Ibáñez-Álamo et al., 2017; Sol et al., 2017), but higher functional diversity

118 (Oliveira Hagen et al., 2017). Studies investigating the effect of these two types of urban

119 development on taxonomic, functional and phylogenetic diversity will therefore provide an

120 extremely interesting new perspective on the topic, potentially showing unknown effects that

121 might lead to additional conservation recommendations.

122   Here, using birds and a continental spatial scale approach in two different seasons, we

123 (1) investigated whether land-sharing urban areas are associated with lower biodiversity

124 measures (taxonomic, functional and phylogenetic diversity) than land-sparing urban areas.

125 The prediction regarding taxonomic diversity is based on previous local studies (see above).

126 No clear prediction regarding the other two components of biodiversity can be made given

127 the lack of previous information and studies that found contrasting effects for these different

128 components using a similar geographical scale (e.g. Morelli et al., 2016). We also (2)

129 explored the temporal consistency in results analyzing data from two different seasons

130 (breeding and wintering seasons). To our knowledge, this temporal perspective has not been

131 investigated so far in the land-sharing/sparing context, despite being crucial for designing

132 effective conservation plans to help guide the construction of cities (Stott et al., 2015).

133 Murgui (2010) found seasonal variation in urban bird assemblages in the city of Valencia

134 (Spain), with a more structured distribution of species during the breeding season than in

135 other seasons. We predict then higher differences in diversity for the breeding than the

136 wintering season. Finally, to provide more specific conservation recommendations for city

137 planners and policymakers, we (3) studied the effect of local scale characteristics of cities

138 (e.g. built cover, vegetation structure or presence of bird feeders) that determine richer

139 taxonomic, functional and phylogenetic avian communities in each season. To our

140 knowledge, there is only one local scale study that has investigated this question using

141 proxies for all three major components of biodiversity for the specific case of Beijing's parks

142 (China) (Morelli et al., 2017a), which highlight the novelty of this last objective. This

143 approach complements classical analyses based on building density alone, taking into account

144 the potential role of different configurations of the urban landscape as well as the influence of

different local factors (e.g. type of green space, human activities…) in towns and cities. We have used birds as our model group because they are key components of ecosystems (Sekercioglu, 2006), good bioindicators for other taxa (Rodrigues et al., 2007), with a widely validated phylogeny (Jetz et al., 2012; Prum et al., 2015) and are well-studied within the urban ecology context (Gil and Brumm, 2014; Lepczyk and Warren, 2012; Marzluff et al., 2001).

2. Methods

2.1. Study area and classification of urban areas

We assessed bird assemblages in nine cities from six different European countries encompassing large latitudinal variation from Granada (latitude 37.2º N) in Southern Spain to Rovaniemi (latitude 66.5º N), northern Finland (Fig. 1). In each city we selected 10 different 500 m x 500 m squares, half of them with a land-sharing urban development and the other half corresponding with land-sparing urban areas (Fig. 1). Individual squares were separated by a mean minimum distance of 570 ($\pm$ 65 m SD). The squares within each city were initially assigned to either one or another type by visual inspection of satellite images available on Google Earth. Land-sharing squares consisted in areas with low-density housing (i.e. single-family houses) and fragmented green areas, while land-sparing squares corresponded with high-density housing areas (i.e. multi-storey buildings), and the majority (>50%) of its green surfaces aggregated into a single patch. We made no distinction on whether the green space was fully natural (i.e. forest remnants) or partially managed (i.e. parks). Given the known positive relationship between the size of green areas and animal biodiversity (including birds) in urban landscapes (Beninde et al., 2015), every land-sharing square in a given city was paired with another land-sparing square of the same city holding a similar overall green area.

169　This procedure allowed us to test for the effect of urban landscape organization avoiding a

170　potential bias associated with the size of green areas.

171　　　We confirmed the initial assignment of each square to one of two urban development

172　styles with a new land sharing-sparing index. Using the same satellite images and QGIS 2.18,

173　we divided each 500 m x 500 m square into 100 cells (50 x 50 m each) and estimated the

174　percentage of green and built surface for each cell (to the nearest 10%). This information was

175　used to calculate the following variables for each 500 m x 500 m square: (1) Percentage of

176　high vegetation cells (those with more than 50% green area) in a single patch (contiguous

177　cells), (2) number of green patches (a green patch is defined as having at least one high

178　vegetation cell), (3) percentage of built cells of all vegetated cells, (4) percentage of only

179　vegetated cells of all vegetated cells, and (5) number of cells with vegetated surfaces.

180　Variables 1 and 2 provide information on the land-sharing/sparing development style at the

181　500 m x 500 m square level with high values of variable 1 associated with land-sparing urban

182　areas (i.e. vegetation in a single patch), while high values of variable 2 are associated with

183　land-sharing urban areas (i.e. vegetation distributed into many patches). Variables 3 and 4

184　provide information on the within-cell land-sharing or land-sparing urban development,

185　respectively, and variable 5 estimates the overall amount of vegetation in the square. With

186　these five variables, we run a principal component analysis (PCA) using the SPSS 25.0

187　package. The first axis (PC1), that explained 53.4% of the total variation, was used as the

188　land sharing-sparing index (Table S1). Overall, positive values of this index were associated

189　with land-sparing squares while negative values indicated land-sharing squares. We found

190　significant differences in the land sharing-sparing index between the initially classified land-

191　sharing and land-sparing squares ($F = 64.04$, $df = 1, 88$, $p < 0.0001$; city as random factor),

192　confirming the suitability of our initial classification. The second axis (PC2) explained

193　21.44% of the total variation and was negatively associated with the number of vegetated

8

194   cells in the square (Table S1). It was then an inverse measure of the overall amount of

195   vegetation and was independent of the land sharing-sparing index. This fact confirmed the

196   paired design of our study and allowed to analyze the independent effects of urban landscape

197   organization and size of green areas on bird diversity.

198   Finally, we also calculated a commonly used urbanization index for each 500 m x 500

199   m square (Liker et al., 2008) to confirm that land-sharing and land-sparing areas did not

200   differ in their urbanization level (i.e. green or built surfaces). A general mixed model

201   including land-sharing/sparing type as fixed factor and city as a random factor showed that

202   the urbanization index in land-sharing (mean $\pm$ SE = -0.17 $\pm$ 0.26) and sparing squares (0.17

203    $\pm$ 0.32) did not differ significantly (F = 1.01, df = 1, 88, p = 0.320). This result was expected

204   due to the paired selection of land-sharing and sparing squares according to their green cover,

205   and it provided confidence that the potential results associated with our study were strictly

206   related to the landscape organization of urban features rather than differences in the intensity

207   of urbanization.

208   *2.2. Bird data collection*

209   Data on bird species were collected using standardized point counts (Bibby et al.,

210   1992), carried out during the 2016 breeding season (April-June) and the following wintering

211   season (December-February). Point counts provide reliable estimates of relative population

212   density (Blondel et al., 1970), constituting a standardized method in ecology (Bibby et al.,

213   1992) used extensively for monitoring bird populations across Europe (Voříšek et al., 2008).

214   Within each 500 m x 500 m square, 6-7 point counts were randomly selected with a

215   minimum of 100 m distance between them or the border of the square to avoid counting the

216   same individual twice. The location of all point counts was recorded with GPS to quantify

217   birds at the same location both during the breeding and wintering season. We detected birds

218   by sight and sound for 5 min in each point count. Point counts were only carried out during

219   the morning (up to 3 hours after local sunrise) and under favourable weather conditions. We

220   paid special attention to avoid double-counts of the same individual by moving quickly from

221   point to point and by excluding birds that were counted in previous point counts (e.g. clearly

222   conspicuous individuals easily seen or heard). To capture potential temporal changes in bird

223   assemblages within a season (e.g. due to early and late breeders), we carried out two surveys

224   (separated by a month) in each season. We considered all species detected in both surveys for

225   our analyses. We also registered specific landscape characteristics associated with each point

226   count by noting the percentage (to the nearest 10%) of cover with buildings and paved

227   surfaces (i.e. roads), water, vegetation (trees, bushes and grass), and snow (in winter), within

228   a distance of 50 m of each point count (Díaz et al., 2013). In addition, we collected data on

229   the presence of bird feeders and vegetation with berries in winter as potential sources of food

230   for birds. Finally, we counted the number of pedestrians and mammals (e.g. squirrels, cats,

231   dogs) encountered within a distance of 50 m of each point count while assessing birds.

232   Mammals in general, and particularly these species increase their abundance in urban habitats

233   and can have important implications for bird assemblages (Bonnington et al., 2013; Jokimäki

234   et al., 2017; Sims et al., 2008).

235   *2.3. Avian diversity and community metrics*

236   For each season, we estimated three different measures of biodiversity based on bird

237   communities: (1) Bird species richness (BSR) was used as a measure of taxonomic diversity

238   (Magurran, 2004). BSR was calculated as the maximum number of recorded bird species at

239   each sampling site (point count) considering the two surveys within each season. The

240   biodiversity metrics based on species-trait approaches focused on functional aspects of

241   biodiversity (functional diversity metrics), constitute an additional tool to the traditional

taxonomic approach (de Bello et al., 2010). Therefore, we used (2) Rao's quadratic entropy

(Rao's Q) as a measure of the functional diversity of bird communities. Rao's Q is a measure

of functional diversity in a community based on multiple traits, and is a measure not

mathematically constrained to be positively correlated with species richness (Zoltan, 2005).

The Rao's Q was calculated using the avian niche traits provided in Pearman et al. (2014),

which are based on bird traits related to their feeding and breeding ecology. The trait table

consisted of 53 variables that describe the niche of each bird species, including variables

across body mass, food types (13 variables), behavior used for acquiring food (9 variables),

substrate from which food was taken (9 variables), period of day during which a species

foraged actively (3 variables), and nesting habitats (18 variables) (Pearman et al., 2014). All

variables except the body mass were binomial (scored as either 0 or 1). Finally, to explore

changes in bird communities in terms of phylogenetic diversity, we used (3) the evolutionary

distinctiveness (ED) score as a measure of species uniqueness (Jetz et al., 2014). The ED

score for each species is calculated by dividing the total phylogenetic diversity of a clade

amongst its members (Isaac et al., 2007; "www.edgeofexistence.org" 2015). Then, using the

ED score for each bird species present in a community, we calculated the community

evolutionary distinctiveness (CED) of the community as the mean ED for the entire

assemblage (Ibáñez-Álamo et al., 2017; Morelli et al., 2016; Tucker et al., 2016).

2.4. Statistical analyses

To check for spatial autocorrelation issues in the dataset, we performed a Mantel test

(Legendre and Fortin, 2010; Mantel, 1967), based on a matrix with geographic distance

among points and a matrix of differences in bird species richness, functional diversity and

community evolutionary distinctiveness among points, applying Monte Carlo permutations

with 9999 randomizations (Oksanen et al., 2016). Sampling sites were treated as statistically

11

independent observations because the value of spatial autocorrelation was not significant for all tests (e.g. for species richness: r_M = 0.0047, 9999 randomizations, p = 0.554). A preliminary exploration of variables was done by using a Principal Component Analysis (PCA), which is appropriate for detecting potential multicollinearity issues, and then to select the most adequate and less redundant variables for modelling procedures (Janželkovič and Novak, 2012).

We used Generalized Linear Mixed Models (GLMMs) to study the patterns of bird species richness, functional diversity (Rao's Q) and community evolutionary distinctiveness (CED) in relation to land-sharing and land-sparing urban development, amount of green areas, latitude, point-count-level landscape characteristics, presence of bird feeders, berries, and the average number of pedestrians and mammals (cats, dogs, squirrels...) modelled as predictors. We decided to include latitude as a geographical predictor because it could be related to large-scale changes in biodiversity (Mannion et al., 2014; Morelli et al., 2016). Potential interactive effects of latitude, urban development mode and amount of vegetation on bird diversity (Beninde et al., 2015; Díaz et al., 1998) were tested by the corresponding two-way interactions. City (n = 9) was included as a random factor to account for possible consistent differences among cities, and square pair (nested in city) to account for the paired design of the study. The model using bird species richness as response variable was fitted assuming a Poisson distribution after having explored the variable distribution as suggested in Box and Cox (1964). Models were run separately for the breeding or wintering seasons using the SPSS 25.0 package. Full models were tested, and effect sizes of terms with p<0.10 were computed from t statistics following Becker (1999).

3. Results

290   In total, we detected 119 bird species in 593 point counts carried out during the

291   breeding season and 73 bird species in 322 point counts performed during the wintering

292   season. Only three species were identified as introduced (*Alopochen aegyptiacus*, *Myiopsitta*

293   *monachus* and *Phasianus colchicus*), which represented a very small proportion of bird

294   assemblages (2.4%). All squares were visited both seasons, although the number of census

295   points differed among seasons for logistic reasons (e.g. harsh climate, snow cover…). The list

296   of all bird species recorded in this study for both urban development styles, with their ED

297   score, is provided in the Electronic Supplementary Material (Table S3).

298   The urban development style was significantly and negatively associated with

299   functional and, to a lesser extent, taxonomic diversity, especially in winter (Fig. 2; Table S2).

300   Our results indicated that land-sharing urban areas partially supported more diverse bird

301   communities, although the difference was on average small (Fig. 3). The amount of

302   vegetation at the square level had a consistent positive effect on bird diversity that was

303   additive to the effect of the urban development style (Fig. 2). There were no latitudinal trends

304   in bird diversity, although latitude modulated the positive effect of vegetation on taxonomic

305   and phylogenetic diversity, especially in winter (Fig. 2). Positive effects of vegetation were

306   higher at higher latitudes. Effect sizes of square-level (landscape) traits ranged from 7 to 19%

307   (Fig. 2, Table S2).

308   Regarding small-scale (local) predictors, bird species richness during the breeding

309   season was positively associated with bushes and water as well as with the abundance of

310   mammals, but negatively associated with the coverage of built surfaces and the density of

311   pedestrians (Fig. 2). The functional diversity metric (Rao's Q) was only significantly

312   explained by the presence of water and, to a lesser extent, grass. In contrast, phylogenetic

313   diversity (CED) was positively associated with the coverage of trees but negatively correlated

314　with the coverage of built areas (Fig. 2). During the wintering season, all diversity metrics

315　were positively associated with the presence of bird feeders and bushes with berries, and with

316　local abundance of mammals. Tree cover also increased taxonomic diversity, which was in

317　turn negatively associated with the percentage of built areas (Table 2). Functional diversity

318　was negatively associated to bushes and positively to water and pedestrians, whereas the

319　CED of winter bird communities was significantly and negatively associated with the tree

320　and bush cover (Fig. 2). Effect sizes for these associations ranged between 9 and 20%, with a

321　peak 35% effect size of bird feeders on winter bird species richness (Fig. 2, Table S2).

322

4. Discussion

4.1. Land sharing versus land sparing city development

325　　　Our study using for the first time spatial (9 cities), temporal (2 seasons) and multiple

326　biodiversity measurements (taxonomic, functional and phylogenetic metrics) suggests that the

327　urban development style (land sharing or sparing) can be relevant for the conservation of

328　avian biodiversity in European urban environments. Although the urban development style

329　seems to be of little importance during the breeding season (i.e. only a marginally significant

330　effect for functional diversity), it is important during winter (i.e. significant effects for

331　taxonomic and functional diversity), which highlights the relevance of integrating a temporal

332　component to study urban biodiversity. This result does not fit our prediction that avian

333　biodiversity will show larger differences associated with urban development style in the

334　breeding than in the wintering season. Murgui's study (2010) on which we have based our

335　prediction investigated only urban parks while ours used a wider variety of urban habitats.

336　Thus it is possible that his findings only apply to urban parks and not to the city as a whole.

14

337   Alternatively, our contrasting findings could be due to local (i.e. city of Valencia) versus

338   continental (i.e. 9 European cities) effects.

339   Our results indicated that, in winter, areas with a land sharing model of urban

340   development showed a significantly higher species richness and Rao's Q values than those

341   organized according to a land sparing model. However, it is still possible that certain

342   important species (e.g. area-sensitive species) could benefit from large green patches

343   associated to land-sparing urban areas which suggest caution with our conclusions. Our

344   results fit with those obtained in a long-term study from northern Finland showing higher

345   winter bird assemblages in private-house (shared) areas compared with multistory-building

346   (spared) areas (Jokimäki and Kaisanlahti-Jokimäki, 2012). A similar pattern was observed for

347   butterflies in the city of Tokyo (Japan) (Soga et al., 2014) and trees of the city of Cambridge

348   (UK) (Collas et al., 2017), suggesting that other animals and plants might follow similar

349   patterns. However, they contrasted with our initial prediction based on other local findings

350   for birds (Sushinsky et al., 2013). For example, although avian bird communities in the city

351   of Brisbane (Australia) are negatively affected by any form of urbanization, they seem to be

352   less impacted by a land-sparing model (Sushinsky et al., 2013). The contrasting findings

353   between that and our study could be explained by (i) specific features of the city of Brisbane

354   that prevent its generalization; (ii) regional differences in urbanization between Australia

355   (following an extensive urban design) and Europe (where compact –land sparing– cities are

356   more common) (Stott et al., 2015); (iii) differences in the duration of urbanization (more

357   recent in Australia); (iv) differences in the period of study (breeding vs winter); or even (v)

358   different responses of Australian and European regional bird assemblages to each urban

359   development style. Further studies comparing different continents/bioregions simultaneously

360   will provide critical information on this aspect. The differences from other taxonomic groups

361   such as mammals or ground beetles that also seem to benefit from land sparing (Caryl et al.,

362   2016; Soga et al., 2014; Villaseñor et al., 2017) could be due to the above-mentioned

363   explanations or taxonomic-specific differences. Alternatively, previous studies supporting

364   land sparing as the best strategy assumed (modeled) that the green space associated with this

365   practice is of adequate quality for the focal assemblage (i.e. forest remnants (Collas et al.,

366   2017)), which might not be the case in our dataset as it also includes managed parks and

367   gardens as spared green areas, therefore also potentially explaining inconsistency of findings.

368   Two non-mutually exclusive hypotheses could explain the association of a higher

369   avian taxonomic diversity with land-sharing urban areas. First, it has been suggested that

370   species richness peaks at intermediate levels of disturbance (i.e. suburban areas) in an urban

371   gradient (Callaghan et al., 2019; Jokimäki and Suhonen, 1993; Luck and Smallbone, 2010;

372   Tratalos et al., 2007). This explanation is based on the intermediate disturbance hypothesis

373   that predicts higher levels of diversity at intermediate levels of disturbance due to the higher

374   number of habitats available (Battisti et al., 2016; Connell, 1978). In contrast with land-

375   sparing urban areas, land-sharing areas generally correspond with those offering a higher

376   number of habitats providing support for this possibility. This hypothesis however does not

377   provide a clear explanation for the differences between spring and winter. Second, human

378   practices in land-sharing urban areas favoring certain avian species (e.g. bird feeders) could

379   help to retain additional species promoting higher species richness in comparison with land-

380   sparing areas (Jokimäki and Kaisanlahti-Jokimäki, 2012). For instance, housing density is the

381   main driver explaining bird feeding practices in the UK (Fuller et al., 2008), and it seems that

382   only people with their own backyards feed birds in North America (Horn and Johansen,

383   2013). Our data also point in the same direction as we found a significantly higher number of

384   bird feeders in land-sharing areas (average = 0.38) compared with land-sparing areas (0.08;

385    $W = 44741$, $P < 0.0001$), which supported this assumption. Furthermore, our results suggest

386   that bird feeders are relatively important during winter for all biodiversity measures but not

387   during the breeding season, which could explain the observed differences between these two

388   time periods. More detailed studies in order to detect differences in human practices in each

389   urban development style will certainly help to better understand patterns of urban biodiversity

390   and implement future conservation practices.

391   Interestingly, only the taxonomic and functional diversity metrics showed significant

392   differences between land sharing and sparing urbanization styles. No differences were found

393   regarding phylogenetic diversity for breeding or wintering bird communities. These would

394   indicate that while the additional bird species in land-sharing urban areas compared to land-

395   sparing areas imply additional functions for the bird assemblage, they are probably achieved

396   by the incorporation of phylogenetically close species. These findings also provide several

397   additional important pieces of information. Firstly, these results are in line with previous

398   studies showing that human-induced impacts can differentially affect these three components

399   of biodiversity (e.g. Knapp et al., 2008; Devictor et al., 2010; Hanspach et al., 2015; Battisti

400   et al., 2016; Morelli et al., 2016, 2017a) and are consistent with recent recommendations in

401   nature conservation optimization in favor of using multiple complementary biodiversity

402   metrics (Monnet et al., 2014; Winter et al., 2012). Secondly, considering that cities are

403   associated with changes in phylogenetic and functional diversity of bird and plant

404   assemblages at a regional and global scale level (Čeplová et al., 2015; Ibáñez-Álamo et al.,

405   2017; Morelli et al., 2016; Sol et al., 2017), it seems that these two alternative urban

406   development styles do not alter the phylogenetic composition of European bird assemblages

407   (Fig. 3). This suggests that urbanizing following a land sharing or sparing urban development

408   style does not help to reconcile urbanization with this component of biodiversity (i.e.

409   phylogenetic diversity).

410   Urbanization should accommodate both environmental and human needs for well-

411   being (Gaston, 2010). However, some scientists have highlighted the potential conflict of

412   these two aspects regarding the best way to build cities in the future (Soga et al., 2015;

413   Sushinsky et al., 2013). This is based on previous studies showing that land sparing seems to

414   maximize urban biodiversity (Caryl et al., 2016; Soga et al., 2014; Villaseñor et al., 2017),

415   while human well-being is mostly favored by a land sharing urban development model (Soga

416   et al., 2015; Stott et al., 2015). This dilemma was not supported by our data, which emphasize

417   land sharing as the best strategy for retaining biodiversity in winter and no differences during

418   the breeding season. However, the debate of whether we should develop our cities following

419   a land sharing or land sparing model is still open because several other ecosystem services

420   seem to be maximized by the latter (Stott et al., 2015). Multi-city comparisons in this context

421   are typically lacking (Ziter, 2016). In addition, land sharing is usually associated with a larger

422   altered area typical of extensive urbanization, urban sprawling or sprinkling which are known

423   for their negative impacts in ecosystem function and structure (Romano et al., 2019; Salvati,

424   2014). It is thus still possible that the per capita impact is higher than that associated with

425   land sparing if a larger proportion of the natural habitat surrounding the city is urbanized (Lin

426   and Fuller, 2013; Norton et al., 2016).

427   *4.2. Urban features promoting avian biodiversity*

428   At the local level, we found that areas with a higher built coverage were associated

429   with lower levels of bird species richness and evolutionary distinctiveness during breeding,

430   and also in winter for the former. These results match those of previous studies finding

431   support for the species-area relationship in urban environments by which species richness of

432   different taxa are reduced in cities because of the replacement of suitable habitat (i.e.

433   vegetation) by impervious surfaces (Beninde et al., 2015; McKinney, 2008) or the subsequent

434   reduction in size of vegetated patches (Arca et al., 2012). The negative association between

435   phylogenetic diversity and built cover in the breeding season might suggest that only a few

436   closely related bird species are able to reproduce in areas with many sealed surfaces. The

437   proportion of area covered by water was another important small-scale feature that, in this

438   case, was positively associated with taxonomic (only in the breeding season) and functional

439   diversity (both seasons) of urban bird assemblages. Water cover has previously been linked to

440   higher bird species richness at the point-count level in the parks of Beijing (Morelli et al.,

441   2017a), and a recent meta-analysis also found that it favors intra-urban diversity of several

442   taxa, including birds (Beninde et al., 2015), supporting the generality of our findings. Water

443   might provide extra food and nesting opportunities, hence explaining the higher values of

444   Rao's Q, ultimately promoting the presence of additional bird species in the area. Vegetation

445   variables significantly explained taxonomic, functional and phylogenetic diversity metrics

446   both at the local (50 m radius circles) and landscape level (500 m x 500 m squares)

447   confirming previous findings that support the relevance of these factors for avian diversity

448   (Beninde et al., 2015 and references therein). Overall, vegetation variables were positively

449   associated with avian diversity at both scales (Fig. 2), the only exception being bush cover

450   and functional diversity in winter at the local level. In addition, latitude seems to mediate the

451   positive association of vegetation cover with taxonomic and phylogenetic diversity at the

452   landscape level. Squares with the same amount of green areas hold a higher number of bird

453   species and evolutionary distinctiveness levels toward the north, following a similar pattern

454   detected in other non-urban contexts (Brotons et al., 2018; Díaz et al., 1998).

455   The presence of food sources (bird feeders and berries) during winter seem to be

456   important in explaining part of the variation in all components of avian diversity and could be

457   considered keystone structures sensu Tews et al. (2004) in this season. This result matches

458   previous findings (e.g. Jokimäki & Suhonen, 1998; Suhonen & Jokimäki, 2015) and was

459 expected as the winter is an energetically demanding period (Newton, 1998; Suhonen et al.,

460 2009) during which birds are known to concentrate near food sources such as those presented

461 by bird feeders (Tryjanowski et al., 2015). We also found a positive association between

462 mammals and avian diversity, which was particularly strong in winter. It is possible that

463 urban mammals are more easily detected in winter due to an increase in their activity or,

464 alternatively, that highly diverse urban areas in birds (e.g. green areas) attract also other

465 animals like mammals. For example, red squirrels (*Sciurus vulgaris*) are also attracted to bird

466 feeders (Jokimäki et al., 2017), which are more common in land-sharing urban areas (see

467 above). The differences between winter and breeding in this association could also be related

468 to the important role that some of these mammals (e.g. cats) play as predators of avian nests

469 (Bonnington et al., 2013). The results about the influence of number of pedestrians are

470 complex and difficult to interpret as they are influenced by season and varied depending on

471 the biodiversity component analyzed. We found a negative relationship with taxonomic

472 diversity during the breeding season that is in agreement with the assumption that human

473 population density reduces vertebrate species richness, particularly at small scales (Pautasso,

474 2007). On the contrary, functional diversity of local bird assemblages in winter was

475 positively associated with the number of pedestrians. These results however should be taken

476 with caution because of potential daily variation in pedestrian activity that might obscure the

477 association between this measure (collected during the first hours of the morning) and human

478 population density.

479

480 **5. Conclusions**

481   Our study shows differences in avian biodiversity depending on the urban

482 development style in Europe, partially supporting land-sharing urban areas. However, these

483 differences are complex and vary depending on the season and component of biodiversity

484 considered. The positive effect of land sharing is restricted to winter, having no significant

485 impact for European breeding bird assemblages which highlights important temporal

486 contrasts (i.e. between seasons). Furthermore, the observed effect in winter applies to

487 taxonomic and functional diversity but not to phylogenetic diversity suggesting that the

488 spatial configuration of urban features is insufficient to fully preserve biodiversity. Additional

489 conservation practices might be needed to create more biodiversity-friendly cities. Despite

490 this complexity, our findings provide useful information for the current debate on how to

491 balance biodiversity conservation and human well-being. Large-scale modeling of future

492 urban scenarios will allow the development of more precise tools and suggestions. Our study

493 explores the effect of urban landscape configuration using a specific spatial scale, but land

494 sharing and sparing can be defined at multiple spatial scales (Kremen, 2015) and, therefore,

495 additional studies using different scales will be very interesting to investigate the generality

496 of our findings. Furthermore, despite urbanization being a worldwide phenomenon, urban

497 environments vary at large geographic scales (Forman, 2014). Future studies in other regions

498 are therefore imperative to better understand the relationship between urbanization practices

499 and biodiversity, as well as to provide locally-adjusted conservation recommendations (e.g.

500 Díaz & Concepción, 2016). Particularly interesting would be the focus on high biodiversity

501 areas (i.e. tropics), where a larger urban expansion is predicted to happen (Seto et al., 2012).

502   In our study, we also determined which small-scale urban landscape characteristics

503 (i.e. few impervious surfaces, high water or tree cover) and human practices (i.e. use of bird

504 feeders or berry plants) may help maintain more taxonomic, functional and phylogenetically

505 diverse urban bird assemblages during breeding and/or winter. Consequently, we gave

506 specific management practices for both policymakers and citizens that hopefully will make it

507 easier to reconcile urbanization and biodiversity conservation. Future studies on other human

508 practices and activities not considered here (e.g. traffic, mowing…) that can also disrupt

21

509   biodiversity (Battisti et al., 2016) will be very interesting in this context. It remains unknown

510   whether our recommendations can be applied to other cities outside Europe, but we hope that

511   our findings can be valuable for urban conservationists and policymakers.

512

513   **Competing interest**

514   The authors declare no competing interest.

515

516   **Acknowledgments**

522

523

524   **References**

525   Arca, E., Battisti, C., Fraticelli, F., 2012. Area-effect in breeding bird communities occurring
526   in an archipelago of urban holm oak fragments (Rome, central Italy). Vie Milieu 62,
527   154–169.

528   Battisti, C., Poeta, G., Fanelli, G., 2016. An Introduction to Disturbance Ecology, A Road
529   Map for Wildlife Management and Conservation. https://doi.org/10.1007/978-3-319-
530   32476-0

531   Becker, L.A., 1999. Effect size calculators. University of Colorado Colorado Springs, UCCS
532   [WWW Document].

533 Beninde, J., Veith, M., Hochkirch, A., 2015. Biodiversity in cities needs space: A meta-
534   analysis of factors determining intra-urban biodiversity variation. Ecol. Lett. 18, 581–
535   592. https://doi.org/10.1111/ele.12427

536 Bibby, C.J., Burgess, N.D., Hill, D.A., 1992. Bird Census Techniques. Academic Press,
537   London.

538 Blondel, J., Ferry, C., Frochot, B., 1970. La méthode des indices ponctuels d'abondance (I. P.
539   A.) au des relevés d'avifaune par '"stations d"ecoute''. Alauda 38, 55–71.

540 Bonnington, C., Gaston, K.J., Evans, K.L., 2013. Fearing the feline: Domestic cats reduce
541   avian fecundity through trait-mediated indirect effects that increase nest predation by
542   other species. J. Appl. Ecol. 50, 15–24. https://doi.org/10.1111/1365-2664.12025

543 Box, G.E.P., Cox, D.R., 1964. An analysis of transformations. J. R. Stat. Soc. B 26, 211–252.

544 Brotons, L., Herrando, S., Sirami, C., Kati, V., Díaz, M., 2018. Mediterranean Forest Bird
545   Communities and the Role of Landscape Heterogeneity in Space and Time, in: Ecology
546   and Conservation of Forest Birds. https://doi.org/10.1017/9781139680363.012

547 Callaghan, C.T., Bino, G., Major, R.E., Martin, J.M., Lyons, M.B., Kingsford, R.T., 2019.
548   Heterogeneous urban green areas are bird diversity hotspots: insights using continental-
549   scale citizen science data. Landsc. Ecol. 34, 1231–1246. https://doi.org/10.1007/s10980-
550   019-00851-6

551 Caryl, F.M., Lumsden, L.F., van der Ree, R., Wintle, B.A., 2016. Functional responses of
552   insectivorous bats to increasing housing density support "land-sparing" rather than
553   "land-sharing" urban growth strategies. J. Appl. Ecol. 53, 191–201.
554   https://doi.org/10.1111/1365-2664.12549

555 Čeplová, N., Lososová, Z., Zelený, D., Chytrý, M., Danihelka, J., Fajmon, K., Láníková, D.,
556   Preislerová, Z., Řehořek, V., Tichý, L., 2015. Phylogenetic diversity of central-European
557   urban plant communities: Effects of alien species and habitat types. Preslia 87, 1–16.

558 Collas, L., Green, R.E., Ross, A., Wastell, J.H., Balmford, A., 2017. Urban development,
559   land sharing and land sparing: the importance of considering restoration. J. Appl. Ecol.
560   54, 1865–1873. https://doi.org/10.1111/1365-2664.12908

561 Connell, J.H., 1978. Diversity in Tropical Rain Forests and Coral Reefs. Science 199, 1302–
562   1310. https://doi.org/10.1126/science.199.4335.1302

563 de Bello, F., Lavorel, S., Gerhold, P., Reier, Ü., Pärtel, M., 2010. A biodiversity monitoring
564   framework for practical conservation of grasslands and shrublands. Biol. Conserv. 143,
565   9–17. https://doi.org/10.1016/j.biocon.2009.04.022

566 Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., Mouquet, N., 2010. Spatial
567   mismatch and congruence between taxonomic, phylogenetic and functional diversity:
568   The need for integrative conservation strategies in a changing world. Ecol. Lett. 13,
569   1030–1040. https://doi.org/10.1111/j.1461-0248.2010.01493.x

570 Díaz, M., Carbonell, R., Santos, T., Tellería, J.L., 1998. Breeding bird communities in pine
571   plantations of the Spanish plateaux: Biogeography, landscape and vegetation effects. J.

572   Appl. Ecol. https://doi.org/10.1046/j.1365-2664.1998.3540562.x

573   Díaz, M., Concepción, E.D., 2016. Enhancing the Effectiveness of CAP Greening as a
574   Conservation Tool: a Plea for Regional Targeting Considering Landscape Constraints.
575   Curr. Landsc. Ecol. Reports 1, 168–177. https://doi.org/10.1007/s40823-016-0017-6

576   Díaz, M., Møller, A.P., Flensted-Jensen, E., Grim, T., Ibáñez-Álamo, J.D., Jokimäki, J.,
577   Markó, G., Tryjanowski, P., 2013. The Geography of Fear: A Latitudinal Gradient in
578   Anti-Predator Escape Distances of Birds across Europe. PLoS One 8, e64634.

579   EDGE of Existence, 2015. www.edgeofexistence.org [WWW Document].

580   Fahrig, L., 2003. Effects of Habitat Fragmentation on Biodiversity. Annu. Rev. Ecol. Evol.
581   Syst. 34, 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

582   Fernández-Juricic, E., Jokimäki, J., 2001. A habitat island approach to conserving birds in
583   urban landscapes: Case studies from southern and northern Europe. Biodivers. Conserv.
584   10, 2023–2043. https://doi.org/10.1023/A:1013133308987

585   Finch, T., Gillings, S., Green, R.E., Massimino, D., Peach, W.J., Balmford, A., 2019. Bird
586   conservation and the land sharing-sparing continuum in farmland-dominated landscapes
587   of lowland England. Conserv. Biol. 33, 1045–1055. https://doi.org/10.1111/cobi.13316

588   Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S.,
589   Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A.,
590   Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K.,
591   2005. Global consequences of land use. Science 309, 570–474.
592   https://doi.org/10.1126/science.1111772

593   Forman, R., 2014. Urban Ecology: Science of Cities. Cambridge University Press,
594   Cambridge.

595   Fragkias, M., Güneralp, B., Seto, K.C., Goodness, J., 2013. A Synthesis of Global
596   Urbanization Projections, in: Urbanization, Biodiversity and Ecosystem Services:
597   Challenges and Opportunities. Springer Netherlands, Dordrecht, pp. 409–435.
598   https://doi.org/10.1007/978-94-007-7088-1_21

599   Fuller, R.A., Warren, P.H., Armsworth, P.R., Barbosa, O., Gaston, K.J., 2008. Garden bird
600   feeding predicts the structure of urban avian assemblages. Divers. Distrib. 14, 131–137.
601   https://doi.org/10.1111/j.1472-4642.2007.00439.x

602   Gaston, K., 2010. Urban ecology, Ecological reviews. Cambridge University Press,
603   Cambridge.

604   Gaston, K.J., Spicer, J.I., 2004. Biodiversity : an introduction. Blackwell Publishing Ltd,
605   Cornwall.

606   Gil, D., Brumm, H., 2014. Avian urban ecology: behavioural and physiological adaptations.
607   Oxford University Press, Oxford.

608   Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X., Briggs, J.M.,
609   Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bal, X., Briggs,

610   J.M., 2008. Global Change and the Ecology of Cities. Science (80-.). 319, 756–760.

611 Groom, M.J., Meffe, G.K., Carroll, C.R. (Carl R., Meffe, G.K., 2006. Principles of
612   conservation biology. Sinauer Associates, Sutherland.

613 Hanspach, J., Loos, J., Dorresteijn, I., von Wehrden, H., Moga, C.I., David, A., 2015.
614   Functional diversity and trait composition of butterfly and bird communities in
615   farmlands of Central Romania. Ecosyst. Heal. Sustain. 1, art32.
616   https://doi.org/10.1890/EHS15-0027.1

617 Horn, D.J., Johansen, S.M., 2013. A comparison of bird-feeding practices in the United States
618   and Canada. Wildl. Soc. Bull. 37, 293–300. https://doi.org/10.1002/wsb.281

619 Ibáñez-Álamo, J.D., Rubio, E., Benedetti, Y., Morelli, F., 2017. Global loss of avian
620   evolutionary uniqueness in urban areas. Glob. Chang. Biol. 23, 2990–2998.

621 Isaac, N.J.B., Turvey, S.T., Collen, B., Waterman, C., Baillie, J.E.M., 2007. Mammals on the
622   EDGE: Conservation priorities based on threat and phylogeny. PLoS One 2, e296.
623   https://doi.org/10.1371/journal.pone.0000296

624 Janželkovič, F., Novak, T., 2012. PCA – A Powerful Method for Analyze Ecological Niches,
625   in: Dr. Parinya Sanguansat (Ed.), Principal Component Analysis - Multidisciplinary
626   Applications. InTech, p. 212.

627 Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K., Mooers, A.O., 2012. The global diversity of
628   birds in space and time. Nature 491, 444–448.

629 Jetz, W., Thomas, G.H., Joy, J.B., Redding, D.W., Hartmann, K., Mooers, A.O., 2014. Global
630   Distribution and Conservation of Evolutionary Distinctness in Birds. Curr. Biol. 24,
631   919–930. https://doi.org/10.1016/j.cub.2014.03.011

632 Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., 2012. Residential Areas Support Overwintering
633   Possibilities of Most Bird Species. Ann. Zool. Fennici 49, 240–256.
634   https://doi.org/10.5735/086.049.0404

635 Jokimäki, J., Selonen, V., Lehikoinen, A., Kaisanlahti-Jokimäki, M.L., 2017. The role of
636   urban habitats in the abundance of red squirrels (Sciurus vulgaris, L.) in Finland. Urban
637   For. Urban Green. 27, 100–108. https://doi.org/10.1016/j.ufug.2017.06.021

638 Jokimäki, J., Suhonen, J., 1998. Distribution and habitat selection of wintering birds in urban
639   environments. Landsc. Urban Plan. 39, 253–263. https://doi.org/10.1016/S0169-
640   2046(97)00089-3

641 Jokimäki, J., Suhonen, J., 1993. Effects of urbanization on the breeding bird species richness
642   in Finland: a biogeographical comparison. Ornis Fenn. 70, 71–77.

643 Knapp, S., Kühn, I., Schweiger, O., Klotz, S., 2008. Challenging urban species diversity:
644   Contrasting phylogenetic patterns across plant functional groups in Germany. Ecol. Lett.
645   11, 1054–1064. https://doi.org/10.1111/j.1461-0248.2008.01217.x

646 Kremen, C., 2015. Reframing the land-sparing/land-sharing debate for biodiversity
647   conservation. Ann. N. Y. Acad. Sci. 1355, 52–76. https://doi.org/10.1111/nyas.12845

648   Lee, M.-B., Martin, J.A., 2017. Avian Species and Functional Diversity in Agricultural
649   Landscapes: Does Landscape Heterogeneity Matter? PLoS One 12, e0170540.
650   https://doi.org/10.1371/journal.pone.0170540

651   Legendre, P., Fortin, M.-J., 2010. Comparison of the Mantel test and alternative approaches
652   for detecting complex multivariate relationships in the spatial analysis of genetic data.
653   Mol. Ecol. Resour. 10, 831–844. https://doi.org/10.1111/j.1755-0998.2010.02866.x

654   Lepczyk, C., Warren, P., 2012. Urban bird ecology and conservation. University of California
655   Press, London.

656   Liker, A., Papp, Z., Bókony, V., Lendvai, Á.Z., 2008. Lean birds in the city: Body size and
657   condition of house sparrows along the urbanization gradient. J. Anim. Ecol. 77, 789–
658   795. https://doi.org/10.1111/j.1365-2656.2008.01402.x

659   Lin, B.B., Fuller, R.A., 2013. Sharing or sparing? How should we grow the world's cities? J.
660   Appl. Ecol. 50, 1161–1168. https://doi.org/10.1111/1365-2664.12118

661   Luck, G., Smallbone, L., 2010. Species diversity and urbanisation: patterns, drivers and
662   implications, in: Gaston, K.J. (Ed.), Urban Ecology. Cambridge University Press,
663   Cornwall.

664   Magurran, A., 2004. Measuring Biological Diversity. Blackwell Science: Oxford; UK.

665   Magurran, A.E., McGill, B.J., 2011. Biological diversity: frontiers in measurement and
666   assessment. Oxford University Press.

667   Mannion, P.D., Upchurch, P., Benson, R.B.J., Goswami, A., 2014. The latitudinal
668   biodiversity gradient through deep time. Trends Ecol. Evol. 29, 42–50.
669   https://doi.org/10.1016/j.tree.2013.09.012

670   Mantel, N., 1967. The detection of disease clustering and a generalized regression approach.
671   Cancer Res. 27, 209–220.

672   Marzluff, J., Bowman, R., Donnelly, R., 2001. Avian Ecology and Conservation in an
673   Urbanizing World. Springer Science, New York.

674   McKinney, M.L., 2008. Effects of urbanization on species richness: A review of plants and
675   animals. Urban Ecosyst. 11, 161–176.

676   Monnet, A.C., Jiguet, F., Meynard, C.N., Mouillot, D., Mouquet, N., Thuiller, W., Devictor,
677   V., 2014. Asynchrony of taxonomic, functional and phylogenetic diversity in birds.
678   Glob. Ecol. Biogeogr. 23, 780–788. https://doi.org/10.1111/geb.12179

679   Morelli, F., Benedetti, Y., Ibáñez-Álamo, J.D., Jokimaki, J., Mänd, R., Tryjanowski, P.,
680   Møller, A.P., 2016. Evidence of evolutionary homogenization of bird communities in
681   urban environments across Europe. Glob. Ecol. Biogeogr. 25, 1284–1293.

682   Morelli, F., Benedetti, Y., Su, T., Zhou, B., Moravec, D., Šímová, P., Liang, W., 2017a.
683   Taxonomic diversity, functional diversity and evolutionary uniqueness in bird
684   communities of Beijing's urban parks: effects of land use and vegetation structure.
685   Urban For. Urban Green. 23, 84–92. https://doi.org/10.1016/j.ufug.2017.03.009

686   Morelli, F., Jiguet, F., Sabatier, R., Dross, C., Princé, K., Tryjanowski, P., Tichit, M., 2017b.
687   Spatial covariance between ecosystem services and biodiversity pattern at a national
688   scale (France). Ecol. Indic. 1–13. https://doi.org/10.1016/j.ecolind.2017.04.036

689   Murgui, E., 2010. Seasonality and nestedness of bird communities in urban parks in Valencia,
690   Spain. Ecography 33, 979–984. https://doi.org/10.1111/j.1600-0587.2010.05816.x

691   Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L.,
692   Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-
693   Londoño, S., Edgar, M.J., Fel, A., Scharlemann, J.P.W., Purvis, A., 2015. Global effects
694   of land use on local terrestrial biodiversity. Nature 520, 45–50.

695   Newton, I., 1998. Population limitation in birds. Academic Press, London.

696   Norton, B.A., Evans, K.L., Warren, P.H., 2016. Urban Biodiversity and Landscape Ecology:
697   Patterns, Processes and Planning. Curr. Landsc. Ecol. Reports 1, 178–192.
698   https://doi.org/10.1007/s40823-016-0018-5

699   Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, B.R.,
700   Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2016. vegan: Community
701   Ecology Package. R package version 2.3-4.

702   Oliveira Hagen, E., Hagen, O., Ibáñez-Álamo, J.D., Petchey, O.L., Evans, K.L., 2017.
703   Impacts of Urban Areas and Their Characteristics on Avian Functional Diversity. Front.
704   Ecol. Evol. 5, 84. https://doi.org/10.3389/fevo.2017.00084

705   Pautasso, M., 2007. Scale dependence of the correlation between human population presence
706   and vertebrate and plant species richness. Ecol. Lett. 10, 16–24.
707   https://doi.org/10.1111/j.1461-0248.2006.00993.x

708   Pearman, P.B., Lavergne, S., Roquet, C., Wüest, R., Zimmermann, N.E., Thuiller, W., 2014.
709   Phylogenetic patterns of climatic, habitat and trophic niches in a European avian
710   assemblage. Glob. Ecol. Biogeogr. 23, 414–424. https://doi.org/10.1111/geb.12127

711   Prum, R.O., Berv, J.S., Dornburg, A., Field, D.J., Townsend, J.P., Moriarty Lemmon, E.,
712   Lemmon, A.R., 2015. A comprehensive phylogeny of birds (Aves) using targeted next-
713   generation DNA sequencing. Nature 526, 569–573. https://doi.org/10.1038/nature15697

714   Rodrigues, A.S.L., Brooks, T.M., Rodrigues, A.S.L., Brooks, T.M., 2007. Shortcuts for
715   Biodiversity Conservation Planning : The Effectiveness of Surrogates Linked references
716   are available on JSTOR for this article : Shortcuts for Biodiversity Conservation
717   Planning : The Effectiveness of Surrogates 38, 713–737.

718   Romano, Fiorini, Marucci, 2019. Italy without Urban 'Sprinkling'. A Uchronia for a Country
719   that Needs a Retrofit of Its Urban and Landscape Planning. Sustainability 11, 3469.
720   https://doi.org/10.3390/su11123469

721   Salvati, L., 2014. Agro-forest landscape and the "fringe" city: A multivariate assessment of
722   land-use changes in a sprawling region and implications for planning. Sci. Total
723   Environ. 490, 715–723. https://doi.org/10.1016/j.scitotenv.2014.05.080

724   Sekercioglu, C.H., 2006. Increasing awareness of avian ecological function. Trends Ecol.

725   Evol. 21, 464–471. https://doi.org/10.1016/j.tree.2006.05.007

726   Seto, K.C., Güneralp, B., Hutyra, L.R., 2012. Global forecasts of urban expansion to 2030
727   and direct impacts on biodiversity and carbon pools. Proc. Natl. Acad. Sci. U. S. A. 109,
728   16083–16088. https://doi.org/10.1073/pnas.1211658109

729   Sims, V., Evans, K.L., Newson, S.E., Tratalos, J.A., Gaston, K.J., 2008. Avian assemblage
730   structure and domestic cat densities in urban environments. Divers. Distrib. 14, 387–
731   399. https://doi.org/10.1111/j.1472-4642.2007.00444.x

732   Soga, M., Yamaura, Y., Aikoh, T., Shoji, Y., Kubo, T., Gaston, K.J., 2015. Reducing the
733   extinction of experience: Association between urban form and recreational use of public
734   greenspace. Landsc. Urban Plan. 143, 69–75.
735   https://doi.org/10.1016/j.landurbplan.2015.06.003

736   Soga, M., Yamaura, Y., Koike, S., Gaston, K.J., 2014. Land sharing vs. land sparing: Does
737   the compact city reconcile urban development and biodiversity conservation? J. Appl.
738   Ecol. 51, 1378–1386. https://doi.org/10.1111/1365-2664.12280

739   Sol, D., Bartomeus, I., González-Lagos, C., Pavoine, S., 2017. Urbanisation and the loss of
740   phylogenetic diversity in birds. Ecol. Lett. 20, 721–729.
741   https://doi.org/10.1111/ele.12769

742   Stott, I., Soga, M., Inger, R., Gaston, K.J., 2015. Land sparing is crucial for urban ecosystem
743   services. Front. Ecol. Environ. 13, 387–393. https://doi.org/10.1890/140286

744   Suhonen, J., Jokimäki, J., 2015. Fruit removal from rowanberry (Sorbus aucuparia) trees at
745   urban and rural areas in Finland: A multi-scale study. Landsc. Urban Plan. 137, 13–19.
746   https://doi.org/10.1016/j.landurbplan.2014.12.012

747   Suhonen, J., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., Hakkarainen, H., Huhta, E., Inki, K.,
748   Suorsa, P., 2009. Urbanization and stability of a bird community in winter. Écoscience
749   16, 502–507. https://doi.org/10.2980/16-4-3280

750   Sushinsky, J.R., Rhodes, J.R., Possingham, H.P., Gill, T.K., Fuller, R.A., 2013. How should
751   we grow cities to minimize their biodiversity impacts? Glob. Chang. Biol. 19, 401–410.
752   https://doi.org/10.1111/gcb.12055

753   Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F.,
754   2004. Animal species diversity driven by habitat heterogeneity/diversity: The
755   importance of keystone structures. J. Biogeogr. 31, 79–92.
756   https://doi.org/10.1046/j.0305-0270.2003.00994.x

757   Tratalos, J., Fuller, R.A., Evans, K.L., Davies, R.G., Newson, S.E., Greenwood, J.J.D.,
758   Gaston, K.J., 2007. Bird densities are associated with household densities. Glob. Chang.
759   Biol. 13, 1685–1695. https://doi.org/10.1111/j.1365-2486.2007.01390.x

760   Tryjanowski, P., Sparks, T.H., Biadun, W., Brauze, T., Hetmaski, T., Martyka, R., Skórka, P.,
761   Indykiewicz, P., Myczko, L., Kunysz, P., Kawa, P., Czyz, S., Czechowski, P.,
762   Polakowski, M., Zduniak, P., Jerzak, L., Janiszewski, T., Golawski, A., Dudu, L.,
763   Nowakowski, J.J., Wuczynski, A., Wysocki, D., 2015. Winter bird assemblages in rural
764   and urban environments: A national survey. PLoS One 10, 1–25.

765 Tucker, C.M., Cadotte, M.W., Carvalho, S.B., Davies, T.J., Ferrier, S., Fritz, S.A., Grenyer,
766   R., Helmus, M.R., Jin, L.S., Mooers, A.Ø., Pavoine, S., Purschke, O., Redding, D.W.,
767   Rosauer, D.F., Winter, M., Mazel, F., 2016. A guide to phylogenetic metrics for
768   conservation, community ecology and macroecology. Biol. Rev. 92, 698–715.
769   https://doi.org/10.1111/brv.12252

770 United Nations, 2016. Urbanization and development: Emerging futures. World Cities Report
771   2016. United Nations, Nairobi.

772 United Nations, 2015. World urbanization prospects, the 2014 revision. New York.

773 Villaseñor, N.R., Tulloch, A.I.T., Driscoll, D.A., Gibbons, P., Lindenmayer, D.B., 2017.
774   Compact development minimizes the impacts of urban growth on native mammals. J.
775   Appl. Ecol. 54, 794–804. https://doi.org/10.1111/1365-2664.12800

776 Voříšek, P., Klvaňová, A., Wotton, S., Gregory, R.D., 2008. A best practice guide for wild
777   bird monitoring schemes, Europe. Bruxelles.

778 Winter, M., Devictor, V., Schweiger, O., 2012. Phylogenetic diversity and nature
779   conservation: where are we? Trends Ecol. Evol. 28, 199–204.

780 Ziter, C., 2016. The biodiversity-ecosystem service relationship in urban areas: A quantitative
781   review. Oikos 125, 761–768. https://doi.org/10.1111/oik.02883

782 Zoltan, B.-D., 2005. Rao' s quadratic entropy as a measure of functional diversity based on
783   multiple traits. J. Veg. Sci. 16, 533–540. https://doi.org/10.1658/1100-
784   9233(2005)16[533:RQEAAM]2.0.CO;2

785

786 **Figure legends**

787 Figure 1. Study design and location of the 9 cities used distributed across 6 European

788 countries. Black areas in the second square represent built surfaces, while white ones

789 correspond to green areas. The second square shows a schematic representation of study plots

790 and do not show the real configuration of study plots for that city (i.e. distances between them

791 are not at the proper scale).

LSH Land Sharing
LSP Land Sparing
Circle with 50m radius
Point count

792
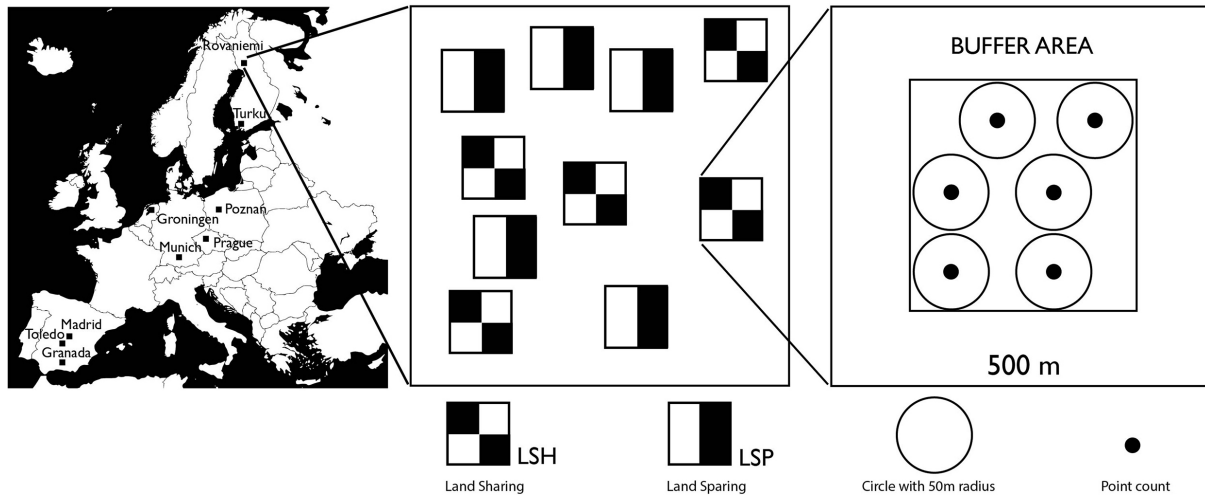
Figure 2. Heat-map of the estimated effects (positive in green, negative in red; effect sizes <10% in lighter colours) of urban development style (sparing-sharing), vegetation features, and presence of pedestrians and mammals on the taxonomic (TAX), functional (FUN) and phylogenetic (PHY) diversity of breeding and wintering bird communities in European cities. See detailed results in Table S2.

	breeding				wintering		
	TAX	FUN	PHY		TAX	FUN	PHY
Latitude							
Sparing-sharing		red			red	red	
Vegetation cover	green				green	green	
Latitude x Sparing-sharing							
Latitude x Vegetation			light green		green		green
Built	red		red		red		green
Tree			green		green		green
Bush	green					red	light green
Grass		light green					
Water	light green	green				green	
Snow							
Bird feeders					green	green	green
Berries					green	green	green
Pedestrians	red					green	
Mammals	light green				green		light green

Figure 3. Comparison of overall bird species richness, functional diversity and average community evolutionary distinctiveness between land sharing (LSH) and land sparing (LSP) urban areas, in breeding and wintering seasons, merging all data from 9 cities. The y-axis represents the estimated variable. The boxplots show the mean (yellow rhombus), median (bar in the middle of rectangles), upper and lower quartiles and extreme values.

805

806