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

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

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

#### Introduction

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Urbanisation is a major cause of biodiversity loss at global scale (Aronson et al., 2014; Millenium Ecosystem Assessment, 2005), but careful habitat management and provision of green space within cities can help to mitigate the negative effects of this land use change on wild plants and animals (Lepczyk et al., 2017; McKinney, 2002). It has also been highlighted that biological diversity in urban parks, of habitats and species, contributes to human well-being of people in cities (Cameron et al., 2020). It is therefore important to understand how urban and semi-urban landscapes can be planned to provide space for wildlife while simultaneously accommodating a range of human needs (housing, transport infrastructure, recreational opportunities). Therefore, a current challenge for land planners and conservationists is to optimise the quantity, quality and spatial configuration of semi-natural habitats in and around cities to preserve biodiversity, while ensuring compatibility with the multiple functions of urban green space (Aronson et al., 2017; Norton et al., 2016). Birds are a conspicuous and well-known component of urban biodiversity. They respond quickly to land use change and are sensitive to urbanisation, making them particularly suitable as biodiversity indicators of anthropogenic influence (e.g. Guetté et al., 2017); even when highly intensively farmed land is urbanised they may demonstrate a negative response (Gillings, 2019). The ways in which birds exploit habitats within cities and also along urban-rural gradients have therefore received considerable attention (Blair, 2004; Chace and Walsh, 2006; Clergeau et al., 2006). Much of this attention has taken the form of city-scale studies involving a mosaic of habitat types, which is relevant as birds are highly mobile and often exploit different habitats for nesting or feeding. Urban bird assemblages are strongly influenced by local habitat characteristics, such as structural and compositional complexity of vegetation or supplementary feeding and by regional or landscape-

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

scale factors, in particular patch size and to a lesser extent patch isolation (Evans et al., 2009).

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

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

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

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

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

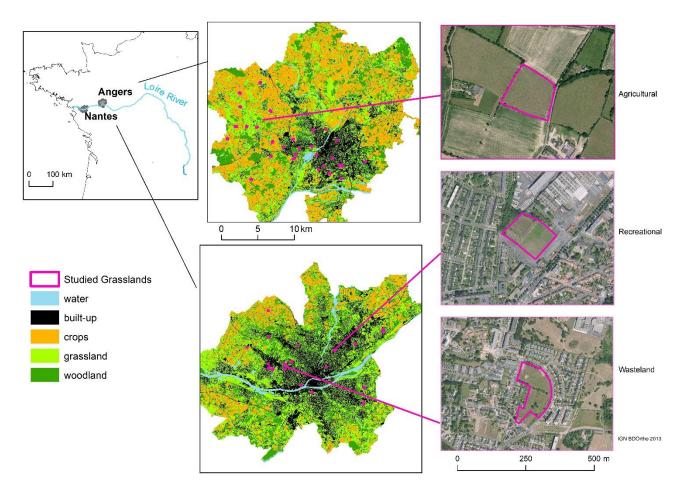
A better knowledge of how birds use grasslands, as influenced by landscape-scale and local habitat factors, in relation to land use and management, might help to inform urban planning for nature conservation. We examined grassland use by birds during the breeding season along an urban-rural gradient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

#### Methods

114 Study areas, land cover mapping and site selection

We focused on the urban-rural gradient of two medium-sized cities of north-western France situated approximately 100 km apart (Fig. 1): Nantes (47°13' N; 1°33' W, conurbation 523 km², 609 000 inhabitants) and Angers (47°28' N; 0° 33'W, conurbation 540 km², 270 000 inhabitants). These two cities share a temperate, oceanic climate and are situated at low altitude (< 65m). By choosing two cities sharing relatively similar biogeographical and climatic conditions, we were able to compare two urban-rural gradients extending well into relatively close rural areas. Both cities are surrounded by mixed farmland with annual and perennial

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



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

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

RAPIDEYE imagery (2011, 5 m spatial resolution, obtained by GEOSUD http://geosud.teledetection.fr). All layers were merged to produce a land cover map with five different classes: built-up areas (including buildings, roads and impervious areas), water bodies, woody areas (including forests and hedgerows), crops (including temporary sown grasslands) and permanent grasslands (including non-farmed open vegetation) (Cochard et al., 2019). Third, we mapped the presence of residential gardens as no such maps existed for the two studied cities, as do in other cities (see for example(Al-Kofahi et al., 2019). Our method was simple in comparison with existing methods (Mathieu et al., 2007); residential gardens were defined as areas of vegetation (woody or grassy) contained in "residential parcels", defined as ownership parcels less than 5000m² (BD Parcellaire® IGN, 2013) containing individual private houses.

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

Environmental variables: habitat surveys and landscape metrics

Habitat surveys were conducted at all the sites. Firstly, each site was assigned to one of the three following grassland use types: recreational, wasteland or agricultural (Fig. 2). Recreational sites were mostly city parks and extensively managed sportsgrounds, wastelands were mostly abandoned plots awaiting development.

Only permanent (>5 years) agricultural grasslands were included. We chose these land use categories as they

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



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

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

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

#### Bird surveys

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

### Statistical analysis

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

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

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

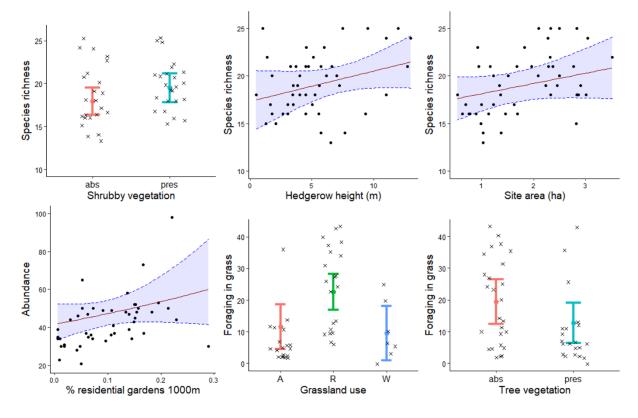
We further investigated bird communities using urban grasslands at the species level. We looked at species distributions and ground foraging activity across grassland use types and according to species habitat affinity. For species that occurred in at least 1/3 of grassland sites we carried out an indicator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

# **Results**

- Effects of local habitat and landscape context on birds using grasslands
- In total, 71 species of bird were observed in grasslands, but for only 33 among these were more than 10 individuals observed, and only 22 were observed in more than 1/3 of the investigated sites. Mean site-level

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

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



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

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

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

Response of bird habitat affinity groups

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

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

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

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

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

Bird communities in grasslands

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

**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).

		Sn	ecies richne	ess.	Abundanc		re Foraging in grass				
	n / range	Estimate	lower CI		Estimate	lower CI	upper CI	Estimate	lower CI	upper CI	
(Intercept)	11/141190	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	
Grassland use type <sup>1</sup>											
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	
Local habitat variables <sup>2</sup>											
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	
Landscape variables at 20	00m-radius										
% 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	
Landscape variables at 10	000m-radius										
% 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 Sp			ecies richne	SS		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
Grassland use type <sup>1</sup>												
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
Local habitat variables	2											
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
Landscape variables at	200m-radiu	S										
% 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
Landscape variables at	1000m-radi	us										
% 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						
	Sı	oecies richne	ess		Abundance S			oecies richne	ess		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	
Grassland use type <sup>1</sup>													
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	
Local habitat variable	$s^2$												
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	
Landscape variables a	t 200m-radiu	S											
% 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	
Landscape variables a	t 1000m-radi	us											
% 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.

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

#### Discussion

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

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

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

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

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

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

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

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

Our focus on grassland habitats may have concealed some of this variation in species richness, observed when considering the full diversity of forms of urban green space. The influence of landscape context was clearer for species affinity groups. Forest specialists responded positively to increasing woody cover at both scales while avoiding areas with a high proportion of herbaceous cover at the 1000m scale. Urban specialists in grasslands naturally preferred urban contexts, but also more open landscapes, with less woodland and more herbaceous cover. More precise mapping of certain land cover types could enhance such landscape analyses. The land cover databases we used did not allow us to finely quantify the proportions of more intermediate vegetation classes such as scrub or extensively managed grass, the very variables influencing bird diversity at site level. Mapping of informal urban green space shows that between 5 and 40% of urban areas can be made up of Informal Urban Green-space, not easily attributable to main land-use categories (Rupprecht and Byrne, 2014a). It is also difficult to obtain information about management practices of green space at landscape scale.

Significantly more ground foraging was observed in recreational grasslands, in comparison with wastelands and agricultural grasslands, but this mainly concerned just two species of insectivorous feeders in short grass, Blackbird *Turdus merula* and Starling *Sturnus vulgaris*. Both are generalists, which were more abundant in this type of grassland. One possible reason is that recreational sites are usually closely cropped, contrasting with the higher grass of wastelands and the variable grass height of agricultural grasslands (Supplementary material, Fig. S5). Studies in agricultural grasslands have shown that both species prefer feeding in shorter grass swards, where prey availability is greater (Whitehead et al. 1995; Perkins et al. 2000). However, it has also been shown experimentally that although Starlings forage more efficiently on recently mown swards this may only represent a short-term benefit, as more frequent mowing reduces invertebrate abundance in the long-term (Devereux et al. 2006). There is also evidence that grasslands in cities indeed provide important feeding resources for breeding Starlings, but that reproductive success may be lower because adults are able to bring less food to nestlings in urban environments (Mennechez and Clergeau 2006). This example illustrates the

importance of understanding how habitat quality in cities influences key activities such as breeding

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

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

#### Conclusion

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

**Declarations** 424 425 All authors have given their consent for publication and declare that this work has not been submitted 426 for publication elsewhere. 427 Data availability The research was built upon public material and field data. The data produced can be made available 428 429 upon request via email to the corresponding author. Conflicts of interest 430 431 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 manuscript. 433 434 **Funding** This study was funded by: Pays de la Loire Region (France), the French ministry for the environment 435 436 DIVA 3 Programme, Angers Loire Metropole (France) and Kone Foundation (Finland). 437 **Author contributions** 438 439 Véronique Beaujouan, Hervé Daniel, Guillaume Pain and Josephine Pithon contributed to the study conception and design. All authors contributed to data collection and data analysis was led by Rémi 440 Duflot. The first draft of the manuscript was written by Josephine Pithon and all authors commented 441 on subsequent versions of the manuscript. All authors read and approved the final manuscript. 442 443 444 Acknowledgements We thank Vincent Oury, Cindy Schrader, Frédéric Vaidie and Pascal Bellion for their assistance with 445 fieldwork. This study was funded by the Pays de la Loire Region (URBIO: Biodiversity of Urban 446 447 Areas) and by the French ministry for the environment via the DIVA 3 programme. Rémi Duflot was supported by a postdoctoral grant from Angers Loire Metropole in France and by a postdoctoral 448 449 fellowship from the Kone Foundation in Finland. 450

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# **Electronic Supplementary Material**

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

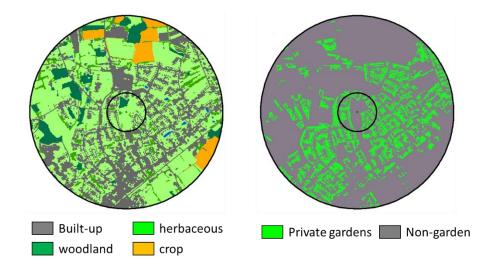


Fig. S2. Relationship across continuous variables

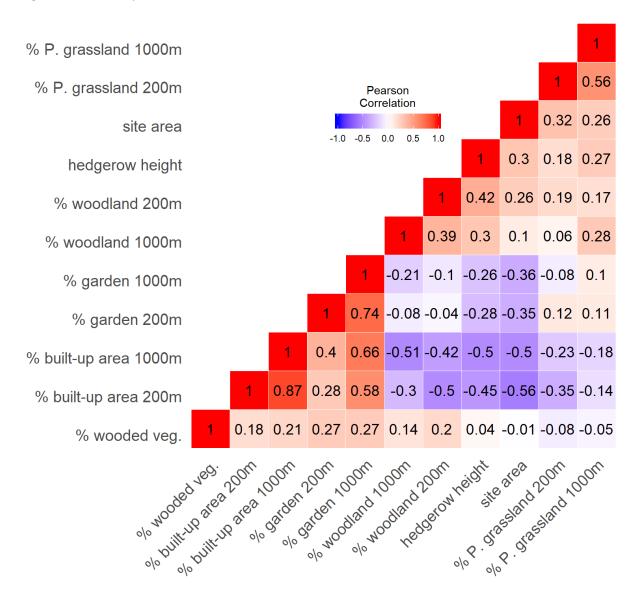


Fig. S3. Relationship across categorical variables

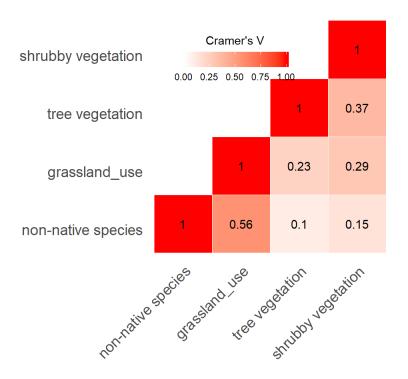


Fig. S4. Relationship between categorical and continuous variables

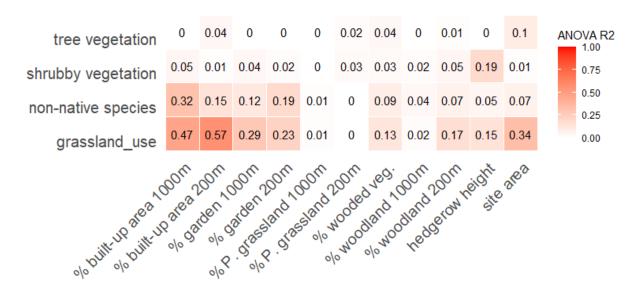
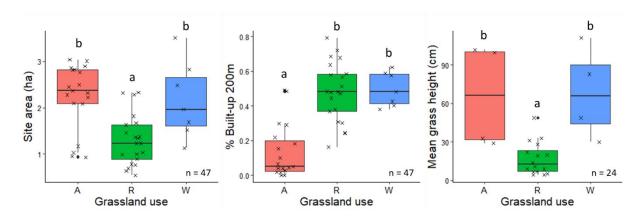


Fig. S5. Analysis of different grassland use types



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-Wilcoxson 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.