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1 Grasslands provide diverse opportunities for bird species along an urban-rural gradient

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16

17 **Abstract**

18 Urbanisation is a major cause of biodiversity loss but careful habitat management and provision of green  
19 space within cities can help to mitigate its negative effects. Grasslands occupy large surface areas and have  
20 many functions but only a few studies have begun to explore how birds exploit these habitats in urban  
21 contexts. We hypothesized that the value of grasslands for nesting and feeding birds is likely to depend both  
22 on landscape context, and on local characteristics (grassland size, use and vegetation structure). We surveyed  
23 local habitat characteristics, breeding bird presence, abundance and foraging activity in 47 grassland sites,  
24 distributed along an urban-rural gradient in two French cities, and varying in the proportions of grassland,  
25 built-up land and residential gardens in the neighbouring landscape. Species richness was influenced by local  
26 rather than landscape variables; larger sites with scrub within the grassland and taller hedgerow vegetation  
27 were more species rich. Total bird abundance, however, depended on landscape context, and increased in  
28 suburban grasslands with a higher proportion of gardens in the landscape. Foraging in grass was more  
29 frequently observed in shorter, regularly mown, recreational grasslands. These were more common in urban  
30 contexts and favoured by species requiring easily accessible and visible invertebrate prey. Less intensively  
31 managed wastelands were species rich despite being in urban contexts and favoured by seedeaters and one  
32 farmland specialist. A diversity of use and management of grasslands along the urban-rural gradient could  
33 allow birds with various requirements to co-exist at landscape scale.

34

35 **Keywords:** wasteland, urban parks, residential gardens, agricultural grassland, ground-foraging, France

36

## 37 **Introduction**

38 Urbanisation is a major cause of biodiversity loss at global scale (Aronson et al., 2014; Millenium Ecosystem  
39 Assessment, 2005), but careful habitat management and provision of green space within cities can help to  
40 mitigate the negative effects of this land use change on wild plants and animals (Lepczyk et al., 2017;  
41 McKinney, 2002). It has also been highlighted that biological diversity in urban parks, of habitats and species,  
42 contributes to human well-being of people in cities (Cameron et al., 2020). It is therefore important to  
43 understand how urban and semi-urban landscapes can be planned to provide space for wildlife while  
44 simultaneously accommodating a range of human needs (housing, transport infrastructure, recreational  
45 opportunities). Therefore, a current challenge for land planners and conservationists is to optimise the  
46 quantity, quality and spatial configuration of semi-natural habitats in and around cities to preserve  
47 biodiversity, while ensuring compatibility with the multiple functions of urban green space (Aronson et al.,  
48 2017; Norton et al., 2016).

49  
50 Birds are a conspicuous and well-known component of urban biodiversity. They respond quickly to land use  
51 change and are sensitive to urbanisation, making them particularly suitable as biodiversity indicators of  
52 anthropogenic influence (e.g. Guetté et al., 2017); even when highly intensively farmed land is urbanised they  
53 may demonstrate a negative response (Gillings, 2019). The ways in which birds exploit habitats within cities  
54 and also along urban-rural gradients have therefore received considerable attention (Blair, 2004; Chace and  
55 Walsh, 2006; Clergeau et al., 2006). Much of this attention has taken the form of city-scale studies involving a  
56 mosaic of habitat types, which is relevant as birds are highly mobile and often exploit different habitats for  
57 nesting or feeding. Urban bird assemblages are strongly influenced by local habitat characteristics, such as  
58 structural and compositional complexity of vegetation or supplementary feeding and by regional or landscape-  
59 scale factors, in particular patch size and to a lesser extent patch isolation (Evans et al., 2009).

60  
61 It can also be important to consider the specific contribution of single habitat or land-uses types. Urban green  
62 space can take many forms and it could be useful for land managers to assess the individual contribution of  
63 each. Lepczyk et al. (2017) propose a continuum of habitat types ranging from intact remnant patches of  
64 native vegetation, brownfields, gardens, and yards to green roofs and heavily maintained terraformed patches

65 in the city core. The value for birds of certain habitats in urban contexts, in particular woodland habitats of  
66 different kinds such as treelines and urban woodlands (Croci et al., 2008; Taylor et al., 2016), or of certain  
67 land-use types such as residential gardens, has been widely investigated. Private, residential gardens provide a  
68 diversity of resources that may not be equally available in other land-use categories, such as artificial bird  
69 feeders, which have been shown to boost bird abundance if not diversity (Fuller et al., 2008). Gardens are  
70 generally botanically rich (Thompson et al., 2003) and correlated with high invertebrate diversity and it is  
71 thought that they could play a key part in ecological land-use complementation if located close to city parks,  
72 for example (Colding, 2007). It has more recently been suggested that the complementary use of private and  
73 public green space by wildlife requires more attention (Mimet et al., 2020).

74

75 Among these types of urban green space, grasslands are of particular importance. They occupy large surface  
76 areas, sometimes dominating green space, as in the UK for example (Evans et al., 2009). Turf grasses in urban  
77 areas have been estimated to cover 2% of the total land surface of the United States of America (Milesi et al.,  
78 2005). Some attempts have been made to quantify grassland use types within urban areas and their potential  
79 contribution to urban biodiversity conservation (Fischer et al., 2013). But these grasslands are associated with  
80 a range of functions and take a variety of forms in and around urban areas. Depending on context, they range  
81 from intensively managed grass, receiving artificial irrigation and fertilizers and excluding agricultural usage  
82 (Milesi et al., 2005) to vacant or abandoned wastelands, where reduced management leads to the development  
83 of spontaneous vegetation somewhere between pioneer or pre-forest successional stages. Such wastelands are  
84 often beneficial for biodiversity (Bonthoux et al., 2014), including birds in densely built-up contexts  
85 (Villaseñor et al., 2020; Zuniga-Palacios et al., 2020). This diversity of land use types corresponds to an equal  
86 diversity of land managers to whom these categories represent meaningful management units (Manning et al.,  
87 2019).

88

89 Relatively few studies have begun to explore how birds exploit urban grasslands (but see Šálek et al. 2004;  
90 Meffert et al. 2012; Šálek et al. 2018) and there is a need for more investigation of how grassland structure  
91 and diversity influence bird communities in urban contexts (Evans et al., 2009). Relatively few species nest in  
92 grassy vegetation but many can nest in scrubby or woody vegetation in or near grassland areas, as these

93 provide valuable food resources for insectivores, granivores and more generalist feeders. We hypothesized  
94 that, if extensively managed and accompanied by a certain amount of scrub or woodland, or embedded in  
95 landscapes with woodland or residential gardens, grasslands could be valuable feeding sites for tree and scrub  
96 nesters.

97

98 Further, grasslands in cities may provide much-needed habitat for species of open or farmland habitats, whose  
99 populations are declining at European levels. Some of these species nest on the ground and lack suitable  
100 breeding sites in intensively managed farmland. However, these open land specialists tend not to penetrate  
101 urban landscapes (Jokimäki et al., 2016; Sorace and Gustin, 2010), also outside Europe (Leveau & Leveau,  
102 2005), and the reasons for this are not always clear. One possibility is the absence of large enough grassland  
103 patches, distant from trees or hedgerows, or too little habitat at landscape scale.

104

105 A better knowledge of how birds use grasslands, as influenced by landscape-scale and local habitat factors, in  
106 relation to land use and management, might help to inform urban planning for nature conservation. We  
107 examined grassland use by birds during the breeding season along an urban-rural gradient in two French  
108 cities. Our specific aims were 1) to study how variation in species richness and abundance of breeding birds in  
109 these grasslands depends on local habitat characteristics as well as landscape-scale variation, particularly the  
110 amount of built-up land or residential gardens, 2) to examine whether use of grasslands for ground foraging  
111 varies along the urban-rural gradient.

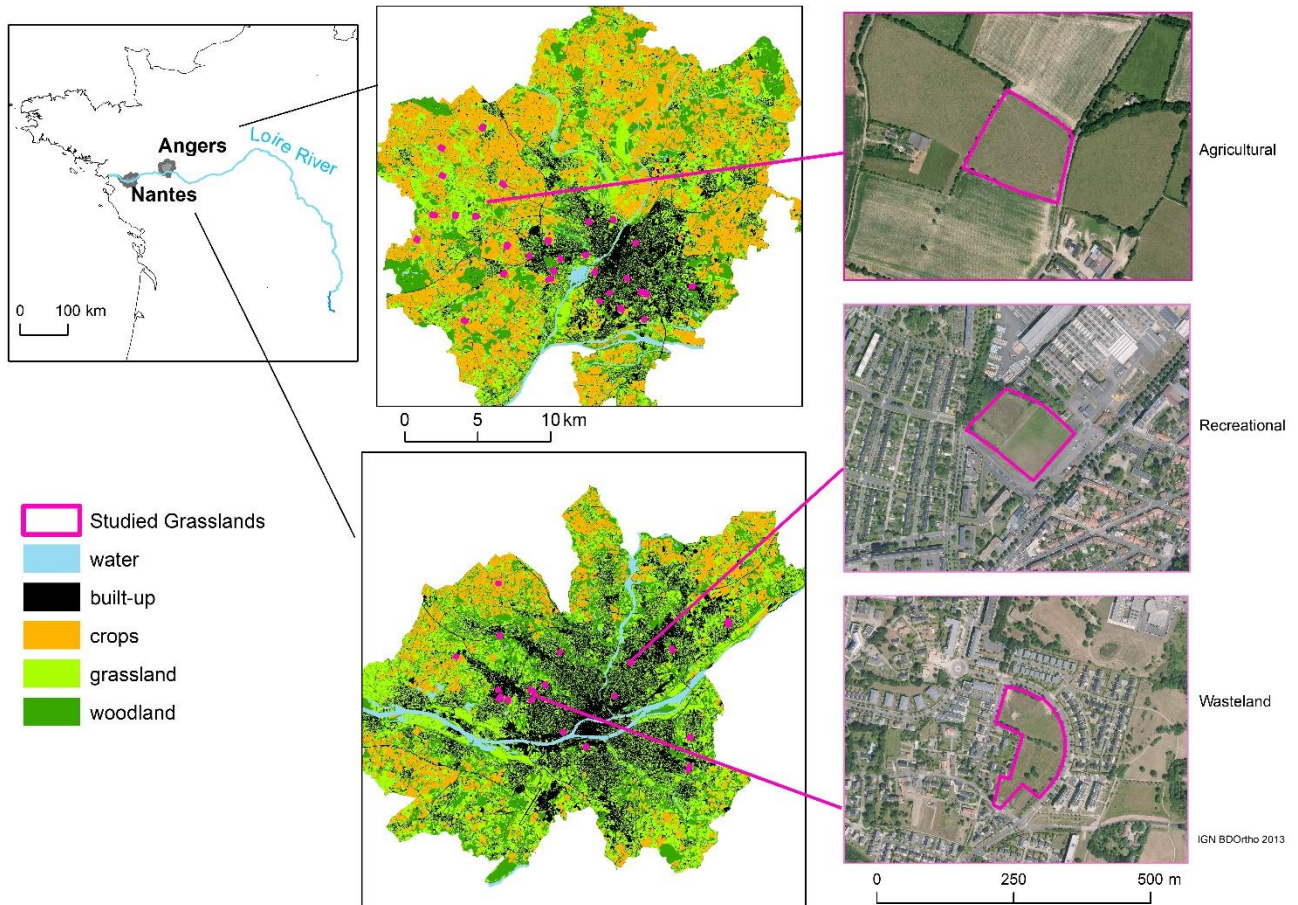
112

## 113 **Methods**

### 114 *Study areas, land cover mapping and site selection*

115 We focused on the urban-rural gradient of two medium-sized cities of north-western France situated  
116 approximately 100 km apart (Fig. 1): Nantes (47°13' N; 1°33' W, conurbation 523 km<sup>2</sup>, 609 000 inhabitants)  
117 and Angers (47°28' N; 0° 33'W, conurbation 540 km<sup>2</sup>, 270 000 inhabitants). These two cities share a  
118 temperate, oceanic climate and are situated at low altitude (< 65m). By choosing two cities sharing relatively  
119 similar biogeographical and climatic conditions, we were able to compare two urban-rural gradients extending  
120 well into relatively close rural areas. Both cities are surrounded by mixed farmland with annual and perennial

121 crops, temporary and permanent grasslands, and a generally low proportion of woodland habitat but relatively  
 122 well-preserved hedgerow networks. Therefore, our studied gradients were dominated by human activities  
 123 from urban centres to rural outskirts.



124  
 125 **Figure 1.** Geographical location of the two study cities and distribution and types of studied grassland sites  
 126 along urban-rural gradients in each.

127  
 128 We produced land cover maps of the Nantes and Angers conurbations in a three-step process using QGIS  
 129 software (different versions from 2015 to 2020; <http://qgis.org>). First, we extracted vector data from national,  
 130 high resolution databases (BD TOPO® (2013) IGN: water, built-up areas, roads, forests and hedgerows and  
 131 Graphical Parcel Register (RPG 2012, [www.data.gouv.fr](http://www.data.gouv.fr)): agricultural areas and permanent grasslands).  
 132 Secondly, surfaces not included in the previously cited IGN database land cover types needed to be  
 133 categorised. These unassigned areas were differentiated between open, grassland vegetation or impervious  
 134 surfaces by calculating NDVI (Normalized Difference Vegetation Index) at 3 different dates using

135 RAPIDEYE imagery (2011, 5 m spatial resolution, obtained by GEOSUD <http://geosud.teledetection.fr>). All  
136 layers were merged to produce a land cover map with five different classes: built-up areas (including  
137 buildings, roads and impervious areas), water bodies, woody areas (including forests and hedgerows), crops  
138 (including temporary sown grasslands) and permanent grasslands (including non-farmed open vegetation)  
139 (Cochard et al., 2019). Third, we mapped the presence of residential gardens as no such maps existed for the  
140 two studied cities, as do in other cities (see for example (Al-Kofahi et al., 2019)). Our method was simple in  
141 comparison with existing methods (Mathieu et al., 2007); residential gardens were defined as areas of  
142 vegetation (woody or grassy) contained in “residential parcels”, defined as ownership parcels less than  
143 5000m<sup>2</sup> (BD Parcellaire® IGN, 2013) containing individual private houses.

144

145 For site selection, we firstly extracted from the land cover maps all areas likely to contain grassland elements  
146 (building sites, wastelands, parks and gardens, sports fields, campsites, agricultural grasslands or abandoned  
147 farmland), at least 50m from water bodies or woodlands. We set a limit to the length of our urban-rural  
148 gradients from the city centre of 6 km for Angers and 11 km for Nantes, enabling us to include completely  
149 rural contexts in each case and to examine the distributions of farmland species along the gradient. After field  
150 checks, we selected 47 extensively managed grasslands (29 in Angers and 18 in Nantes) aiming at maximising  
151 variation in the proportion of built-up area and of residential gardens in the surrounding landscape. Sites  
152 selected ranged from 0.5 to 4 ha in area, smaller sites being excluded as too small for bird sampling and larger  
153 sites as they occurred exclusively in rural areas. We excluded intensively managed grasslands and sites with a  
154 complete absence of associated shrubby or woody vegetation within the grassland or on the periphery so as to  
155 ensure sites would be comparable. Nearby cover is known to strongly influence birds’ use of open habitats,  
156 particularly when foraging (Visscher et al., 2018).

157

158 *Environmental variables: habitat surveys and landscape metrics*

159 Habitat surveys were conducted at all the sites. Firstly, each site was assigned to one of the three following  
160 grassland use types: recreational, wasteland or agricultural (Fig. 2). Recreational sites were mostly city parks  
161 and extensively managed sportsgrounds, wastelands were mostly abandoned plots awaiting development.  
162 Only permanent (>5 years) agricultural grasslands were included. We chose these land use categories as they



163 correspond to different land-use management (city green space, abandonment or farming) and therefore  
164 represent meaningful units for land managers and policy makers (Manning et al., 2019). Grass height  
165 measurements were carried out in the first year of the study on a sample of these grasslands and revealed clear  
166 differences in grass management between grassland use types (see Supplementary material, Fig. S5).  
167 Secondly, we surveyed variation in local vegetation structure likely to influence site use by birds: i) the  
168 presence or absence of shrubby vegetation or trees within the grassland (rather than on the perimeter), and ii)  
169 mean height of hedgerows on the grassland perimeter (hereafter referred to as mean hedgerow height) and an  
170 estimation of the total amount of woody vegetation (both shrubs and trees) of the grassland site (hereafter  
171 referred to as proportion of woody vegetation). We recorded the presence/absence of non-native vegetation as  
172 follows: if perimeter hedgerows were dominated by non-native ornamental species we noted “present” while  
173 if the presence of non-native vegetation was judged absent or negligible we noted “absent”.



175 **Figure 2.** Illustrative photographs of the three grassland use types: (a) agricultural, (b) recreational and (c)  
176 wasteland.

177  
178 Landscape composition metrics used in this study were the proportion of built-up area, permanent grassland  
179 vegetation, woodland and residential gardens surrounding each sampled site. The landscape metrics were  
180 calculated in 200m and 1000m-radius buffer zones around site centroids (see Supplementary material, Fig. S1  
181 for a graphical representation). We also calculated the surface area of each grassland site. Spatial analysis was  
182 carried out using CHLOE 2012 (Boussard and Baudry, 2014). We checked for relationship between  
183 environmental variables (see Supplementary material, Figs. S2-S4). Percentage of built-up area was strongly  
184 correlated across the two study scales, *i.e.* 200m and 1000m (Pearson’s  $r > 0.8$ ). To a lesser extent, this was  
185 also true for the percentage of residential gardens (Pearson’s  $r > 0.7$ ). Grassland use type was also related to

186 the percentage of built-up area at the two scales (ANOVA R-square = 0.57 and 0.47 at 200m and 1000m  
187 scales respectively), and to a lesser extent site area (ANOVA R-square = 0.34). Unsurprisingly, grasslands  
188 used for agriculture were found in significantly less urban contexts than grasslands used for recreational  
189 activities and wastelands, while sites in the recreational use type were significantly smaller in area compared  
190 with agricultural and wasteland sites (see Supplementary material Fig. S5).

191

### 192 *Bird surveys*

193 Each site was visited 3 times during the breeding season in April, May and June, in two consecutive years  
194 (2014 and 2015 or 2015 and 2016). The observer first walked the site perimeter before completing the visit by  
195 a zigzag walk across the centre of the grassland to flush hidden birds. Each survey lasted about 15 minutes  
196 and was carried out between 1 and 4 hours after sunrise on days without continuous rain or wind. All  
197 individuals detected by sight or song were recorded along with information about territorial and/or feeding  
198 behaviour. Data from 2 years and 3 visits were pooled to calculate species richness per site. Species  
199 abundance per site was the maximum number of individuals detected in a single visit over the two years. At  
200 each site the total numbers of birds seen foraging in grass were pooled for the 3 visits and 2 years. Further,  
201 each species was assigned to a habitat affinity class (generalist, farmland specialist, urban specialist or forest  
202 specialist), based on national-scale indicators (Jiguet, 2010) or regional habitat preferences for unclassified  
203 species (Marchadour, 2014). Species richness and total abundance were calculated for these four habitat  
204 affinity groups.

205

### 206 *Statistical analysis*

207 Local habitat and landscape variables were included together in multiple regression models to estimate their  
208 relative effects on bird species richness and abundance and number of observations of ground foraging. The  
209 same approach was repeated for richness and abundance of the four habitat affinity groups. These models  
210 were analysed using multi-model inference (MMI) and model averaging. MMI analyses are robust against  
211 model selection uncertainty as several supported models are taken into account (Burnham and Anderson,  
212 2002) and are less sensitive to correlation among descriptors (Smith et al., 2009). All continuous variables  
213 were mean-centred and divided by the standard deviation to make the coefficients comparable (Smith et al.,

214 2009). In the MMI procedure, linear models for each possible combination of all local and landscape variables  
215 were tested and ranked based on the corrected Akaike information criterion (AICc). Then, we computed  
216 standardised average regression coefficients weighted by the Akaike weights across supported best models  
217 ( $\Delta AICc < 7$ ) and tested their significance using unconditional 95% confidence intervals (Burnham and  
218 Anderson, 2002; Smith et al., 2009).

219

220 Residuals of averaged models were tested for normality (Shapiro-Wilcoxon test and quantile–quantile plots).  
221 For some of the bird abundance measures, residuals were not normally distributed. Hence, a second average  
222 model was built in a generalized linear model using negative binomial distribution rather than Poisson, as data  
223 showed over-dispersion. We checked for a potential effect of city (Angers or Nantes) by including a random  
224 factor using mixed models. As no differences between cities were detected, data from the two cities were  
225 pooled in the final analyses. All statistical tests were performed using R software 3.6.1 (R Core Team, 2019)  
226 using the ‘MuMin’ package for MMI analyses (Barton, 2016), the ‘lme4’ package for generalized linear  
227 mixed-effects models (Bates et al., 2015), and the ‘qcc’ package for over-dispersion testing (Scrucca,  
228 2004).

229

230 We further investigated bird communities using urban grasslands at the species level. We looked at species  
231 distributions and ground foraging activity across grassland use types and according to species habitat affinity.  
232 For species that occurred in at least 1/3 of grassland sites we carried out an indicator species analysis (Dufrêne  
233 and Legendre, 1997), which took into account both frequency and abundance of species in the grassland use  
234 types and produced an indicator value for each species corresponding to its affinity for each grassland use  
235 type. We tested the statistical significance using a Monte-Carlo randomization approach (999 permutations  
236 were used). Indicator species analyses were carried out using PC-ORD Version 5.

237

## 238 **Results**

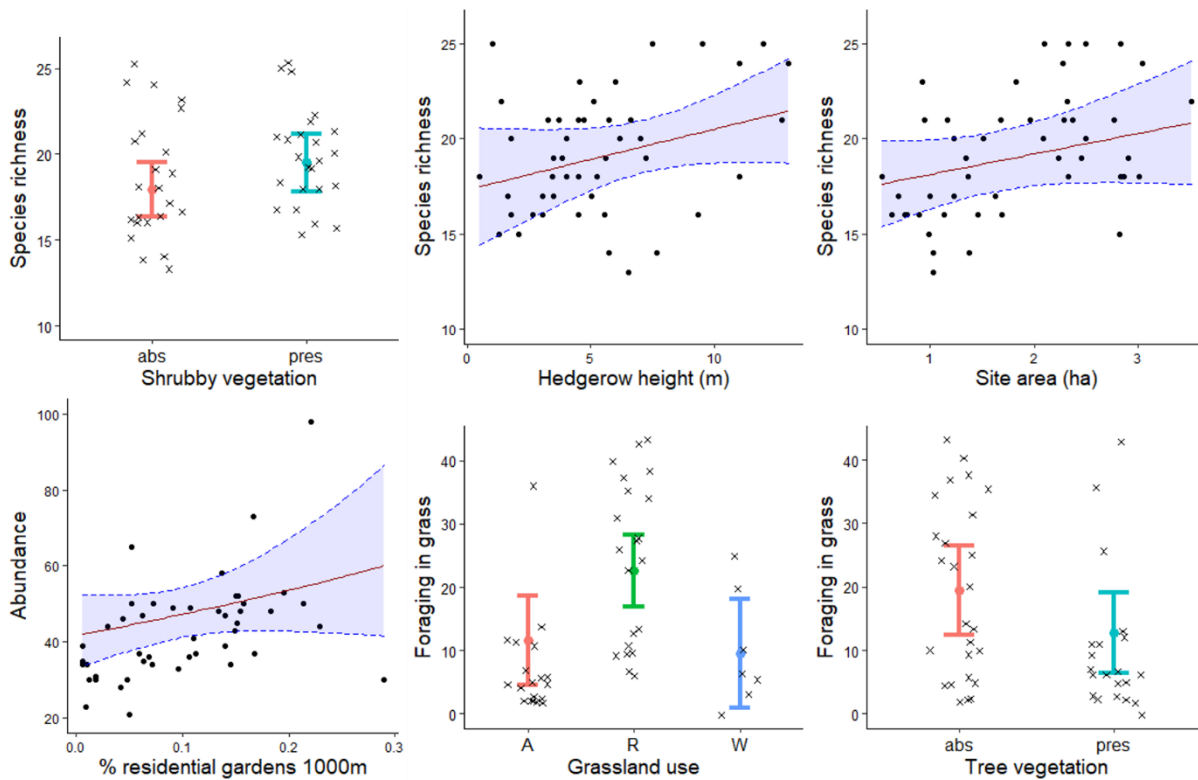
### 239 *Effects of local habitat and landscape context on birds using grasslands*

240 In total, 71 species of bird were observed in grasslands, but for only 33 among these were more than 10  
241 individuals observed, and only 22 were observed in more than 1/3 of the investigated sites. Mean site-level

242 species richness was 19 (min = 13, max = 25) and we observed a mean of 42.8 individuals (min = 21, max =  
243 98) per site.

244

245 Bird species richness was positively influenced by particular aspects of local vegetation structure (Table 1,  
246 Fig. 3); it was significantly higher when shrubby vegetation was present within the grassland site (2.1 more  
247 species on average), and also when perimeter hedgerows were taller. However, the proportion of woody  
248 vegetation per site was not a good indicator of either bird species richness or abundance. Grassland sites of  
249 larger area also had significantly greater species richness. These three variables showed very low pairwise  
250 correlation (Supplementary material, Figs. S2 and S4), denoting independent effects.



251

252 **Figure 3.** Graphical representation of significant effects of local habitat and landscape variables on bird  
253 species richness, abundance and foraging observations in grass. Observed (crosses and dots), predicted values  
254 and 95% confidence interval of prediction. Refer to Table 1 for full results.

255

256 Overall bird abundance was higher in grasslands whose environments contained a higher percentage of  
257 residential gardens (Table 1, Fig. 3). This effect was significant at the 1000m scale, bearing in mind that this  
258 variable was correlated with the percentage of gardens at the 200m scale.

259

260 Ground foraging by birds showed a different pattern. There were significantly more observations of ground  
261 feeding in recreational grasslands than in agricultural grasslands or wastelands (Table 1, Fig. 3). This  
262 behaviour was also strongly negatively affected by presence of trees within grasslands. These two variables  
263 were weakly correlated (Supplementary material, Fig. S3).

264

#### 265 *Response of bird habitat affinity groups*

266 Generalist species richness was positively related to grassland site area, while generalist abundance was  
267 higher in recreational grasslands compared with agricultural grasslands and wasteland sites (Table 2). Both  
268 richness and abundance of generalist species increased with the surface of woody vegetation within the  
269 grassland. Generalist species were not significantly affected by landscape context.

270

271 Both richness and abundance of farmland species increased in grassland sites of larger area, while they  
272 strongly decreased in recreational grasslands in comparison with agricultural grasslands and wasteland sites  
273 (Table 2). Farmland species were more abundant in landscapes with a higher percentage of woodland at the  
274 1000m scale.

275

276 Unsurprisingly, forest specialists responded positively to woody vegetation at the local scale, as their richness  
277 increased in grassland sites with shrubs or surrounded by taller hedgerows, while their abundance increased  
278 with area of woody vegetation within the grassland (Table 3). At the 200m scale, also, forest species richness  
279 increased with proportion of woodland. On the other hand, forest species richness declined with increasing  
280 proportion of permanent grassland at the 1000m scale.

281

282 Urban species responded differently to local scale woody habitats; their richness decreased with increasing  
283 surface of woody vegetation within the grassland, and their abundance decreased at grassland sites with taller  
284 hedgerows (Table 3). Urban species richness also decreased with increasing proportion of woody habitat at  
285 the 200m scale. Among species affinity groups, urban species richness was the only group positively  
286 influenced by the proportion of private gardens at the 200m scale. Both richness and abundance of urban

287 specialists increased with the proportion of built-up area at the 200m scale (correlated with the same measure  
288 at the 1000m scale). Abundance of urban species also increased with increasing proportion of permanent  
289 grassland at the 1000m scale.

290

#### 291 *Bird communities in grasslands*

292 Table 4 focuses on the 22 species occurring in more than one third of sampled sites, classified into three  
293 habitat affinity groups: urban, generalist or farmland specialists. Sixteen of these species were more abundant,  
294 on average, in either recreational grasslands or wastelands compared with agricultural grasslands. Most  
295 species were generalists apart from 4 urban specialists, 5 forest specialists and two farmland specialists, Cirl  
296 bunting *Emberiza circlus* and Whitethroat *Sylvia communis*. The latter, despite its affinity for farmland at  
297 national scale, was more abundant in wastelands than in agricultural grasslands. Ten species can be considered  
298 indicators of one grassland use type. The three species typifying agricultural grasslands were Chaffinch  
299 *Fringilla coelebs*, Nuthatch *Sitta europaea* and Cirl Bunting *Emberiza circlus*, each with a different habitat  
300 affinity at national scale. One urban specialist, the Magpie *Pica pica*, and three generalist species were typical  
301 of recreational grasslands. Finally, three indicator species in wastelands were Greenfinch *Chloris chloris*,  
302 Melodious warbler *Hippolais polyglotta* and Whitethroat *Sylvia communis*, again, each of different habitat  
303 affinity at national scale. Thirty-four species were observed foraging in grass (a total of 629 foraging  
304 observations) but most were very occasional foragers in grass; only 6 species were involved in more than 2%  
305 of foraging observations with Blackbird and Starling being by far the two most frequent grassland foragers.

306

**Table 1.** Estimates (standardised, averaged regression coefficients) and their 95% confidence intervals from model averaging (MMI) for bird species richness, abundance and observations of ground foraging. Significant results, *i.e.* estimates whose 95 % confidence interval do not include zero, are in bold. All models were performed using a Gaussian distribution except abundance for which a negative binomial distribution was used. <sup>1</sup> for grassland use types, agricultural use was used as intercept; <sup>2</sup> for local habitat categorical variable, absence was used as intercept. n / range indicate the number of replicates per category (pres. = presence) or range of variation for categorical and continuous variables respectively (total n = 47).

	n / range	Species richness			Abundance			Foraging in grass		
		Estimate	lower CI	upper CI	Estimate	lower CI	upper CI	Estimate	lower CI	upper CI
(Intercept)		18.34	16.67	20.00	3.71	3.56	3.85	13.44	6.10	20.77
site area	[0.5 - 3.5ha]	<b>1.07</b>	<b>0.05</b>	<b>2.08</b>	0.07	-0.03	0.16	1.44	-2.62	5.50
<i>Grassland use type<sup>1</sup></i>										
Recreational	n = 21	-1.84	-4.12	0.45	0.17	-0.05	0.39	<b>11.03</b>	<b>2.02</b>	<b>20.04</b>
Wasteland	n = 7	-0.21	-3.01	2.59	0.22	-0.02	0.47	-2.11	-12.81	8.58
<i>Local habitat variables<sup>2</sup></i>										
non-native species	pres = 22	0.19	-1.69	2.07	0.11	-0.06	0.28	0.78	-7.19	8.75
shrubby vegetation	pres = 24	<b>2.09</b>	<b>0.05</b>	<b>4.14</b>	0.02	-0.14	0.18	2.10	-5.20	9.39
tree vegetation	pres = 21	0.83	-1.09	2.75	-0.04	-0.20	0.12	<b>-7.25</b>	<b>-13.62</b>	<b>-0.88</b>
hedgerow height	[0.5 - 13m]	<b>1.18</b>	<b>0.08</b>	<b>2.29</b>	-0.02	-0.11	0.07	-2.45	-6.01	1.10
% woody veg.	[1 - 87%]	0.22	-0.70	1.15	0.06	-0.01	0.14	-1.33	-5.25	2.59
<i>Landscape variables at 200m-radius</i>										
% built-up area	[0 - 79%]	-0.31	-1.53	0.90	0.08	-0.06	0.22	0.69	-5.00	6.39
% P. grassland	[0 - 84%]	0.64	-0.32	1.60	0.07	-0.02	0.15	0.42	-3.28	4.11
% woodland	[0 - 19%]	0.26	-0.70	1.21	0.00	-0.10	0.09	0.24	-3.58	4.06
% residential gardens	[0 - 46%]	0.24	-0.75	1.24	0.07	-0.05	0.19	1.21	-3.38	5.80
<i>Landscape variables at 1000m-radius</i>										
% built-up area	[2 - 72%]	-0.24	-1.46	0.98	0.03	-0.13	0.19	2.26	-4.03	8.56
% P. grassland	[12 - 66%]	0.02	-0.99	1.02	0.06	-0.03	0.14	2.48	-0.97	5.94
% woodland	[5 - 34%]	0.37	-0.51	1.26	0.01	-0.07	0.09	-3.21	-6.57	0.15
% residential gardens	[1 - 29%]	-0.02	-1.06	1.01	<b>0.11</b>	<b>0.02</b>	<b>0.21</b>	3.65	-0.32	7.62

**Table 2.** Estimates (standardised, averaged regression coefficients) and their 95% confidence intervals from model averaging (MMI) for richness and abundance of generalist and farmland bird species. Significant results, i.e. estimates whose 95 % confidence interval do not include zero, are in bold. All models were performed using a Gaussian distribution except for farmland abundance and richness for which a negative binomial distribution was used. 1 for grassland use types, agricultural use was used as intercept; 2 for local habitat categorical variable, absence was used as intercept.

	Generalists						Farmland specialists					
	Species richness			Abundance			Species richness			Abundance		
	Estimate	lower CI	upper CI	Estimate	lower CI	upper CI	Estimate	lower CI	upper CI	Estimate	lower CI	upper CI
(Intercept)	8.45	7.89	9.01	18.07	14.37	21.77	0.42	-0.20	1.05	0.68	-0.03	1.39
site area	<b>0.45</b>	<b>0.06</b>	<b>0.84</b>	1.88	-0.30	4.07	<b>0.38</b>	<b>0.05</b>	<b>0.70</b>	<b>0.44</b>	<b>0.09</b>	<b>0.80</b>
<i>Grassland use type<sup>1</sup></i>												
Recreational	-0.79	-1.73	0.14	<b>6.38</b>	<b>1.19</b>	<b>11.57</b>	<b>-1.30</b>	<b>-2.33</b>	<b>-0.27</b>	<b>-1.46</b>	<b>-2.50</b>	<b>-0.42</b>
Wasteland	0.11	-1.02	1.24	-1.46	-7.78	4.86	0.26	-0.59	1.11	0.70	-0.28	1.68
<i>Local habitat variables<sup>2</sup></i>												
non-native species	-0.35	-1.10	0.41	-0.77	-5.08	3.53	0.12	-0.60	0.84	0.59	-0.26	1.45
shrubby vegetation	0.21	-0.47	0.90	1.86	-1.88	5.61	0.37	-0.27	1.01	0.45	-0.33	1.23
tree vegetation	-0.06	-0.76	0.64	0.46	-3.35	4.26	0.03	-0.55	0.62	-0.36	-1.03	0.31
hedgerow height	0.06	-0.32	0.43	-1.28	-3.29	0.73	0.16	-0.19	0.51	0.23	-0.15	0.61
% woody veg.	<b>0.43</b>	<b>0.08</b>	<b>0.77</b>	<b>2.62</b>	<b>0.70</b>	<b>4.54</b>	-0.25	-0.55	0.06	-0.25	-0.58	0.08
<i>Landscape variables at 200m-radius</i>												
% built-up area	-0.15	-0.66	0.37	-1.28	-4.40	1.83	-0.14	-0.78	0.51	0.17	-0.85	1.19
% P. grassland	0.10	-0.27	0.46	1.14	-0.74	3.03	0.06	-0.18	0.30	0.02	-0.25	0.29
% woodland	-0.02	-0.39	0.36	-0.56	-2.69	1.57	-0.11	-0.44	0.21	-0.34	-0.70	0.01
% residential gardens	-0.22	-0.61	0.18	1.26	-0.90	3.42	-0.38	-0.88	0.13	-0.27	-0.74	0.19
<i>Landscape variables at 1000m-radius</i>												
% built-up area	0.06	-0.49	0.60	-0.39	-3.35	2.56	-0.19	-0.68	0.30	-0.48	-1.10	0.15
% P. grassland	0.09	-0.26	0.44	0.28	-1.70	2.26	-0.01	-0.22	0.21	-0.08	-0.34	0.19
% woodland	-0.10	-0.44	0.25	-0.42	-2.26	1.43	0.04	-0.27	0.35	<b>0.31</b>	<b>0.01</b>	<b>0.60</b>
% residential gardens	-0.21	-0.62	0.20	0.51	-1.87	2.90	-0.32	-0.74	0.09	-0.26	-0.70	0.18



**Table 3.** Estimates (standardised, averaged regression coefficients) and their 95% confidence intervals from model averaging (MMI) for richness and abundance of forest and urban bird species. Significant results, i.e. estimates whose 95 % confidence interval do not include zero, are in bold. All models were performed using a Gaussian distribution except abundance of urban specialists for which a negative binomial distribution was used. 1 for grassland use types, agricultural use was used as intercept; 2 for local habitat categorical variable, absence was used as intercept.

	Forest specialists						Urban specialists					
	Species richness			Abundance			Species richness			Abundance		
	Estimate	lower CI	upper CI	Estimate	lower CI	upper CI	Estimate	lower CI	upper CI	Estimate	lower CI	upper CI
(Intercept)	4.23	3.21	5.25	8.02	5.93	10.11	4.04	3.33	4.75	2.13	1.78	2.48
site area	-0.05	-0.69	0.59	0.88	-0.61	2.38	-0.05	-0.65	0.55	-0.09	-0.30	0.12
<i>Grassland use type<sup>1</sup></i>												
Recreational	-0.88	-2.42	0.66	-1.86	-5.64	1.92	0.44	-1.00	1.88	0.37	-0.17	0.91
Wasteland	-1.67	-3.91	0.57	-3.83	-8.73	1.07	-0.06	-1.99	1.88	0.23	-0.39	0.84
<i>Local habitat variables<sup>2</sup></i>												
non-native species	0.26	-0.93	1.45	1.52	-1.24	4.27	0.76	-0.28	1.79	0.34	0.00	0.68
shrubby vegetation	<b>1.37</b>	<b>0.18</b>	<b>2.57</b>	1.87	-1.11	4.85	-0.35	-1.36	0.66	-0.35	-0.71	0.02
tree vegetation	0.49	-0.68	1.66	1.01	-1.55	3.57	0.59	-0.31	1.48	-0.13	-0.49	0.23
hedgerow height	<b>1.05</b>	<b>0.35</b>	<b>1.74</b>	1.34	-0.16	2.84	-0.21	-0.76	0.34	<b>-0.33</b>	<b>-0.56</b>	<b>-0.10</b>
% woody veg.	0.33	-0.33	1.00	<b>2.05</b>	<b>0.66</b>	<b>3.45</b>	<b>-0.50</b>	<b>-0.99</b>	<b>-0.01</b>	-0.08	-0.25	0.09
<i>Landscape variables at 200m-radius</i>												
% built-up area	-0.36	-1.16	0.44	-2.17	-4.38	0.05	<b>1.04</b>	<b>0.32</b>	<b>1.76</b>	<b>0.49</b>	<b>0.21</b>	<b>0.76</b>
% P. grassland	0.61	-0.06	1.27	0.81	-0.57	2.18	0.25	-0.31	0.80	0.12	-0.15	0.39
% woodland	<b>0.99</b>	<b>0.37</b>	<b>1.61</b>	1.36	-0.19	2.90	<b>-0.56</b>	<b>-1.12</b>	<b>-0.01</b>	-0.08	-0.28	0.13
% residential gardens	0.40	-0.20	1.00	0.85	-1.05	2.74	<b>0.53</b>	<b>0.02</b>	<b>1.03</b>	0.10	-0.11	0.31
<i>Landscape variables at 1000m-radius</i>												
% built-up area	-0.19	-1.09	0.71	0.81	-2.29	3.90	0.27	-1.13	1.68	0.25	-0.22	0.72
% P. grassland	<b>-0.76</b>	<b>-1.43</b>	<b>-0.09</b>	-0.26	-1.70	1.17	0.45	0.00	0.90	<b>0.38</b>	<b>0.16</b>	<b>0.59</b>
% woodland	0.36	-0.23	0.94	0.02	-1.35	1.39	0.32	-0.22	0.85	-0.06	-0.23	0.11
% residential gardens	0.27	-0.52	1.07	1.59	-0.11	3.30	0.45	-0.28	1.18	0.16	-0.04	0.37

**Table 4.** Mean abundance and ground foraging activity of birds. Species occurring in more than a third of sampled grasslands are shown, in order of habitat affinity, in different grassland use types. Numbers in bold type highlight species which are typical of one type of grassland use (Indicator value analysis; \*\*\* p < 0.001, \*\* p < 0.01, \* p < 0.05). Shaded cells are maximum mean abundance values for each species. Habitat affinity is derived from common bird monitoring at national scale (Jiguet, 2010). For species foraging in grass, the total number of birds detected foraging is given, with species involved in >2% of all foraging observations highlighted in bold.

Species	Latin name	Habitat affinity	Mean abundance			Number foraging
			Agricultural (n = 19)	Recreational (n = 21)	Wasteland (n = 7)	
Goldfinch	<i>Carduelis carduelis</i>	Urban	0.37	0.90	1.29	8
Greenfinch	<i>Chloris chloris</i>	Urban	0.21	0.67	<b>3.14 ***</b>	1
House sparrow	<i>Passer domesticus</i>	Urban	0.95	3.29	3.29	<b>13</b>
Magpie	<i>Pica pica</i>	Urban	1.05	<b>2.48 *</b>	1.57	<b>24</b>
Blackbird	<i>Turdus merula</i>	Generalist	2.68	<b>5.52 ***</b>	3.29	<b>227</b>
Blackcap	<i>Sylvia atricapilla</i>	Generalist	<b>3.16</b>	2.33	3.00	0
Blue tit	<i>Cyanistes caeruleus</i>	Generalist	2.16	<b>3.52</b>	1.71	0
Carrion crow	<i>Corvus corone</i>	Generalist	0.47	<b>1.19 *</b>	0.14	<b>30</b>
Chaffinch	<i>Fringilla coelebs</i>	Generalist	<b>2.95 ***</b>	2.24	1.29	1
Dunnock	<i>Prunella modularis</i>	Generalist	1.05	1.86	<b>2.14</b>	5
Great tit	<i>Parus major</i>	Generalist	1.74	<b>2.57</b>	2.14	0
Melodious warbler	<i>Hippolais polyglotta</i>	Generalist	0.79	0.14	<b>1.57 *</b>	0
Woodpigeon	<i>Columba palumbus</i>	Generalist	1.21	<b>3.86 ***</b>	1.71	<b>25</b>
Chiffchaff	<i>Phylloscopus collybita</i>	Forest	2.42	1.29	2.43	4
Nuthatch	<i>Sitta europaea</i>	Forest	<b>0.79 *</b>	0.00	0.71	0
Robin	<i>Erithacus rubecula</i>	Forest	1.47	1.52	1.14	8
Song thrush	<i>Turdus philomelos</i>	Forest	0.79	0.76	0.43	7
Wren	<i>Troglodytes troglodytes</i>	Forest	1.58	1.29	2.57	0
Cirl Bunting	<i>Emberiza circlus</i>	Farmland	<b>0.95 *</b>	0.14	0.43	0
Whitethroat	<i>Sylvia communis</i>	Farmland	0.95	0.10	<b>1.43 ***</b>	0
Long-tailed tit	<i>Aegithalos caudatus</i>	-	0.84	1.38	0.57	1
Starling	<i>Sturnus vulgaris</i>	-	1.11	4.71	4.71	<b>201</b>

257 **Discussion**

258 Our results from two cities in western France show that both local scale vegetation structure,  
259 reflecting management practices, and landscape context have important effects on shaping breeding  
260 and foraging bird communities. This is in accordance with the results of other studies of breeding birds  
261 in urban environments, showing the importance of both local and landscape variables in explaining  
262 habitat selection (Lepczyk et al. 2017a). Grassland use type was less important in our study, despite  
263 the diversity of functions and forms of management they represented, indicating that, with careful  
264 management, any grassland use type may have potential value for birds.

265

266 Total bird species richness was firstly and most importantly influenced by local habitat characteristics,  
267 while landscape context was less important, in agreement with general results on bird-habitat  
268 relationships in urban contexts (Evans et al. 2009). Unlike many other studies of bird richness along  
269 urban-rural gradients, we did not observe a decrease in bird species richness from rural to urban  
270 grasslands, or more exactly, no effect of proportion of built up land, except for an increase in both  
271 richness and abundance of urban specialists. A recent systematic review (Batáry et al. 2018) reported  
272 general decreases in species richness in urban environments, especially those in which recreational or  
273 amenity parklands were observed. In our study urban grasslands were not necessarily less species rich,  
274 but this richness depended on the management of woody vegetation in and around the site. Presence of  
275 scrubby vegetation inside the grassland site as well as the maintenance of well-developed, tall  
276 hedgerows on the perimeter were associated with higher species richness of breeding birds, especially  
277 forest specialists, in our study. Such habitats are well-known local scale drivers of bird diversity  
278 (Lepczyk et al. 2017b). We found no influence of the total area of woody vegetation (both trees and  
279 shrubs) at site level on total richness or abundance. However, species responded differently according  
280 to habitat affinity; generalists and forest species benefited from larger areas of woody vegetation,  
281 while urban species avoided.

282

283 The proportion of non-native vegetation did not influence bird richness or abundance although bird  
284 communities have been shown to be sensitive to vegetation composition in urban areas (Chace and

285 Walsh 2006). A recent study in Chile (Villaseñor et al. 2020) found that richness and abundance of  
286 native bird species was higher in vacant lands composed of native vegetation than in urban parks and  
287 residential areas dominated by exotic vegetation. However the opposite was true for exotic bird  
288 species; bird communities of Santiago had high proportion of exotic bird species (approximately one  
289 third of birds recorded). Bird and bat species richness both also increased with the proportion of native  
290 vegetation in an Australian study of urban parks and green space, again with a strong presence of  
291 exotic breeding species (Threlfall et al. 2016). So far, bird communities of urban areas in western  
292 France are dominated by native species, apart from occasional occurrences of Ring-necked parakeets  
293 *Psittacula krameri* (recorded in Nantes during our study) and which are expected to increase (Pârâu et  
294 al. 2016).

295  
296 Size of grassland patch also influenced species richness, even though we were only able to study a  
297 relatively narrow range of grassland sizes and could not include any large grassland patches at the  
298 urban end of our study gradients. Despite this, generalist species richness increased with site area and  
299 larger grasslands also favoured the abundance of generalists and of farmland specialists. Most of our  
300 smaller sites were used for recreation and it would have been preferable to include larger recreational  
301 areas if they had existed in our study cities. Again, habitat affinity groups differed in their response to  
302 grassland use type; farmland species clearly avoided recreational grassland sites, while generalists  
303 were more abundant. The positive effect of larger areas of urban green space on biodiversity is  
304 known (Matthies et al. 2017), but this type of land-use is often fragmented, as in our study area.  
305 Similarly, in the UK, only 13% of green space is > 0.25 ha although larger areas are advisable for bird  
306 conservation (Fernández-Juricic and Jokimäki 2001; Evans et al. 2009). Bird species richness would  
307 be expected to increase further if larger patches of grassland could be sampled. In larger cities the  
308 effects of increasing patch size have been more fully demonstrated, revealing that much larger  
309 grassland patches in urban areas may indeed attract species more typical of open habitats, like the  
310 farmland specialists in our study. For example, in Chicago metropolitan area, grassland patch size had  
311 clear positive effects on conservation priority grassland bird species (Buxton and Benson 2016) and  
312 similarly, larger patches of grassland in Berlin were more favourable for populations of wheatear, an

313 open habitat species (Meffert et al. 2012). Very few open habitat specialists were common in the  
314 grasslands we studied in our smaller sized cities and their immediate rural interface. Their presence in  
315 our study also seemed to be related to grassland use type and grass management, as discussed below.

316

317 Bird abundance was driven by landscape context rather than local grassland conditions. Grasslands  
318 with a high proportion of residential gardens in their neighbourhood, which also tended to be in areas  
319 of intermediate levels of built-up land, had higher bird abundance. We detected a positive effect of  
320 residential gardens at a 1km scale, suggesting an influence of a relatively large neighbourhood rather  
321 than immediate surrounding of studied grasslands, but note that this variable was correlated at the two  
322 scales. Grassland sites with more gardens in their immediate neighbourhood (200m scale) attracted  
323 more urban species, however this may simply have been due to the positive effects of built-up land on  
324 this species group. General patterns of bird abundance along urban-rural gradients often reveal peak  
325 abundance values in intermediate, suburban areas (Blair 2004; Batáry et al. 2018), though we did not  
326 find reports of higher densities of birds in areas with residential gardens elsewhere in the  
327 literature. Tratalos et al. (2007) directly studied the influence of variation in housing densities on bird  
328 densities, finding that bird abundance peaked in areas with intermediate housing densities. Residential  
329 gardens may be an important source of complementary resources for breeding birds e.g. nesting sites  
330 for birds feeding in grass, additional food resources for birds nesting and feeding in grasslands.  
331 Gardens form a large part of urban green space but are highly fragmented so that individual gardens  
332 are too small to maintain viable populations of many species. Therefore understanding these  
333 interactions between gardens and other forms of urban green space may help to define strategies for  
334 collective action by residential gardeners and the promotion of wildlife-friendly gardening practices  
335 (Goddard et al. 2010).

336

337 Besides the effect of residential garden density, we detected no other effects of the other landscape  
338 variables, proportion of built-up land, woody habitats or permanent grassland, on total species richness  
339 or abundance. The proportion of built-up land, in particular, is generally shown to be a strong driver of  
340 urban bird assemblages, including in cities of comparable size to those studied here (Bino et al. 2008).

341 Our focus on grassland habitats may have concealed some of this variation in species richness,  
342 observed when considering the full diversity of forms of urban green space. The influence of  
343 landscape context was clearer for species affinity groups. Forest specialists responded positively to  
344 increasing woody cover at both scales while avoiding areas with a high proportion of herbaceous  
345 cover at the 1000m scale. Urban specialists in grasslands naturally preferred urban contexts, but also  
346 more open landscapes, with less woodland and more herbaceous cover. More precise mapping of  
347 certain land cover types could enhance such landscape analyses. The land cover databases we used did  
348 not allow us to finely quantify the proportions of more intermediate vegetation classes such as scrub or  
349 extensively managed grass, the very variables influencing bird diversity at site level. Mapping of  
350 informal urban green space shows that between 5 and 40% of urban areas can be made up of Informal  
351 Urban Green-space, not easily attributable to main land-use categories (Rupprecht and Byrne, 2014a).  
352 It is also difficult to obtain information about management practices of green space at landscape scale.  
353  
354 Significantly more ground foraging was observed in recreational grasslands, in comparison with  
355 wastelands and agricultural grasslands, but this mainly concerned just two species of insectivorous  
356 feeders in short grass, Blackbird *Turdus merula* and Starling *Sturnus vulgaris*. Both are generalists,  
357 which were more abundant in this type of grassland. One possible reason is that recreational sites are  
358 usually closely cropped, contrasting with the higher grass of wastelands and the variable grass height  
359 of agricultural grasslands (Supplementary material, Fig. S5). Studies in agricultural grasslands have  
360 shown that both species prefer feeding in shorter grass swards, where prey availability is greater  
361 (Whitehead et al. 1995; Perkins et al. 2000). However, it has also been shown experimentally that  
362 although Starlings forage more efficiently on recently mown swards this may only represent a short-  
363 term benefit, as more frequent mowing reduces invertebrate abundance in the long-term (Devereux et  
364 al. 2006). There is also evidence that grasslands in cities indeed provide important feeding resources  
365 for breeding Starlings, but that reproductive success may be lower because adults are able to bring less  
366 food to nestlings in urban environments (Mennechez and Clergeau 2006). This example illustrates the  
367 importance of understanding how habitat quality in cities influences key activities such as breeding

368 and feeding, in order to avoid potentially creating ecological traps when managing green space for  
369 wildlife in cities (Lepczyk et al. 2017a).

370

371 More generally, short-mown, recreational grassland, a dominant form of grassland in many cities, has  
372 been shown to be of poor value for plant and insect groups (Watson et al. 2020) and recent studies  
373 have begun to explore the benefits of different management approaches, such as urban meadows  
374 (Norton et al. 2019). Wastelands in our study were relatively species rich and favoured abundance of  
375 generalists and farmland specialists, despite being situated in urban areas and many studies point to  
376 their potential for nature conservation (Bonthoux et al. 2014; Villaseñor et al. 2020). Several species  
377 of seedeaters (Goldfinch, Greenfinch and House Sparrow) whose populations are declining at national  
378 level were more abundant in wasteland grasslands than in the other two grassland use types. Even  
379 Whitethroat, considered a farmland specialist at national scale, was more abundant in wasteland sites  
380 than in agricultural grasslands. This agrees with observations in other cities showing that bird  
381 specialists of open habitats may be enticed into urban sites, with the right management or indeed less  
382 formal management (Meffert et al. 2012; Villaseñor et al. 2020). It has also been shown that urban-  
383 agricultural parkland i.e. extensive, wildlife-friendly farmland in an urban environment could be  
384 another way to provide more suitable habitat for such declining open-land bird species (Sorace  
385 2001). However, most species of farmland and open habitats were infrequent in the urban contexts we  
386 studied. Our sample of wastelands was small due to rapid modifications to these areas, generally  
387 destined for urban development, but despite this, with their more extensive grass management and  
388 scrubby vegetation they show us the potential of less managed sites in comparison with traditional  
389 public parkland and probably more closely resemble newer urban meadows. Although we found  
390 agricultural areas to have a limited contribution as compared with wastelands, the importance of  
391 grassland size may mean that maintaining agricultural grasslands and the farmers that manage them, in  
392 the context of urban expansion, could provide alternative habitats to smaller or more ephemeral  
393 wastelands, to more wooded sites like parklands or to more intensively managed sites like sports  
394 grounds.

395

396 **Conclusion**

397 We conclude that managers and planners of urban green space should carefully consider the interplay  
398 between local site characteristics and possible interactions with other neighbouring land cover types, if  
399 they wish to maximise benefits to birds of urban grassland habitats. The contribution of urban  
400 grasslands to biodiversity conservation will require preservation of large sites managed to provide a  
401 heterogeneity of vegetation structure, and strategically located in urban landscapes with high density  
402 of residential gardens. A diversity of use and management will allow birds with various requirements  
403 to co-exist at landscape scale. Grass management varies according to grassland use type, favouring  
404 different bird communities. Varied mowing regimes, allowing the development of longer grass in  
405 some areas are becoming more common and should be encouraged. This type of management made  
406 lead to new challenges, as other studies have shown. Complex public perception of Informal Urban  
407 Greenspace ranges from disapproval to opportunity for nature exploration (Rupprecht and Byrne,  
408 2014b), but generally, public acceptance of the untidy appearance of certain wildlife habitats may be  
409 difficult to obtain (Filibeck et al., 2016; Rega-Brodsky et al., 2018). Alternating mown and unmown  
410 areas may be more acceptable (Hunter and Hunter 2008), thereby enabling managers to reconcile  
411 human needs and biodiversity maintenance. Areas currently considered as “waste” lands should not be  
412 transformed before taking into consideration their ecological value (Villaseñor et al. 2020). Scrubby  
413 habitats which may look unattractive are valuable habitats for many species of bird. At neighbourhood  
414 and city scales, a better integration of residential gardens may enhance the overall capacity of urban  
415 green space to support bird populations and associated biodiversity (Goddard et al. 2010). The  
416 challenge is to motivate small, private landowners, or indeed groups of gardens, to adopt biodiversity  
417 friendly management (van Heezik et al. 2012); a promising example is the use of GardenApp, a GIS-  
418 based web application, to coordinate action between garden owners and green space managers  
419 (Schneider et al. 2019). Finally, in the context of urban spread, as described by Güneralp et al. (2020),  
420 maintaining large areas of agricultural land, managed by farmers, may provide a complementary  
421 alternative to the forms of urban agriculture currently being developed, which generally correspond to  
422 small-scale horticulture without large grassland areas (Lin et al. 2015).

423



424 **Declarations**

425 All authors have given their consent for publication and declare that this work has not been submitted  
426 for publication elsewhere.

427 *Data availability*

428 The research was built upon public material and field data. The data produced can be made available  
429 upon request via email to the corresponding author.

430 *Conflicts of interest*

431 All authors certify that they have no affiliations with or involvement in any organization or entity with  
432 any financial interest or non-financial interest in the subject matter or materials discussed in this  
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437

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439 Véronique Beaujouan, Hervé Daniel, Guillaume Pain and Josephine Pithon contributed to the study  
440 conception and design. All authors contributed to data collection and data analysis was led by Rémi  
441 Duflot. The first draft of the manuscript was written by Josephine Pithon and all authors commented  
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443

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581

**Electronic Supplementary Material**

Fig. S1. Graphical representation of land-cover maps for a selected site

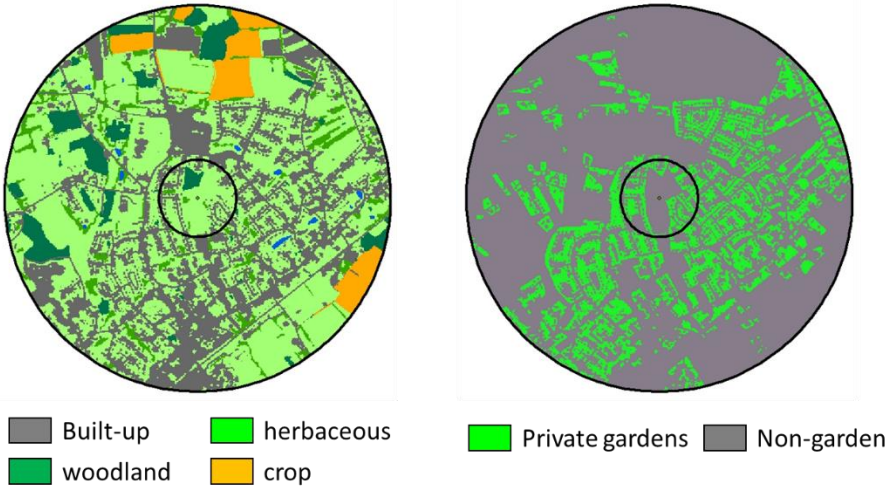


Fig. S2. Relationship across continuous variables

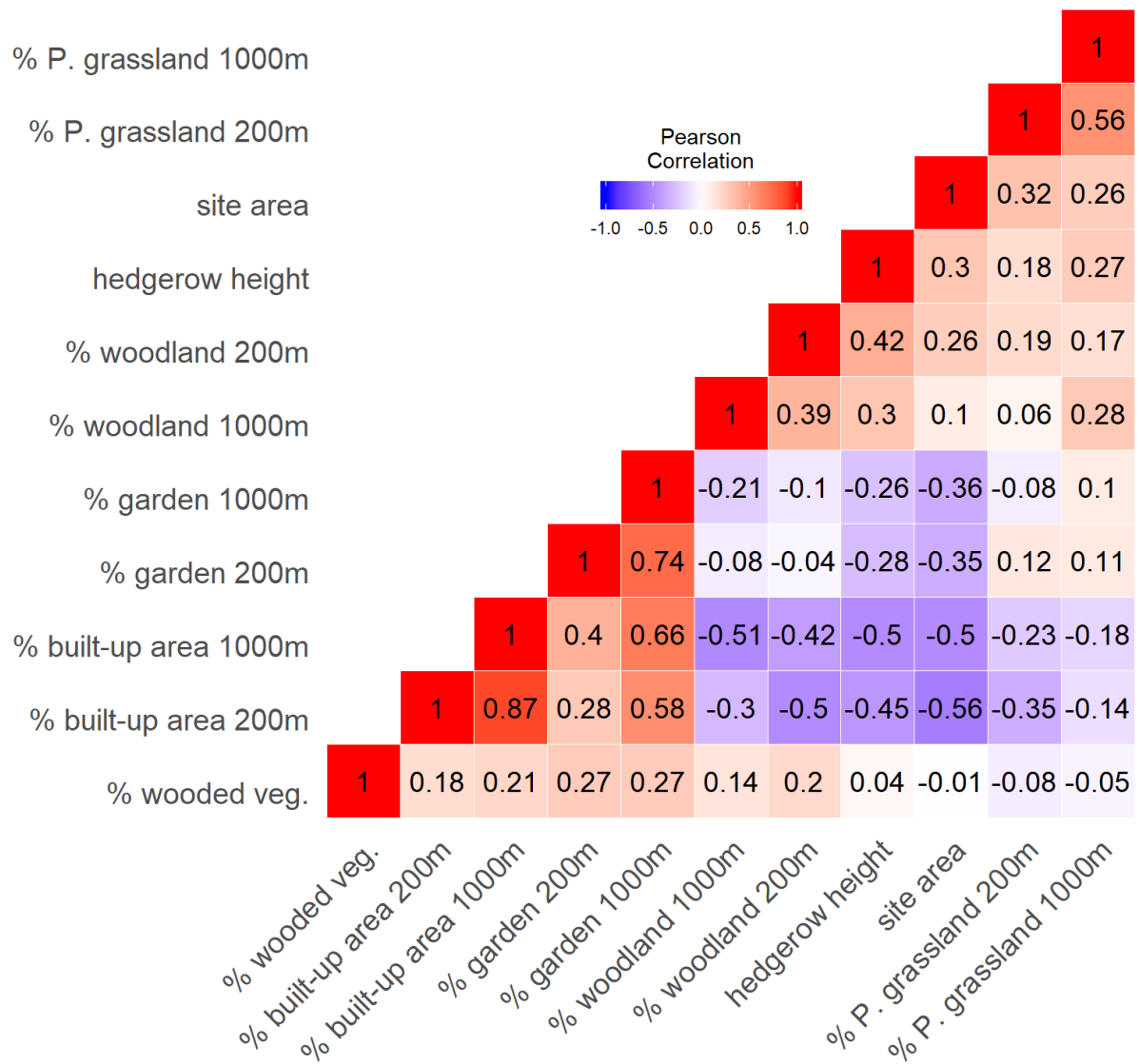




Fig. S3. Relationship across categorical variables

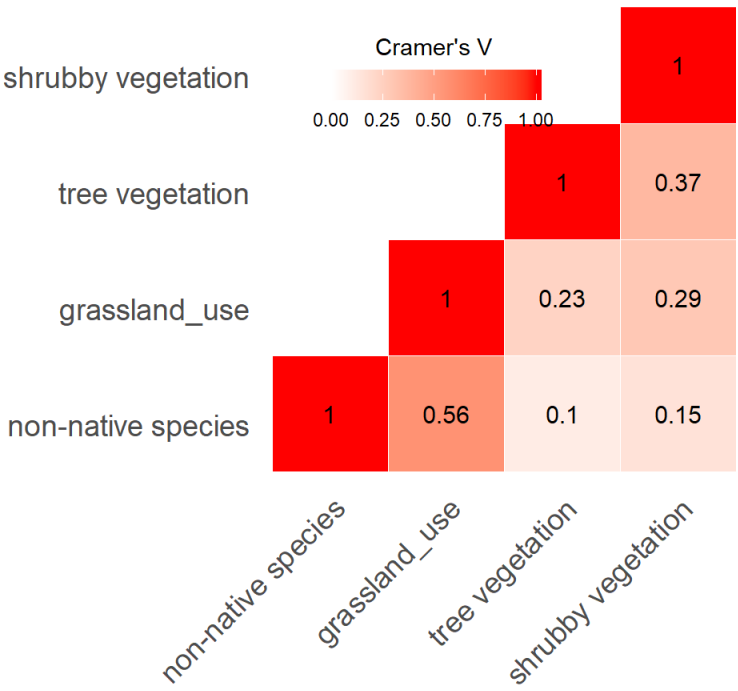


Fig. S4. Relationship between categorical and continuous variables

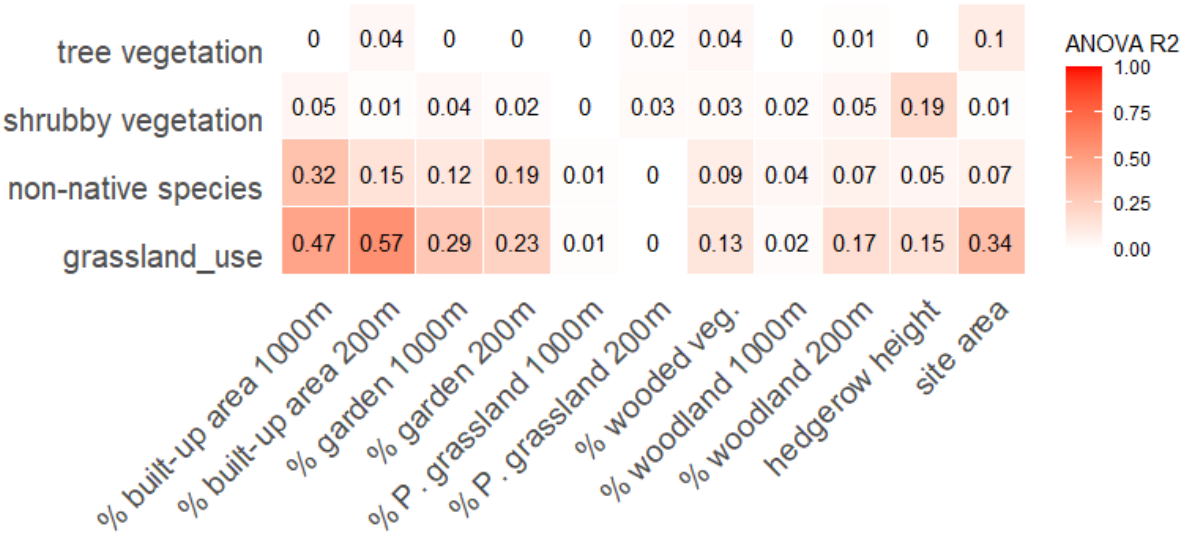
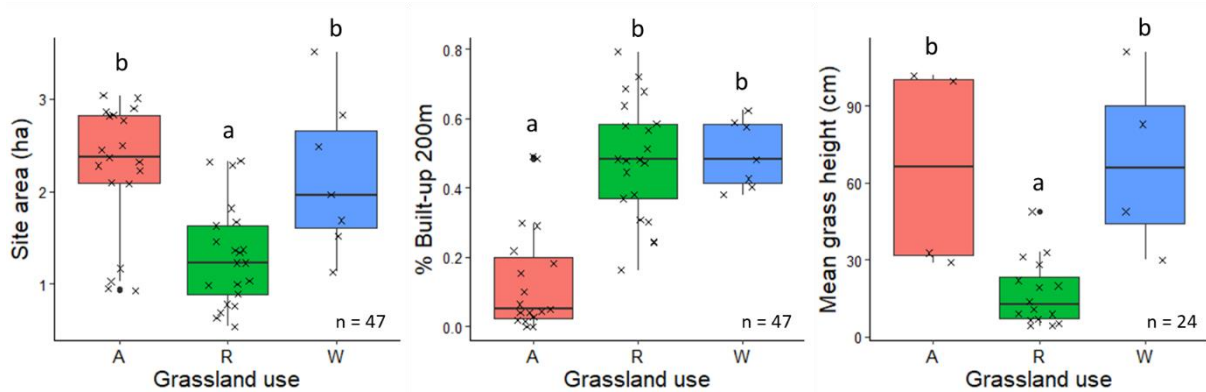


Fig. S5. Analysis of different grassland use types



Site area (ha), percentage of built-up area in a 200m-radius (%), and mean grass height (cm) in agricultural (A), recreational (R) and wasteland (W) grassland sites. Differences were significant in one-way ANOVA test ( $p$ -value  $< 0.001$ , mean grass height was log-transformed for the test). Different letters denote significant differences (Tukey post-hoc test  $\alpha = 5\%$ ).

The average size of sampled grassland sites was 1.8 ha (minimum = 0.54 and maximum = 3.5).

We investigated how the three grassland use types (agricultural, recreational and wasteland) varied in their distribution along the rural-urban gradient, considering the percentage of built up area in 200m-radius to represent level of urbanisation. We also examined how mean grass height varied between grassland use types. Differences were tested using one-way ANOVA followed by a Tukey post hoc test for pairwise multiple comparisons. ANOVA tests were validated by checking for homogeneity of variances across groups using Bartlett test and normality of residuals using a Shapiro-Wilcoxon test. To meet with the assumption of homogeneity of variances, grass height was log-transformed to perform the tests.

Grass land use types were of unequal size (area) and unevenly distributed along the rural-urban gradient, as shown by significant differences in percentage of built-up area ( $p$ -value  $< 0.001$ ). Sites in the recreational category were significantly smaller in area compared with agricultural and wasteland sites ( $p$ -value  $< 0.001$  and  $= 0.013$  respectively). Unsurprisingly, grasslands used for agriculture were found in significantly less urban contexts than grasslands used for recreational activities and wastelands ( $p$ -value  $< 0.001$ ). However, though some recreational grasslands were in suburbs close to rural areas, the urban context of recreational and wasteland sites did not differ significantly.

Our results showed clear differences in mean grass height between grassland use types ( $p$ -value  $< 0.001$ ). Recreational sites had significantly lower grass height than agricultural and wasteland sites ( $p$ -value  $< 0.001$  and  $= 0.013$  resp.), while agricultural and wasteland sites were not significantly different from each other. Mean grass height in agricultural grassland varied most, ranging from approximately 30 to 95 cm.