

This is a self-archived version of an original article. This version may differ from the original in pagination and typographic details.

Author(s): Pithon, Josephine A.; Duflot, Rémi; Beaujouan, Véronique; Jagaille, M.; Pain, Guillaume; Daniel, Hervé

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

Year: 2021

Version: Accepted version (Final draft)

Copyright: © 2021 the Authors

Rights: In Copyright

Rights url: <http://rightsstatements.org/page/InC/1.0/?language=en>

Please cite the original version:

Pithon, J. A., Duflot, R., Beaujouan, V., Jagaille, M., Pain, G., & Daniel, H. (2021). Grasslands provide diverse opportunities for bird species along an urban-rural gradient. *Urban Ecosystems*, 24(6), 1281-1294. <https://doi.org/10.1007/s11252-021-01114-6>

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

2 Pithon, J. A.^{a*} Dufлот R.^{a, b, c}, Beaujouan V.a, Jagaille M.^{a, d}, Pain G.^a, and Daniel H.^a

3 Urban Ecosystems 24, 1281–1294 (2021). <https://doi.org/10.1007/s11252-021-01114-6>

4

5 ^a BAGAP, INRAE, Institut Agro, ESA, 49000, Angers, France

6 ^b Department of Biological and Environmental Science, University of Jyväskylä, Finland

7 ^c School of Resource Wisdom, University of Jyväskylä, Finland

8 ^d GIS Bretagne Télédétection, IMT Atlantique, Technopôle Brest-Iroise CS 83818, 29238 Brest Cedex 3, France

9

10 *Corresponding author: Josephine PITHON, j.pithon@groupe-esa.com ORCID: 0000-0002-2976-961X

11 ORCID ID of authors:

12 Rémi DUFLOT: 0000-0002-5070-903X

13 Hervé DANIEL: 0000-0003-1522-9556

14 Véronique BEAUJOUAN: 0000-0003-1606-1724

15 Guillaume PAIN: 0000-0001-7977-337X

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.

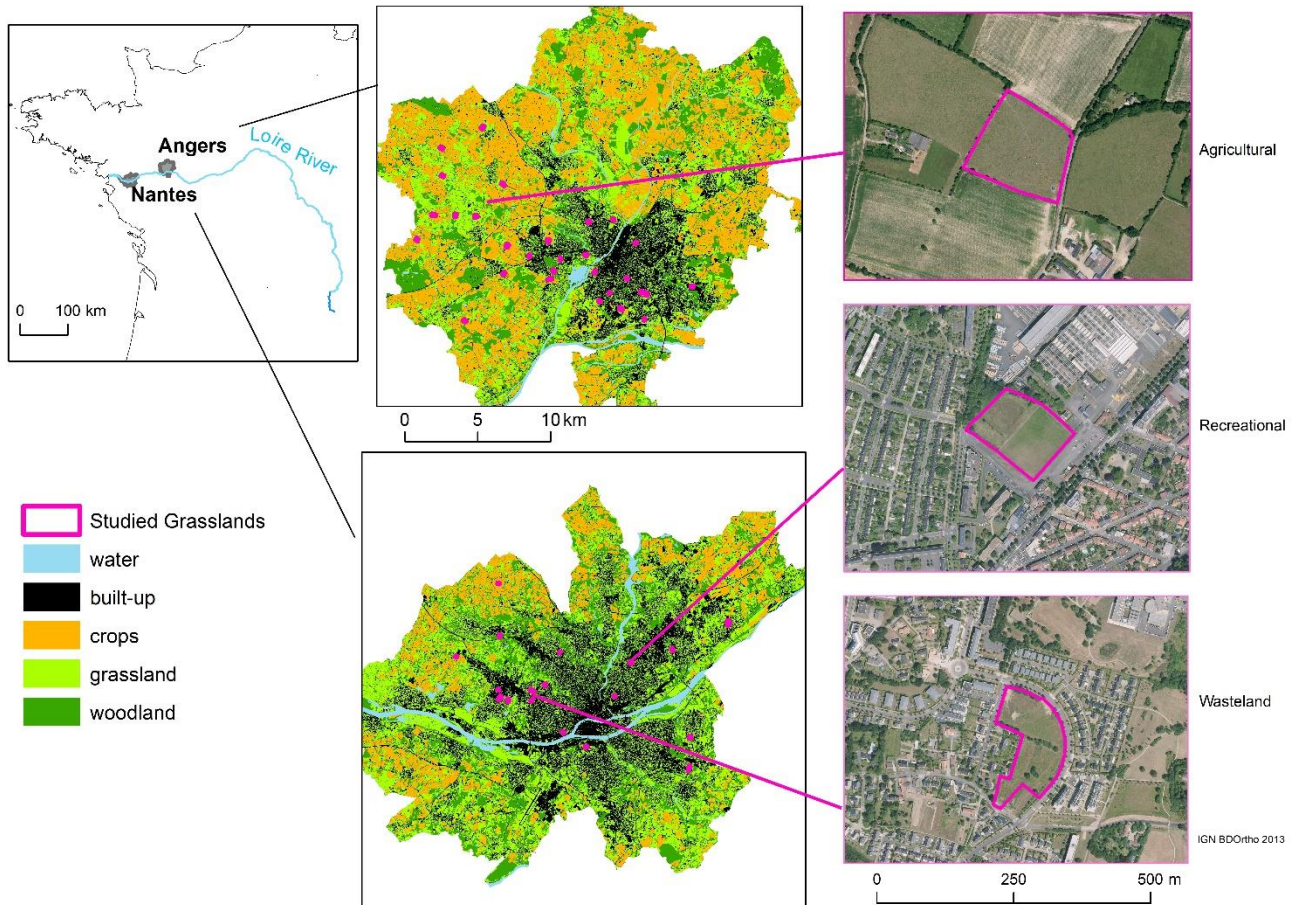
112

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 km², 609 000 inhabitants)
117 and Angers (47°28' N; 0° 33'W, conurbation 540 km², 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): 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 5000m² (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**

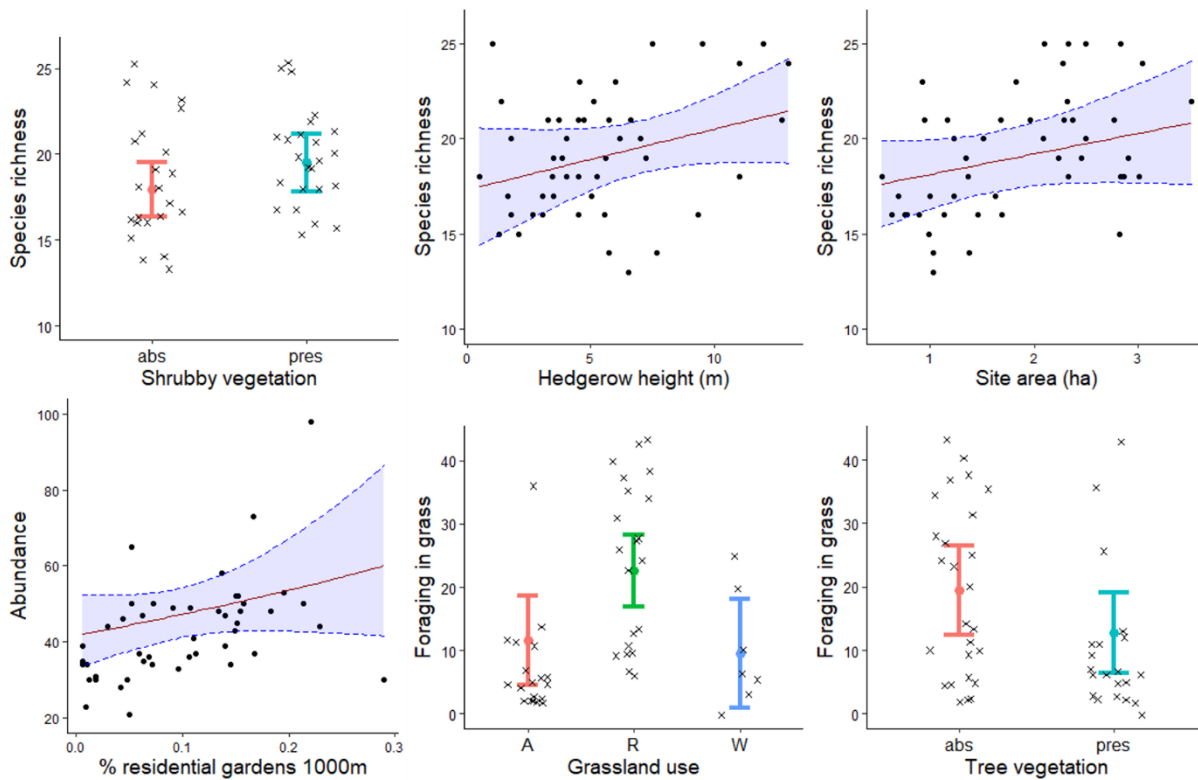
239 *Effects of local habitat and landscape context on birds using grasslands*

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. ¹ for grassland use types, agricultural use was used as intercept; ² 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]	1.07	0.05	2.08	0.07	-0.03	0.16	1.44	-2.62	5.50
<i>Grassland use type¹</i>										
Recreational	n = 21	-1.84	-4.12	0.45	0.17	-0.05	0.39	11.03	2.02	20.04
Wasteland	n = 7	-0.21	-3.01	2.59	0.22	-0.02	0.47	-2.11	-12.81	8.58
<i>Local habitat variables²</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	2.09	0.05	4.14	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	-7.25	-13.62	-0.88
hedgerow height	[0.5 - 13m]	1.18	0.08	2.29	-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	0.11	0.02	0.21	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	0.45	0.06	0.84	1.88	-0.30	4.07	0.38	0.05	0.70	0.44	0.09	0.80
<i>Grassland use type¹</i>												
Recreational	-0.79	-1.73	0.14	6.38	1.19	11.57	-1.30	-2.33	-0.27	-1.46	-2.50	-0.42
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 variables²</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.	0.43	0.08	0.77	2.62	0.70	4.54	-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	0.31	0.01	0.60
% 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 type¹</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 variables²</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	1.37	0.18	2.57	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	1.05	0.35	1.74	1.34	-0.16	2.84	-0.21	-0.76	0.34	-0.33	-0.56	-0.10
% woody veg.	0.33	-0.33	1.00	2.05	0.66	3.45	-0.50	-0.99	-0.01	-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	1.04	0.32	1.76	0.49	0.21	0.76
% 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	0.99	0.37	1.61	1.36	-0.19	2.90	-0.56	-1.12	-0.01	-0.08	-0.28	0.13
% residential gardens	0.40	-0.20	1.00	0.85	-1.05	2.74	0.53	0.02	1.03	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	-0.76	-1.43	-0.09	-0.26	-1.70	1.17	0.45	0.00	0.90	0.38	0.16	0.59
% 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	3.14 ***	1
House sparrow	<i>Passer domesticus</i>	Urban	0.95	3.29	3.29	13
Magpie	<i>Pica pica</i>	Urban	1.05	2.48 *	1.57	24
Blackbird	<i>Turdus merula</i>	Generalist	2.68	5.52 ***	3.29	227
Blackcap	<i>Sylvia atricapilla</i>	Generalist	3.16	2.33	3.00	0
Blue tit	<i>Cyanistes caeruleus</i>	Generalist	2.16	3.52	1.71	0
Carrion crow	<i>Corvus corone</i>	Generalist	0.47	1.19 *	0.14	30
Chaffinch	<i>Fringilla coelebs</i>	Generalist	2.95 ***	2.24	1.29	1
Dunnock	<i>Prunella modularis</i>	Generalist	1.05	1.86	2.14	5
Great tit	<i>Parus major</i>	Generalist	1.74	2.57	2.14	0
Melodious warbler	<i>Hippolais polyglotta</i>	Generalist	0.79	0.14	1.57 *	0
Woodpigeon	<i>Columba palumbus</i>	Generalist	1.21	3.86 ***	1.71	25
Chiffchaff	<i>Phylloscopus collybita</i>	Forest	2.42	1.29	2.43	4
Nuthatch	<i>Sitta europaea</i>	Forest	0.79 *	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	0.95 *	0.14	0.43	0
Whitethroat	<i>Sylvia communis</i>	Farmland	0.95	0.10	1.43 ***	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	201

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
433 manuscript.

434 *Funding*

435 This study was funded by: Pays de la Loire Region (France), the French ministry for the environment
436 DIVA 3 Programme, Angers Loire Metropole (France) and Kone Foundation (Finland).

437

438 **Author contributions**

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
442 on subsequent versions of the manuscript. All authors read and approved the final manuscript.

443

444 **Acknowledgements**

445 We thank Vincent Oury, Cindy Schrader, Frédéric Vaidie and Pascal Bellion for their assistance with
446 fieldwork. This study was funded by the Pays de la Loire Region (URBIO: Biodiversity of Urban
447 Areas) and by the French ministry for the environment via the DIVA 3 programme. Rémi Duflot was
448 supported by a postdoctoral grant from Angers Loire Metropole in France and by a postdoctoral
449 fellowship from the Kone Foundation in Finland.

450

451

452 **References**

- 453 Al-Kofahi, S., Gharaibeh, A., Bsoul, E., Othman, Y., St. Hilaire, R., 2019. Investigating domestic gardens'
454 densities, spatial distribution and types among city districts. *Urban Ecosyst.*
455 <https://doi.org/10.1007/s11252-019-0833-7>
- 456 Aronson, M.F., Lepczyk, C.A., Evans, K.L., Goddard, M.A., Lerman, S.B., MacIvor, J.S., Nilon, C.H., Vargo,
457 T., 2017. Biodiversity in the city: key challenges for urban green space management. *Front. Ecol.*
458 *Environ.* 15, 189–196. <https://doi.org/10.1002/fee.1480>
- 459 Aronson, M.F.J., La Sorte, F.A., Nilon, C.H., Katti, M., Goddard, M.A., Lepczyk, C.A., Warren, P.S., Williams,
460 N.S.G., Cilliers, S., Clarkson, B., Dobbs, C., Dolan, R., Hedblom, M., Klotz, S., Kooijmans, J.L., Kühn,
461 I., MacGregor-Fors, I., McDonnell, M., Mörtberg, U., Pyšek, P., Siebert, S., Sushinsky, J., Werner, P.,
462 Winter, M., 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals
463 key anthropogenic drivers. *Proc. R. Soc. B Biol. Sci.* 281, 20133330.
464 <https://doi.org/10.1098/rspb.2013.3330>
- 465 Barton, K., 2016. MuMIn: Multi-Model Inference.
- 466 Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat.*
467 *Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- 468 Blair, R., 2004. The effects of urban sprawl on birds at multiple levels of biological organisation. *Ecol. Soc.* 9,
469 article 2.
- 470 Bonthoux, S., Brun, M., Pietro, F.D., Greulich, S., Bouché-Pillon, S., 2014. How can wastelands promote
471 biodiversity in cities? A review. *Landsc. Urban Plan.* 132, 79–88.
472 <http://dx.doi.org/10.1016/j.landurbplan.2014.08.010>
- 473 Boussard, H., Baudry, J., 2014. Chloé2012 : a software for landscape pattern analysis,
474 <http://www.rennes.inra.fr/sad/Outils-Produits/Outils-informatiques/Chloe>.
- 475 Burnham, K.P., Anderson, D.R., 2002. Model selection and Multi-Model Inference. A practical information-
476 theoretic Approach, 2nd Ed. ed. Springer-Verlag, New York, USA.
- 477 Cameron, R.W.F., Brindley, P., Mears, M., McEwan, K., Ferguson, F., Sheffield, D., Jorgensen, A., Riley, J.,
478 Goodrick, J., Ballard, L., Richardson, M., 2020. Where the wild things are! Do urban green spaces with
479 greater avian biodiversity promote more positive emotions in humans? *URBAN Ecosyst.*
480 <https://doi.org/10.1007/s11252-020-00929-z>

481 Chace, J.F., Walsh, J.J., 2006. Urban effects on native avifauna: a review. *Landsc. Urban Plan.* 74, 46–69.
482 <http://dx.doi.org/10.1016/j.landurbplan.2004.08.007>

483 Clergeau, P., Croci, S., Jokimaki, J., Kaisanlahti-Jokimaki, M., Dinetti, M., 2006. Avifauna homogenisation by
484 urbanisation: analysis at different European latitudes. *Biol. Conserv.* 127, 336–344.

485 Cochard, A., Pithon, J., Braud, F., Beaujouan, V., Bulot, A., Daniel, H., 2019. Intraspecific trait variation in
486 grassland plant communities along urban-rural gradients. *Urban Ecosyst.* 22, 583–591.
487 <https://doi.org/10.1007/s11252-019-0827-5>

488 Colding, J., 2007. ‘Ecological land-use complementation’ for building resilience in urban ecosystems. *Landsc.*
489 *Urban Plan.* 81, 46–55. <https://doi.org/10.1016/j.landurbplan.2006.10.016>

490 Croci, S., Butet, A., Georges, A., Aguejdad, R., Clergeau, P., 2008. Small urban woodlands as biodiversity
491 conservation hot-spot: a multi-taxon approach. *Landsc. Ecol.* 23, 1171–1186.
492 <https://doi.org/10.1007/s10980-008-9257-0>

493 Dufrière, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible
494 asymmetrical approach. *Ecol. Monogr.* 67, 345–366.

495 Evans, K.L., Newson, S.E., Gaston, K.J., 2009. Habitat influences on urban avian assemblages. *Ibis* 151, 19–39.
496 <https://doi.org/10.1111/j.1474-919X.2008.00898.x>

497 Filibeck, G., Petrella, P., Cornelini, P., 2016. All ecosystems look messy, but some more so than others: A case-
498 study on the management and acceptance of Mediterranean urban grasslands. *URBAN For. URBAN*
499 *Green.* 15, 32–39. <https://doi.org/10.1016/j.ufug.2015.11.005>

500 Fischer, L.K., von der Lippe, M., Kowarik, I., 2013. Urban land use types contribute to grassland conservation:
501 The example of Berlin. *URBAN For. URBAN Green.* 12, 263–272.
502 <https://doi.org/10.1016/j.ufug.2013.03.009>

503 Fuller, R.A., Warren, P.H., Armsworth, P.R., Barbosa, O., Gaston, K.J., 2008. Garden bird feeding predicts the
504 structure of urban avian assemblages: Garden bird feeding and avian assemblages. *Divers. Distrib.* 14,
505 131–137. <https://doi.org/10.1111/j.1472-4642.2007.00439.x>

506 Gillings, S., 2019. Bird responses to housing development in intensively managed agricultural landscapes. *Urban*
507 *Ecosyst.* 22, 1007–1017. <https://doi.org/10.1007/s11252-019-00895-1>

508 Guetté, A., Gaiüzère, P., Devictor, V., Jiguet, F., Godet, L., 2017. Measuring the synanthropy of species and
509 communities to monitor the effects of urbanization on biodiversity. *Ecol. Indic.* 79, 139–154.
510 <https://doi.org/10.1016/j.ecolind.2017.04.018>

511 Jiguet, F., 2010. Les résultats nationaux du programme STOC de 1989 à 2010.

512 Jokimäki, J., Suhonen, J., Jokimäki-Kaisanlahti, M.-L., Carbó-Ramírez, P., 2016. Effects of urbanization on
513 breeding birds in European towns: Impacts of species traits. *Urban Ecosyst.* 19, 1565–1577.
514 <https://doi.org/10.1007/s11252-014-0423-7>

515 Lepczyk, C.A., Aronson, M.F.J., Evans, K.L., Goddard, M.A., Lerman, S.B., MacIvor, J.S., 2017. Biodiversity
516 in the City: Fundamental Questions for Understanding the Ecology of Urban Green Spaces for
517 Biodiversity Conservation. *BioScience* 67, 799–807. <https://doi.org/10.1093/biosci/bix079>

518 Manning, P., Loos, J., Barnes, A.D., Batáry, P., Bianchi, F.J.J.A., Buchmann, N., De Deyn, G.B., Ebeling, A.,
519 Eisenhauer, N., Fischer, M., Fründ, J., Grass, I., Isselstein, J., Jochum, M., Klein, A.M., Klingenberg,
520 E.O.F., Landis, D.A., Lepš, J., Lindborg, R., Meyer, S.T., Temperton, V.M., Westphal, C., Tschamtkke,
521 T., 2019. Transferring biodiversity-ecosystem function research to the management of ‘real-world’
522 ecosystems, in: *Advances in Ecological Research*. Elsevier, pp. 323–356.
523 <https://doi.org/10.1016/bs.aecr.2019.06.009>

524 Marchadour, B., 2014. Oiseaux nicheurs des Pays de la Loire. Coordination régionale LPO Pays de la Loire,
525 Delachaux et Niestlé, Paris, France.

526 Mathieu, R., Freeman, C., Aryal, J., 2007. Mapping private gardens in urban areas using object-oriented
527 techniques and very high-resolution satellite imagery. *Landsc. Urban Plan.* 81, 179–192.
528 <https://doi.org/10.1016/j.landurbplan.2006.11.009>

529 McKinney, M.L., 2002. Urbanization, Biodiversity, and Conservation: The impacts of urbanization on native
530 species are poorly studied, but educating a highly urbanized human population about these impacts can
531 greatly improve species conservation in all ecosystems. *BioScience* 52, 883–890.
532 [https://doi.org/10.1641/0006-3568\(2002\)052\[0883:UBAC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2)

533 Meffert, P.J., Marzluff, J.M., Dziock, F., 2012. Unintentional habitats: Value of a city for the wheatear
534 (*Oenanthe oenanthe*). *Landsc. URBAN Plan.* 108, 49–56.
535 <https://doi.org/10.1016/j.landurbplan.2012.07.013>

536 Milesi, C., Running, S., Elvidge, C., Dietz, J., Tuttle, B., Nemani, R., 2005. Mapping and Modeling the
537 Biogeochemical Cycling of Turf Grasses in the United States. *Environ. Manage.* 36, 426–38.
538 <https://doi.org/10.1007/s00267-004-0316-2>

539 Millenium Ecosystem Assessment, 2005. *Ecosystems and Human Well-Being: Biodiversity Synthesis*. Island
540 Press, Washington DC.

541 Mimet, A., Kerbiriou, C., Simon, L., Julien, J.-F., Raymond, R., 2020. Contribution of private gardens to habitat
542 availability, connectivity and conservation of the common pipistrelle in Paris. *Landscape Urban Plan.* 193,
543 103671. <https://doi.org/10.1016/j.landurbplan.2019.103671>

544 Norton, B.A., Evans, K.L., Warren, P.H., 2016. Urban Biodiversity and Landscape Ecology: Patterns, Processes
545 and Planning. *Curr. Landscape Ecol. Rep.* 1, 178–192. <https://doi.org/10.1007/s40823-016-0018-5>

546 R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical
547 Computing, Vienna, Austria.

548 Rega-Brodsky, C., Nilon, C., Warren, P., 2018. Balancing Urban Biodiversity Needs and Resident Preferences
549 for Vacant Lot Management. *Sustainability* 10, 1679. <https://doi.org/10.3390/su10051679>

550 Rupprecht, C.D.D., Byrne, J.A., 2014a. Informal Urban Green-Space: Comparison of Quantity and
551 Characteristics in Brisbane, Australia and Sapporo, Japan. *PLOS ONE* 9, 1–17.
552 <https://doi.org/10.1371/journal.pone.0099784>

553 Rupprecht, C.D.D., Byrne, J.A., 2014b. Informal urban greenspace: A typology and trilingual systematic review
554 of its role for urban residents and trends in the literature. *Urban For. Urban Green.* 13, 597–611.
555 <https://doi.org/10.1016/j.ufug.2014.09.002>

556 Šálek, M., Hula, V., Kipson, M., Daňková, R., Niedobová, J., Gamero, A., 2018. Bringing diversity back to
557 agriculture: Smaller fields and non-crop elements enhance biodiversity in intensively managed arable
558 farmlands. *Ecol. Indic.* 90, 65–73. <https://doi.org/10.1016/j.ecolind.2018.03.001>

559 Šálek, M., Marhoul, P., Pintíř, J., Kopecký, T., Slabý, L., 2004. Importance of unmanaged wasteland patches for
560 the grey partridge *Perdix perdix* in suburban habitats. *Acta Oecologica* 25, 23–33.
561 <https://doi.org/10.1016/j.actao.2003.10.003>

562 Scrucca, L., 2004. qcc: an R package for quality control charting and statistical process control. *R News* 4/1, 11–
563 17.

564 Smith, A.C., Koper, N., Francis, C.M., Fahrig, L., 2009. Confronting collinearity: comparing methods for
565 disentangling the effects of habitat loss and fragmentation. *Landscape Ecol.* 24, 1271–1285.

566 Sorace, A., Gustin, M., 2010. Bird species of conservation concern along urban gradients in Italy. *Biodivers.
567 Conserv.* 19, 205–221. <https://doi.org/10.1007/s10531-009-9716-1>

568 Taylor, J.J., Lepczyk, C.A., Brown, D.G., 2016. Patch and matrix level influences on forest birds at the rural–
569 urban interface. *Landscape Ecol.* 31, 1005–1020. <https://doi.org/10.1007/s10980-015-0310-5>

570 Thompson, K., Austin, K.C., Smith, R.M., Warren, P.H., Angold, P.G., Gaston, K.J., 2003. Urban domestic
571 gardens (I): Putting small-scale plant diversity in context. *J. Veg. Sci.* 14, 71–78.
572 <https://doi.org/10.1111/j.1654-1103.2003.tb02129.x>

573 Villaseñor, N.R., Chiang, L.A., Hernández, H.J., Escobar, M.A.H., 2020. Vacant lands as refuges for native
574 birds: An opportunity for biodiversity conservation in cities. *Urban For. Urban Green.* 49, 126632.
575 <https://doi.org/10.1016/j.ufug.2020.126632>

576 Visscher, D.R., Unger, A., Grobbelaar, H., DeWitt, P.D., 2018. Bird foraging is influenced by both risk and
577 connectivity in urban parks. *J. Urban Ecol.* 4. <https://doi.org/10.1093/jue/juy020>

578 Zuniga-Palacios, J., Zuria, I., Moreno, C.E., Carlos Almazan-Nunez, R., Gonzalez-Ledesma, M., 2020. Can
579 small vacant lots become important reservoirs for birds in urban areas? A case study for a Latin
580 American city. *URBAN For. URBAN Green.* <https://doi.org/10.1016/j.ufug.2019.126551>
581

Electronic Supplementary Material

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

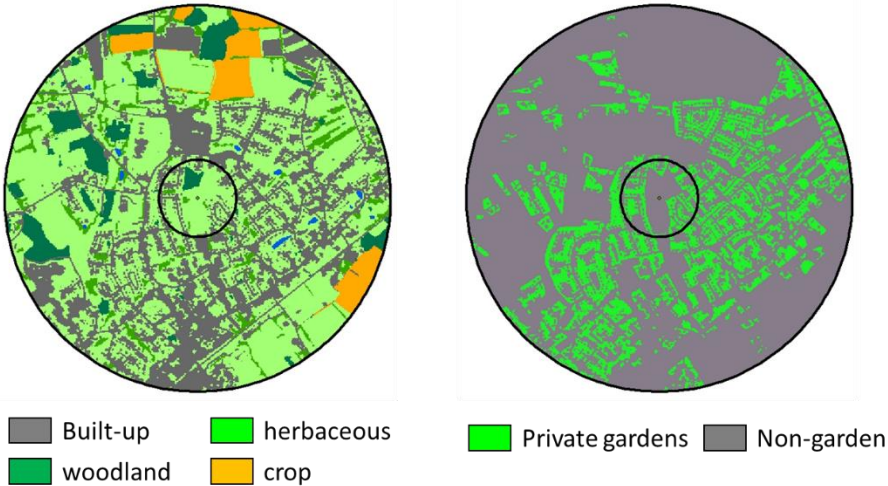


Fig. S2. Relationship across continuous variables

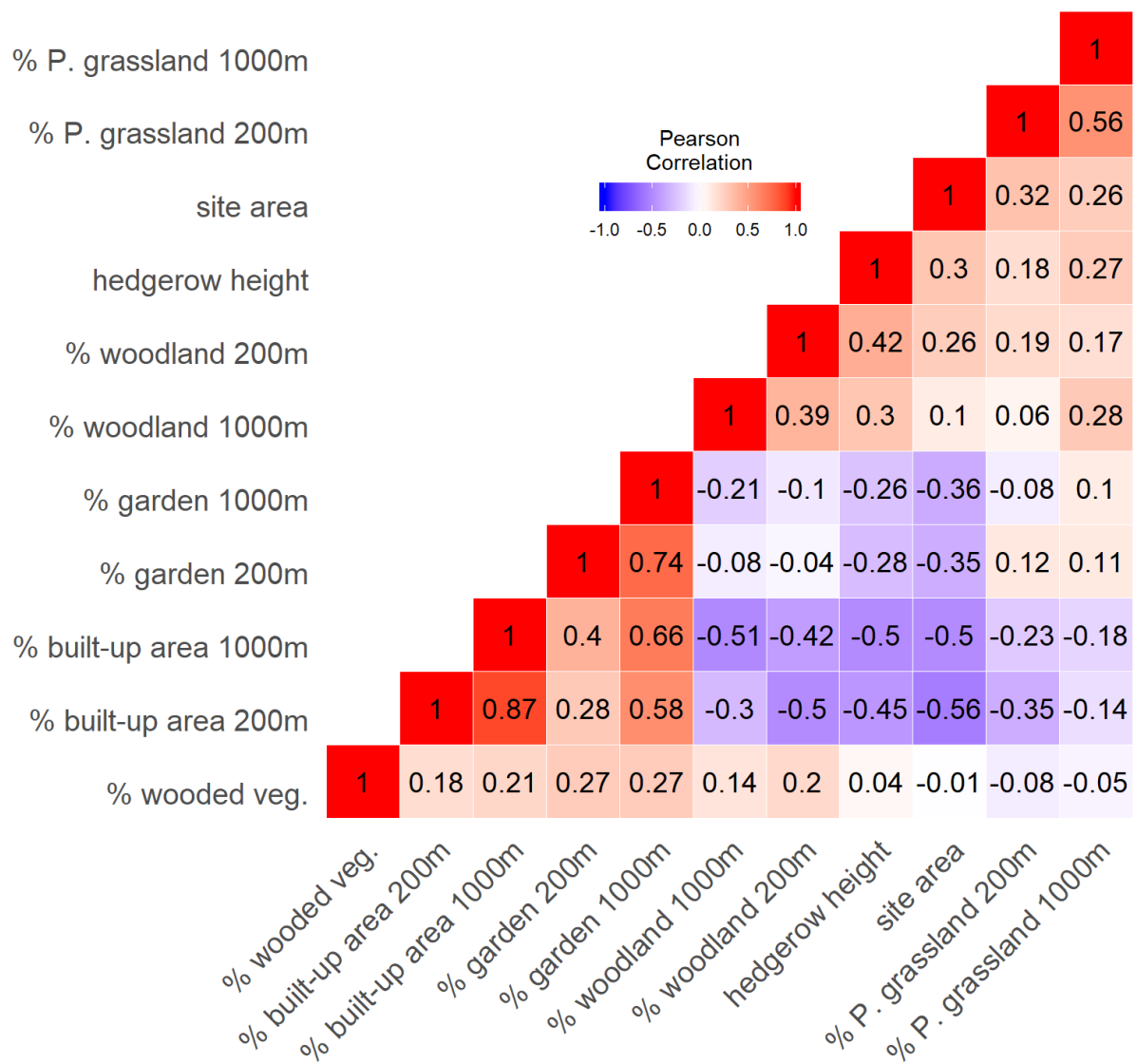


Fig. S3. Relationship across categorical variables

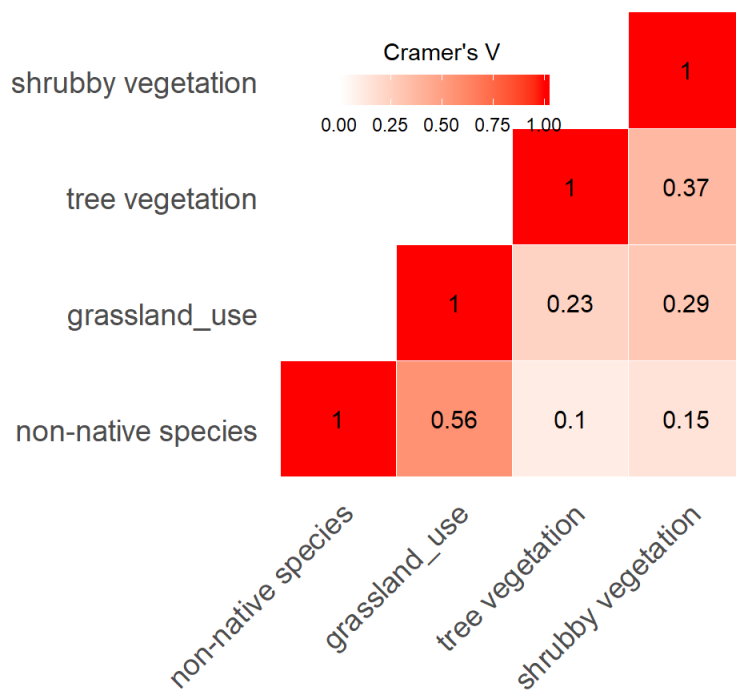


Fig. S4. Relationship between categorical and continuous variables

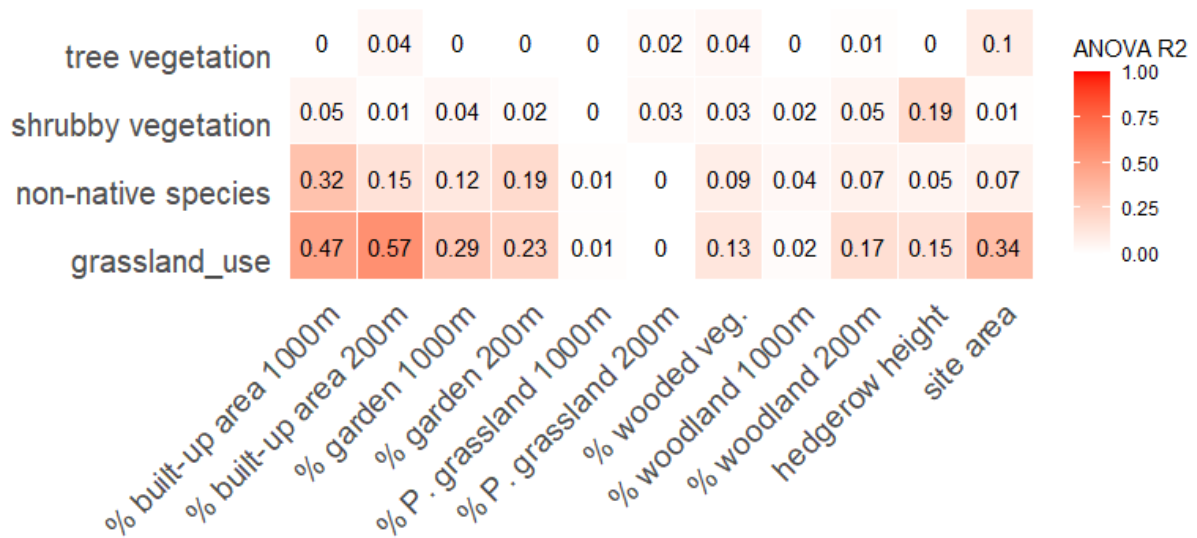
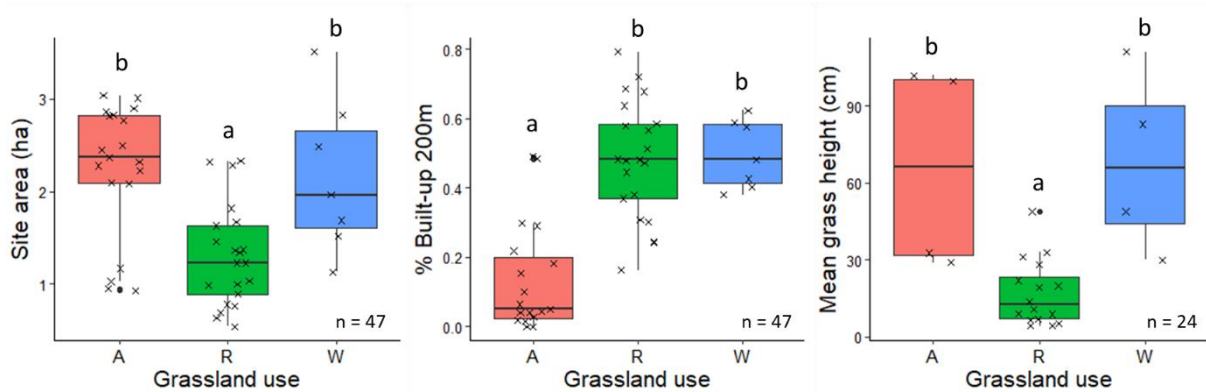


Fig. S5. Analysis of different grassland use types



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.