



Urban influence on birds at a regional scale: A case study with the avifauna of northern Madrid province

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Abstract

Bird fauna of the Madrid province (Central Spain) was analyzed according to urban development in a landscape mosaic of 700 km². Bird distribution and abundance was studied in urban versus several rural habitats and along a gradient of urban typologies. By means of tree regression analyses we identified the most important habitat structure variables affecting bird species richness and density in urban environments. Bird communities in urban environments were globally less diverse and had higher densities than any natural habitat of the study region. The number of urban-avoider species ($n = 37$) was greater than the number of species favoured by urban habitats ($n = 8$). Current housing developments of extensive crowded terraced-houses, with shortage of gardens, supported the least diverse and dense bird populations. Nevertheless, differences in bird species abundance between urban and natural habitats mitigated in many species when considering the older gardened developments. The plots with the highest species richness (average of 14.5 spp./0.8 ha) were those with 15–28% of building cover, more than 43 medium-sized trees/ha (10–30 cm dbh), and 13–54 small trees/ha (less than 10 cm dbh). Subsequently, future land-use planning should stress the exclusion of urban developments from the most valuable habitats, such as open wooded valley areas devoted to cattle-grazing (mainly ash-groves), and the negative effect of dense, low-gardened housing developments.

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1. Introduction

Urban sprawl is one of the most obvious human impacts on nature, leading to perturbation, fragmenta-

tion or total disappearance of native landscapes and wildlife communities. The impressive rate at which current humankind is changing from rural to urban life styles (O'Meara, 1999; Antrop, 2004), makes precise principles on urban ecology especially necessary (Niemelä, 1999; Bowman and Marzluff, 2001; Marzluff et al., 2001). However, urban environments have been poorly studied when compared with other habitats (Marzluff et al., 2001; Chace and Walsh, 2006),

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in spite of interesting characteristics such as their worldwide ubiquity, marked structural heterogeneity, or novel resources provided.

Urban ecologists have primarily focused on birds when testing for urbanization effects on wildlife (e.g., Beissinger and Osborne, 1982; Friesen et al., 1995; Blair, 1996; Germaine et al., 1998; Clergeau et al., 1998; Kluza et al., 2000; Reynaud and Thioulouse, 2000; Green and Baker, 2003; Lim and Sodhi, 2004). Birds are an ecological and taxonomically diversified taxa, widespread and conspicuous, and with a marked sensitivity to environmental changes (Furness et al., 1993). Therefore, urban environments may have a great potential for defining management practices favouring the conservation of birds (Savard et al., 2000; Marzluff and Erwing, 2001). Nevertheless, few studies analyze the effects of urbanization on avian community patterns, with details on precise responses of species to particular features of urban structure (but see Bolger et al., 1997 or Melles et al., 2003). Moreover, urban habitats analyzed are usually located in relatively homogeneous matrices of natural environments, where the finding of clear human impacts of avian communities is easier than in landscape mosaics where urbanizations are widely scattered.

The northern region of the Madrid province (Central Spain) is currently undergoing an intense urban sprawl. Nevertheless, urban habitats were almost negligible before 1960, being limited to isolated cottages and small rural villages within an extensive mosaic of farming stands of low-intensity management (mainly pastures and parklands for cattle-grazing), combined with natural shrublands, oakwoods and pine forests. The formerly small rural areas have undergone an intense urban sprawl, transforming their surrounding natural habitats into built-up environments. This is because of housing demands of 2nd residences closer to natural environments, by people living in the city of Madrid (3.5 million people, 40 km away). As a consequence, the cities in the study region increased urban surface an average 25% between 1992 and 2000 (Comunidad Autónoma de Madrid, 2004). The developments firstly established were predominantly spread single-detached houses, with big gardens that have become mature after 20–40 years. Contrastingly, more recent urban developments mainly consist of tall block buildings or small terraced-houses with no or little areas devoted to gardens. Because these changes from rural

to heavily urbanized model is operating very rapidly, we need to know their effects on native avifauna to develop management actions for the future urban planning of the region. The main goals of this paper are to study the effects of urbanization on the bird community of this region comparing:

- (1) urban versus natural environments, in an extensive landscape mosaic encompassing several habitats markedly different in terms of vegetation and human uses,
- (2) urban typologies in the study region along a gradient ranging from most to least impacting urban development patterns,
- (3) and to analyze habitat preferences of species considering variables describing habitat structure of the urban environment.

2. Material and methods

2.1. Study area and bird census

This study was conducted on the southern slope of the Guadarrama Range (Madrid province, Central Spain), spanning over 700 km² of piedmont and initial mountain ramps (40°35′–40°48′N, 3°45′–4°10′W; 900–1400 m a.s.l.; Fig. 1). This area is located approximately 40 km northwest of Madrid city, with which it is connected by a good network of highways, local roads and railways. The study region has a Mediterranean-continental cold climate, with a mean temperature of 14.5 °C and rainfall of 130 mm during spring time. There is a wide variety of habitats in this area: four main native forests (pinewoods of *Pinus sylvestris*, riparian woods, deciduous oakwoods of *Quercus pyrenaica* and evergreen holm-oakwoods of *Q. rotundifolia*), open wooded habitats of ash (*Fraxinus angustifolia*) and holm-oaks devoted to livestock, several scrublands resulting from forest degradation, artificial pasturelands and urban areas (from small villages to large cities). These habitats are widely scattered in small sized patches due to the land-ownership model in this region and the effects of land-use and environmental factors (e.g., relief, soils, roads and tracks crossing the territory). See Izco (1984) for more details and descriptions of geographic, climatic and botanic characteristics of the study region. New residential

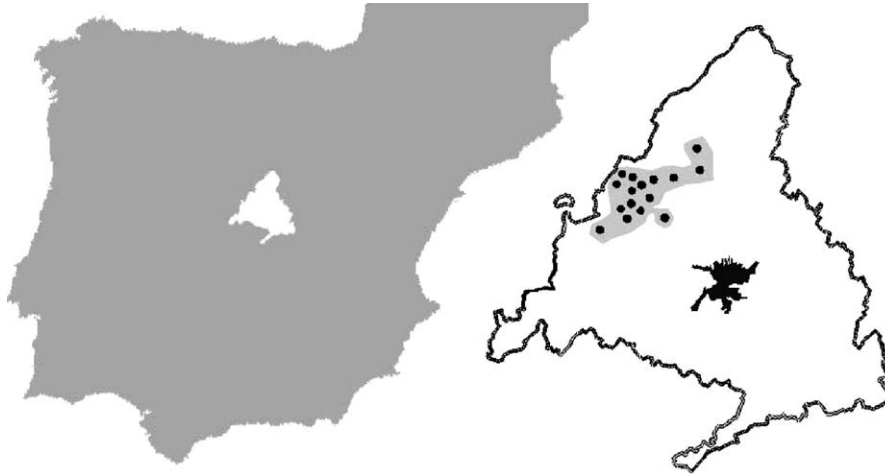


Fig. 1. Location of the study region in the centre of the Iberian Peninsula within Madrid province. Dots represent the 16 small cities surveyed, while shading shows the nearby areas where natural habitats were sampled. Madrid city is shown in black in the middle of the province map.

developments began to grow near town centres on lands formerly devoted to agricultural practices and cattle-grazing.

We assessed bird abundances through 317 single-visit point counts, lasting 20 min, and recording all birds heard or seen within 50 m radius (0.8 ha). These point counts do not efficiently sample all species due to interspecific differences in detectability. However, this is not a major concern in this paper, as the long sampling period of 20 min maximizes the probability of detection of birds within the radius of 50 m, and we are mainly interested in within-species differences across habitats. The censuses were conducted by the same person (DP) during May and early June 2001, 2002 and 2003 (breeding season for all species), between sunrise and 11:00 h GMT in the morning, or between 18:00 h GMT and sunset in the evening. Sampling points were located in order to include only one homogeneous habitat type and were set at least 200 m apart from each other. They were georeferenced with a Garmin 12 GPS (precision of 1 m by means of the average location function). Censuses were carried out on windless and rainless weekdays. Censuses of the different urban and natural environments considered were spanned throughout the study period, avoiding censusing certain habitats in only 1 year.

Habitat structure was sampled within a radius of 25 m centred in each census plot, previously defined considering habitat homogeneity, and was carried out

immediately before bird counts began. We estimated by eye, after training, some structural features of the habitat within a radius of 25 m: percentage cover of herbaceous, shrub and tree layers, average height of the shrub layer, average tree height, number of trunks 5–10, 10–30 and >30 cm in diameter at breast height, and total numbers of coniferous and deciduous trees. Some other variables were also recorded in urban plots: percentage cover of pavement and buildings, average height of buildings, and number of vehicles parked or in movement (as a raw measure of intensity of human transit).

We sampled both urban and main natural habitats surrounding the towns in the study region. The natural habitats surrounding cities and developments consist of four main vegetation types:

- Pine forests (*Pinus sylvestris/pinaster*) spread out above 1100 m a.s.l. They are the most mature woodlands in the region, in spite of being managed for logging. Average tree height = 14.1 m (range: 9.3–20 m); tree density = 1032 trees/ha (178–2415 trees/ha); shrub cover = 14% (0–60%).
- Oak forests (*Quercus pyrenaica*). They are mainly young stands 40–50 years old or younger, predominantly located at 900–1300 m a.s.l. Average tree height = 10 m (range: 4–17 m); tree density = 840 trees/ha (117–2852 trees/ha); shrub cover = 39% (8–85%).

- Dense ash-groves (*Fraxinus angustifolia*) have well-grown canopy cover providing shade. They are established on valley-fields devoted to cattle-grazing. The tree layer is managed through continuous clearance and pruning. Average tree height = 8.3 m (range: 5.2–13.1 m); tree density = 294 trees/ha (86–509 trees/ha); shrub cover = 19% (0–80%).
- Open habitats (mainly pasturelands with scattered trees and tall shrubs). They are devoted to livestock grazing, with low tree density (5–377 trees/ha) of small trees (3.2–10.2 m), and a moderate amount of different shrub species (0–25%; sparse young holm-oaks *Quercus ilex*, or hedgerows of brambles, hawthornes and rock-roses *Rubus* sp., *Rosa* spp., *Prunus* spp., *Crataegus* sp. and *Cistus* spp.).

The towns ($n = 16$) ranged between 0.5 and 15 km² (mean = 3.3 km²), comprising an old commercial core, surrounded by residential areas of four- to seven-storey block buildings, closely placed terraced-houses or sparse detached houses. Public parks are scarce and small, so they were not sampled. Private gardens, however, have a marked range of variability in terms of size and vegetation maturity, structure and composition, useful for defining a gradient of urban typologies which was supposed to have vari-

able impact on birds. This urban gradient ranged from the more densely built-up downtown, almost completely paved and treeless, to residential areas with large detached houses and mature gardens. Urban plots ($n = 194$) were categorized in three typologies according to general appearance, considering the amount of built-up surface, garden cover and tree maturity (Table 1). The most heavily urbanized plots (mainly located in old commercial centres of study cities; typology 1) were characterized by a built-up cover > 50%, lawn cover < 10% and treed surface < 5%. In contrast, the better-gardened category (mainly located in residential areas with the biggest single-family detached houses; typology 3) grouped plots with built-up cover lower than 25%, lawn cover higher than 50% and tree cover exceeding 15%. The remaining plots that did not meet the above-mentioned criteria were included in an intermediate group (several urban developments such as terraced-houses or block buildings surrounded by small gardens outside the town centres; typology 2).

2.2. Statistical analyses

Unifactorial ANOVAs were used to analyze differences in species richness and total bird abundance

Table 1

Average values (\pm one standard error) of habitat variables per circular plot (radius = 25 m; 0.2 ha) in each urban typology, ordered from densely built-up downtown (typ1), to well-gardened residential areas (typ3)

	Typ1, number of plots: 61	Typ2, number of plots: 94	Typ3, number of plots: 39	$F_{2,191}$
%PAVED	19.7 \pm 1.27 ^a	16.9 \pm 1.30 ^a	9.3 \pm 1.34 ^b	11.97*
%BUILT	68.3 \pm 1.10 ^a	32.6 \pm 1.50 ^b	22.0 \pm 1.55 ^c	251.08*
%LAWN	5.4 \pm 0.90 ^a	18.8 \pm 1.23 ^b	52.6 \pm 2.17 ^c	240.13*
%SHRUB	1.7 \pm 0.36 ^a	4.6 \pm 0.84 ^b	5.5 \pm 1.07 ^b	5.64*
%TREES	4.5 \pm 0.50 ^a	11.3 \pm 0.68 ^b	15.8 \pm 1.17 ^c	48.46*
hBUILT	9.3 \pm 0.39	8.2 \pm 0.29	8.1 \pm 0.52	2.67 ns
hTREES	5.8 \pm 0.43 ^a	7.9 \pm 0.23 ^b	9.7 \pm 0.53 ^c	24.29*
VEHICL	28.9 \pm 5.80 ^a	9.2 \pm 2.40 ^b	3.7 \pm 0.80 ^b	10.92*
TREES10	5.1 \pm 0.70 ^a	10.6 \pm 1.17 ^b	8.5 \pm 1.50 ^{ab}	6.57*
TREES30	6.6 \pm 0.83 ^a	16.7 \pm 1.17 ^b	22.4 \pm 2.17 ^c	31.37*
TREES50	0.5 \pm 0.20 ^a	1.1 \pm 0.24 ^a	3.0 \pm 0.58 ^b	12.85*
TREESDEC	9.3 \pm 0.90 ^a	15.6 \pm 1.29 ^b	16.9 \pm 2.28 ^b	7.52*
TREESCON	2.7 \pm 0.58 ^a	10.8 \pm 0.96 ^b	14.7 \pm 2.01 ^b	25.90*

Results of ANOVA tests comparing the three urban typologies are also shown (* $p < 0.01$; ns: non-significant difference). Different superscripts show groups statistically different in post hoc tests at $p < 0.05$. %PAVED = paved cover (in percentage); %BUILT = built-up cover; %LAWN = lawn cover; %SHRUB = shrub cover; %TREES = tree canopy cover; hBUILT = built-up height (in m); hTREES = tree height; VEHICL = number of motor vehicles parked or passing by in 20 min; TREES10 = number of trees 5–10 cm in diameter at breast height (dbh); TREES30 = number of trees 10–30 cm dbh; TREES50 = number of trees >30 cm dbh; TREESDEC = number of deciduous trees; TREESCON = number of coniferous trees.

among different habitats and urban typologies. An a priori planned comparison was made testing for differences between all urban plots and the four natural habitats pooled. Comparisons between the three urban typologies were performed using a linear contrast, ordering categories according to a gradient of building and vegetation cover. Densities at species-specific level were compared using non-parametric tests due to the lack of homocedasticity and normality: Mann–Whitney (urban versus natural habitats pooled) and Kruskal–Wallis (comparisons among the four urban typologies) tests.

Regression trees were used to analyze the effect of habitat and urban variables on species richness and bird abundance in 194 urban plots. The effect of those structural variables on bird species occurrence in these plots was modelled with classification trees. The regression/classification tree analyses allow to interpret datasets where there are complex non-linear relationships between response and predictor variables, and/or high-order interactions among predictor variables (Breiman et al., 1984; Venables and Ripley, 1994; De'ath and Fabricius, 2000). The stopping rules in tree growth applied in our data analyses were (1) groups including at least more than 10 cases and (2) significant reductions in residual deviance (a measure of group heterogeneity) attained by a splitting criterion (according to a χ^2 test).

Variation in total bird density and bird species richness was also analyzed by backward-stepwise multiple regression analysis, using habitat and urban variables as predictors. We checked for normality of residuals of the regression models (density was log-transformed prior to data analysis). All the statistical analyses were carried out using Statistica (StatSoft, 2001) and S-Plus (MathSoft, 1999) software packages.

3. Results

3.1. Bird communities in urban versus natural habitats

There were significant differences between urban and natural habitats comparing both bird species richness and abundance per sampling plot (planned comparisons checking for differences between urban ($n = 194$) and the remaining pooled non-urban habitats ($n = 123$): $F_{1,312} = 9.89$, $p < 0.001$ and $F_{1,312} = 39.47$, $p < 0.001$, respectively). Urban habitats had significantly fewer number of species than open-country habitats and ash-groves, and higher bird density than forests (both pine and oakwoods) and open-country habitats (Fig. 2).

Urban habitats, ash-groves and oakwoods allowed the presence of common species (i.e., more than

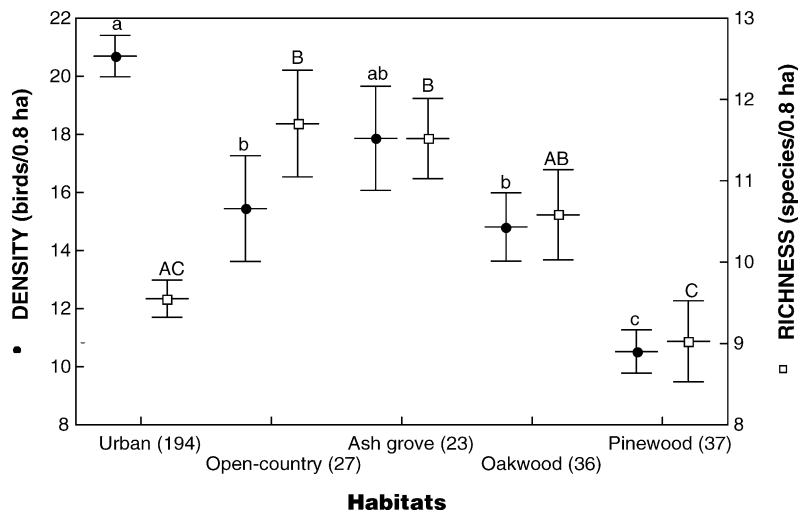


Fig. 2. Inter-habitat differences in total bird density and species richness (mean \pm S.E.). Equal letters (lowercase: density; uppercase: richness) define indistinguishable groups (Dunnett post hoc tests at $p < 0.05$). Sample sizes (number of census plots) in brackets.

Table 2

Mean density values (birds/0.8 ha) in five habitats (PINewoods, OAKwoods, ASH-groves, OPEN-country habitats and URBan), and in three urban typologies ordered from densely built-up downtown (typ1), to well-gardened residential areas (typ3; see Table 1)

	PIN, number of plots (diversity) : 37 (2.94)	OAK, number of plots (diversity) : 36 (2.82)	ASH, number of plots (diversity) : 23 (2.97)	OPEN, number of plots (diversity) : 27 (3.05)	URB, number of plots (diversity) : 194 (2.42)	Typ1, number of plots (diversity) : 61 (1.76)	Typ2, number of plots (diversity) : 94 (2.64)	Typ3, number of plots (diversity) : 39 (2.42)
Urban-exploiters spp.								
<i>Apus apus</i>	0.00	0.00	0.01	0.02	0.20	0.31	0.04	0.42
<i>Carduelis chloris</i>	0.16	0.03	0.14	0.08	0.77	0.64	0.84	0.84
<i>Columba livia</i>	0.00	0.00	0.01	0.01	0.63	1.70	0.33	0.11
<i>Delichon urbica</i>	0.01	0.00	0.00	0.00	1.36	3.15	0.73	1.00
<i>Hirundo rustica</i>	0.01	0.00	0.00	0.05	0.28	0.51	0.20	0.21
<i>Passer domesticus</i>	0.00	0.00	1.43	2.49	7.20	8.07	6.21	8.59
<i>Phoenicurus ochruros</i>	0.00	0.00	0.00	0.00	0.29	0.43	0.27	0.16
<i>Serinus serinus</i>	0.42	0.11	0.75	0.85	1.61	0.56	1.86	2.09
Undetermined spp.								
<i>Acanthis cannabina</i>	0.00	0.00	0.00	0.41	0.01	0.03	0.00	0.00
<i>Loxia curvirostra</i>	0.09	0.00	0.00	0.00	0.35	0.00	0.20	0.95
<i>Merops apiaster</i>	0.00	0.00	0.00	0.01	0.23	0.00	0.39	0.00
<i>Motacilla alba</i>	0.00	0.00	0.00	0.11	0.07	0.12	0.10	0.00
<i>Pica pica</i>	0.05	0.14	1.55	1.69	1.16	0.57	1.15	1.75
<i>Streptopelia decaocto</i>	0.00	0.00	0.04	0.00	0.31	0.07	0.38	0.38
<i>Sturnus unicolor</i>	0.00	0.23	2.30	0.82	1.95	1.60	1.80	2.52
<i>Turdus merula</i>	0.70	1.18	0.83	0.58	1.36	0.64	1.51	1.78
Urban-avoiders spp.								
<i>Aegithalos caudatus</i>	0.14	0.39	0.00	0.30	0.08	0.00	0.13	0.03
<i>Anthus trivialis</i>	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00
<i>Certhia brachydactyla</i>	0.87	0.73	0.57	0.22	0.16	0.05	0.14	0.28
<i>Cettia cetti</i>	0.00	0.00	0.13	0.04	0.01	0.00	0.00	0.03
<i>Ciconia ciconia</i>	0.00	0.00	0.18	0.01	0.03	0.10	0.01	0.01
<i>Columba palumbus</i>	0.15	0.12	0.27	0.12	0.09	0.07	0.09	0.10
<i>Corvus corone</i>	0.04	0.06	0.18	0.06	0.00	0.00	0.00	0.00
<i>C. monedula</i>	0.00	0.00	0.23	0.33	0.02	0.05	0.02	0.00
<i>Cuculus canorus</i>	0.04	0.27	0.02	0.20	0.04	0.00	0.03	0.08
<i>Cyanopica cyana</i>	0.03	0.34	0.43	0.19	0.05	0.00	0.07	0.00
<i>Dendrocopos major</i>	0.14	0.06	0.00	0.00	0.01	0.00	0.01	0.00
<i>Emberiza cirrus</i>	0.00	0.00	0.04	0.19	0.00	0.00	0.00	0.00
<i>Erithacus rubecula</i>	1.05	1.46	0.30	0.11	0.25	0.02	0.21	0.54
<i>Ficedula hypoleuca</i>	0.05	0.11	0.00	0.00	0.00	0.00	0.00	0.00
<i>Fringilla coelebs</i>	1.39	1.88	1.37	1.01	0.19	0.02	0.16	0.37
<i>Garrulus glandarius</i>	0.30	0.31	0.00	0.07	0.00	0.00	0.00	0.00
<i>Hippolais polyglotta</i>	0.00	0.08	0.09	0.19	0.03	0.00	0.05	0.00
<i>Lullula arborea</i>	0.22	0.09	0.09	0.25	0.01	0.00	0.00	0.03
<i>Luscinia megarhynchos</i>	0.03	0.20	1.17	0.63	0.20	0.03	0.26	0.23
<i>Miliaria calandra</i>	0.01	0.00	0.16	0.49	0.00	0.02	0.00	0.00
<i>Oriolus oriolus</i>	0.00	0.18	0.40	0.37	0.05	0.00	0.07	0.05
<i>Parus ater</i>	0.89	0.00	0.00	0.00	0.29	0.00	0.44	0.29
<i>P. caeruleus</i>	0.05	1.29	0.80	0.48	0.13	0.05	0.11	0.21

Table 2 (Continued).

	PIN, number of plots (diversity) : 37 (2.94)	OAK, number of plots (diversity) : 36 (2.82)	ASH, number of plots (diversity) : 23 (2.97)	OPEN, number of plots (diversity) : 27 (3.05)	URB, number of plots (diversity) : 194 (2.42)	Typ1, number of plots (diversity) : 61 (1.76)	Typ2, number of plots (diversity) : 94 (2.64)	Typ3, number of plots (diversity) : 39 (2.42)
<i>P. cristatus</i>	0.81	0.03	0.00	0.00	0.06	0.00	0.09	0.08
<i>P. major</i>	0.27	0.73	1.54	0.49	0.31	0.16	0.26	0.58
<i>Passer montanus</i>	0.00	0.00	0.35	0.33	0.03	0.00	0.01	0.08
<i>Phylloscopus bonelli</i>	0.30	2.21	0.04	0.22	0.02	0.00	0.03	0.03
<i>Picus viridis</i>	0.05	0.10	0.00	0.30	0.06	0.02	0.06	0.11
<i>Regulus ignicapillus</i>	0.72	0.19	0.17	0.04	0.38	0.02	0.36	0.72
<i>Saxicola torquata</i>	0.00	0.00	0.00	0.19	0.00	0.00	0.01	0.00
<i>Sitta europaea</i>	0.19	0.19	0.00	0.00	0.00	0.00	0.00	0.00
<i>Streptopelia turtur</i>	0.03	0.06	0.09	0.15	0.01	0.02	0.01	0.00
<i>Sylvia atricapilla</i>	0.25	0.99	0.65	0.38	0.35	0.10	0.39	0.46
<i>S. cantillans</i>	0.05	0.03	0.26	0.19	0.01	0.00	0.01	0.00
<i>Troglodytes troglodytes</i>	0.44	0.31	0.22	0.11	0.19	0.07	0.21	0.28
<i>Turdus viscivorus</i>	0.23	0.19	0.00	0.00	0.00	0.00	0.00	0.00
<i>Upupa epops</i>	0.00	0.00	0.51	0.27	0.03	0.02	0.03	0.03

Shannon's diversity is shown in brackets in the top of the table. Urban-exploiters and urban-avoiders species subheadings group species according to significant ($p < 0.05$) differences comparing pooled natural habitats (PIN, OAK, ASH and OPEN) with URBAN environments. Bird densities statistically different among urban typologies (Kruskal–Wallis test) are marked in bold.

1 bird/0.8 ha), with higher densities than those observed in pinewoods and open-country habitats (Table 2). Nevertheless, there were subtle differences in the most abundant species within each bird community. For example, total bird density accounted for by the three most abundant species was highest in urban habitats (51.6% of all bird numbers), while it was considerable lower in the four natural habitats (ranging between 31.1 and 38.5%). This striking difference was mainly due to the large density of *Passer domesticus* in urban environments. Accordingly, bird diversity was relatively similar in the five bird communities studied, although the lowest figure was measured in urban habitats.

Only eight species out of 53 (15%) were consistently more abundant in urban than in natural habitats (Table 2). Notably, some species very scarce at a regional scale in natural habitats (maximum abundance lower than 0.1 birds/plot, or 1.25 birds/10 ha), reached significantly greater densities in urban environments: *Apus apus*, *Delichon urbica*, *Columba livia* var. *domestica*, *Hirundo rustica* and *Phoenicurus ochruros*. *Carduelis chloris*, *Passer domesticus* and *Serinus serinus* attained their highest densities in urban areas too, but they were also regionally common species in natural habitats. By contrast, 37 species (70%) were significantly more scarce in urban areas than in non-urban environments. Fourteen species almost completely avoided urban habitats (maximum densities in any single typology below 0.05 birds/plot): *Anthus trivialis*, *Cettia cetti*, *Corvus corone*, *Dendrocopos major*, *Emberiza cirrus*, *Ficedula hypoleuca*, *Garrulus glandarius*, *Lullula arborea*, *Miliaria calandra*, *Saxicola torquata*, *Sitta europaea*, *Streptopelia turtur*, *Sylvia cantillans* and *Turdus viscivorus*. Eight species did not show clear patterns of avoidance nor affinity for urban habitats.

In summary, bird communities in urban environments were less diverse and had higher densities than natural habitats in the study region. The number of urban-avoiding species was greater than the number of species favoured by urban habitats. Considering their European threat status (SPEC index, Hagemeyer and Blair, 1997), five urban-avoider species are under conservation concern (*Ciconia ciconia*, SPEC-2; *Lullula arborea*, SPEC-2; *Picus viridis*, SPEC-2; *Saxicola torquata*, SPEC-3; *Streptopelia turtur*, SPEC-3), while only one relatively endangered species was favoured

by the urban environments (*Hirundo rustica*, SPEC-3) in the study region.

3.2. Bird communities along an urban gradient

There were significant differences among urban typologies both in bird species richness and abundance per sampling plot (planned comparisons ordering typologies from most to least heavily urbanized: $F_{1,191} = 34.34$, $p < 0.001$ and $F_{1,191} = 11.70$, $p < 0.001$, respectively; Fig. 3). Overall, both variables increased towards less heavily built-up, more vegetated sites. However, the increase from the ‘hard urban end’ towards the ‘soft urban end’ was steeper in species richness than in bird density (see results of a posteriori Tukey tests in Fig. 3).

The three most abundant species reached the highest proportion in the most intensely urbanized typology (67.2% of all individuals) and accordingly, the lowest diversity (Table 2). *Columba livia* var. *domestica*, *Delichon urbica*, *Hirundo rustica*, *Motacilla alba* and *Phoenicurus ochruros* were significantly denser in heavily urbanized sites. Conversely, *Certhia brachydactyla*, *Erithacus rubecula*, *Fringilla coelebs*, *Loxia curvirostra*, *P. major*, *Regulus ignicapillus*, *Sturnus unicolor* and *Sylvia atricapilla* were more abundant in

the well-gardened end of the gradient, whereas *Luscinia megarhynchos*, *Parus ater*, *Pica pica*, *Serinus serinus*, *Troglodytes troglodytes* and *Turdus merula* avoided the built-up end of the gradient.

Differences in bird species abundance between urban and natural habitats decreased in many urban-avoider species when considering the highest densities reached within the three distinguished urban typologies (see Table 2). Average density of urban-avoider species in urban environments was 12.4% (S.D. = 13.0, $n = 37$) of the maximum observed in natural habitats, whereas this figure increased to 21.7% (S.D. = 21.8, $n = 37$) when considering the highest densities measured in the three urban typologies (Wilcoxon Matched Pairs Test comparing percentages of change: $Z = 4.54$, $p \ll 0.001$). Nevertheless, statistical differences in bird species abundance between urban and natural habitats disappeared in only two out of 37 species when considering the highest densities in the three distinguished urban typologies (*Regulus ignicapillus* and *Troglodytes troglodytes*; the maximum densities observed in the urban gradient approached the highest measured in the natural environments; Table 2). Thus, there are 35 species whose abundances in the better-gardened urban typology did not attain the maximum densities observed in natural habitats at a regional scale.

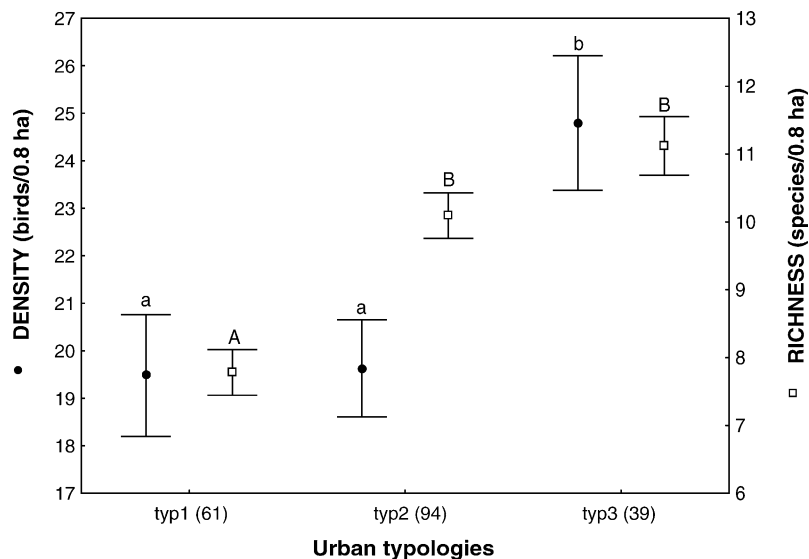


Fig. 3. Bird density and species richness (mean \pm S.E.) in three urban typologies, ordered from densely built-up downtown (typ1), to well-gardened residential areas (typ3; see Table 1 for details). Equal letters (lowercase: density; uppercase: richness) define indistinguishable groups (Dunnnett post hoc tests at $p < 0.05$). Sample sizes (number of census plots) in brackets.

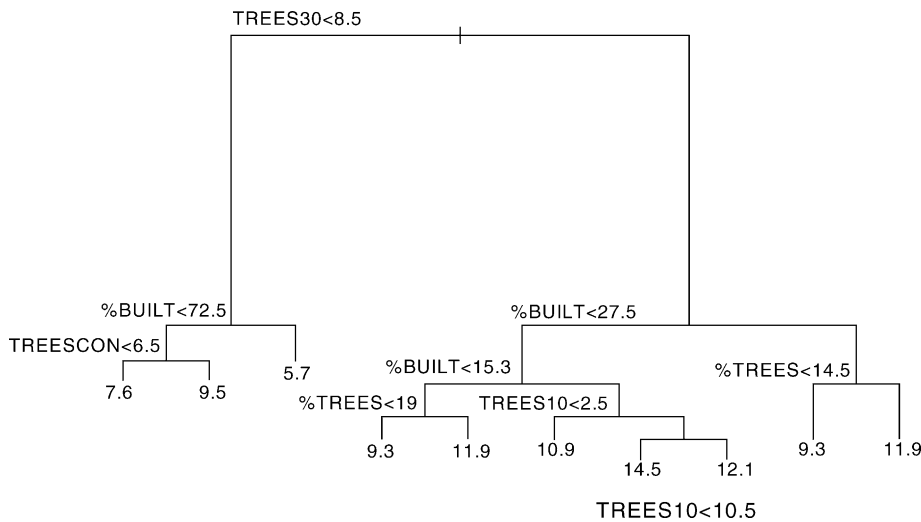


Fig. 4. Regression tree model analyzing species richness per plot in urban environments. Splitting criteria indicate the conditions for the left branches. Numbers at terminal tips are mean richness figures (minimum of 10 cases). Length of the branches are proportional to deviance explained by each split. See Table 1 for variable names.

3.3. Habitat structure and bird distribution in urban environments

Variables describing habitat structure of urban plots accounted for 51.0% of original deviance in species richness in the tree regression analysis ($\chi^2 = 999.9$, d.f. = 14, $p < 0.001$; Fig. 4). The most important variable positively associated with species richness was the density of trees with trunks of 10–30 cm diameter at breast height (dbh). Other important variables were tree canopy and building cover, although their relationships with species richness were complex. The plots with lower species richness (average of 5.7 spp./0.8 ha) were those having less than 43 medium-sized (10–30 cm dbh) trees/ha and a built-up surface cover above 72%. The highest number of species (14.5 spp./0.8 ha) was recorded in urban plots with 15–28% of building cover, more than 43 medium-sized trees/ha, and 13–54 small trees/ha (less than 10 cm dbh). A backward-stepwise linear regression analysis explained a lower proportion (38.7%; $F_{3,190} = 40.05$, $p < 0.001$) of the variance in species richness, selecting negatively built-up surface cover ($\beta = -0.26$, $p = 0.0002$) and number of vehicles ($\beta = -0.14$, $p = 0.019$), and positively density of medium-sized trees ($\beta = 0.40$, $p < 0.0001$) as the main determinants of the variation in this variable.

Bird density was explained by the regression tree shown in Fig. 5 ($\chi^2 = 6150$, d.f. = 13, $p < 0.001$). The proportion of deviance accounted for by this model (32.3%) was lower than that explained for species richness. The best predictors were percentage cover of lawn, height and surface cover of buildings, and number of motor vehicles. The minimum bird density (average of 14 birds per 0.8 ha) was observed in plots with less than 44% of lawn cover, and built-up cover higher than 76%. Conversely, two different urban configurations attained the greatest densities measured: urban plots with either (1) buildings exceeding 8 m high and with more than 44% of lawn cover, or with (2) building cover less than 76%, moderately transited streets (13–68 vehicles/ha), shrub cover below 6% and medium-sized tree density between 10 and 65 trees/ha when lawn cover is lower than 44%. A backward-stepwise linear regression analysis explained a considerably lower proportion (5.9%; $F_{1,192} = 12.14$, $p = 0.0006$) of the variance in bird density, selecting only lawn cover ($\beta = 0.24$) as the main determinant of the variation in this variable.

Significant classification trees, modelling species occurrence, were obtained for 30 species (Table 3). Tree models explained an average 38.2% of the observed variability (range: 12.6–71.3%), with high percentages of correct classification (mean = 87.2%,

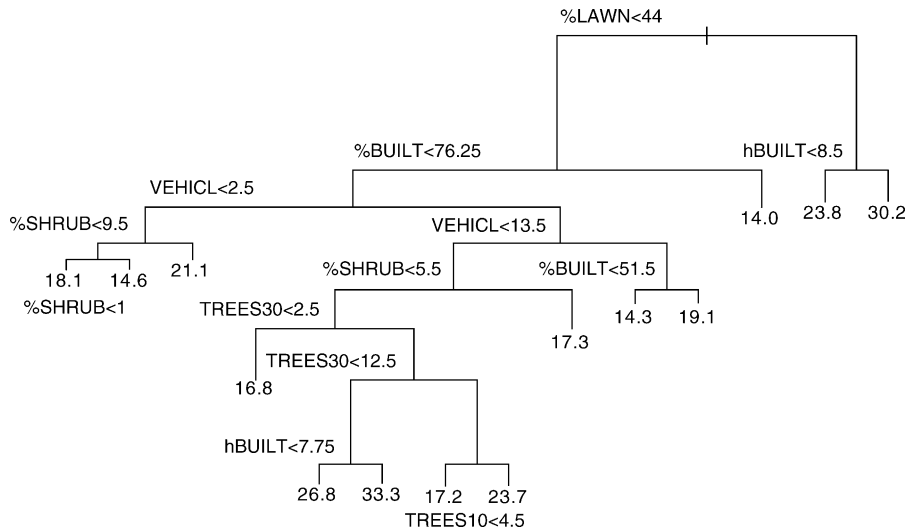


Fig. 5. Regression tree model analyzing bird density per plot in urban environments. Splitting criteria indicate the conditions for the left branches. Numbers at terminal tips are mean richness figures (minimum of 10 cases). Length of the branches are proportional to deviance explained by each split. See Table 1 for variable names.

range: 73.7–96.4%). The most influential predictor variables in the models were percentage cover of buildings, and density of medium-sized trees. Other important variables were density of coniferous trees, average tree height, and tree canopy cover. The most generalized negative effects were found in building height and building cover, while the most positive were observed in the density of medium-sized trees and tree canopy cover.

4. Discussion

In contrast with many previous works on urban bird ecology (Beissinger and Osborne, 1982; Clergeau et al., 1998; Kluza et al., 2000; Reynaud and Thioulouse, 2000; Crooks et al., 2004, and revision in Chace and Walsh, 2006), our study region is a landscape mosaic of relatively small sized habitat patches. The striking deleterious influence of urbanization in ‘binomial’ landscapes (urban versus homogeneous surrounding natural habitats) could be hindered in a heterogeneous matrix of natural habitats, ranging from open treeless pastures to dense forests, and from heavily built areas to sparsely urbanized, well vegetated sites (Wiens, 1976, 1995; Miller et al., 2001). Nevertheless, our results showed that effects of urbanization on the breeding bird

fauna could be clearly detected both at the urban-rural and intra-urban scales.

Urban development in the valleys of northern Madrid has produced, as a whole, a negative effect on the breeding bird fauna. The general trends obtained in many previous works (e.g., Nuorteva, 1971; Emlen, 1974; Lancaster and Rees, 1979; Beissinger and Osborne, 1982; Blair, 1996; Clergeau et al., 1998; Melles et al., 2003; Crooks et al., 2004; Sandström et al., 2006) have been also confirmed here: a decrease of species richness, but a marked increase in total avian density in urban habitats. The large total bird density in urban environments is attained through an over-abundance of a few widespread species that can attain large local densities. These species are highly linked to human environments and are uncommon in the surrounding natural habitats. The main species contributing to this avian homogenization in our studied cities were *Passer domesticus*, *Sturnus unicolor*, *Serinus serinus*, *Delichon urbica* and *Columba livia* var. *domestica*, which account for 60% of all urban bird numbers, whereas in nearby natural habitats they only represent a low proportion of total bird numbers (range 2–27%). Because these are non-endangered species (Martí and Del Moral, 2003), we propose that bird abundance does not provide insights in improving conservation or restoration of bird communities under

Table 3

Summary of classification trees showing the main splits modelling the influence of urban descriptors on the presence/absence of species with greater sample sizes

	Dev ²	%CC	%Prob	Main splits
<i>Apus apus</i>	28.4	78.9	92.5	%LAWN < 11; VEHICL > 5; TREESCON < 6
<i>Carduelis chloris</i>	17.8	73.7	73.4	TREESDEC 5–29; %PAVED < 17
<i>Certhia brachydactyla</i>	26.6	87.6	70.0	%TREES > 16; TREES30 > 35
<i>Columba livia</i>	42.8	83.5	73.9	TREESCON < 6; %LAWN < 24; %TREES > 5
<i>C. palumbus</i>	12.6	92.8	30.0	TREES30 > 35
<i>Corvus monedula</i>	37.7	94.3	23.8	TREESDEC < 17; TREES50 > 3
<i>Cuculus canorus</i>	45.1	94.3	60.0	hTREES > 10; TREESDEC > 17
<i>Delichon urbica</i>	34.7	77.8	82.4	%BUILT > 33; TREESCON < 16; %BUILT > 66
<i>Erithacus rubecula</i>	50.7	90.7	90.9	hTREES > 10; TREES30 > 26
<i>Fringilla coelebs</i>	47.0	89.2	80.0	TREES30 > 11; %TREES > 22
<i>Hirundo rustica</i>	31.4	78.3	100.0	%TREES < 15; %PAVED > 29; TREES10 < 1
<i>Loxia curvirostra</i>	56.4	94.3	50.0	%TREES > 8; %PAVED > 7; %VEHICL < 1
<i>Luscinia megarhynchos</i>	38.9	86.1	76.5	TREES10 > 7; %BUILT < 39; TREESCON < 6
<i>Motacilla alba</i>	33.3	91.2	25.0	%PAVED > 19; %BUILT 24–66
<i>Oriolus oriolus</i>	37.1	94.8	20.0	TREES30 > 10; hBUILT < 7.3; TREESDEC > 9
<i>Parus ater</i>	48.0	88.7	39.7	TREESCON > 3; hTREES > 7; %BUILT < 54
<i>P. caeruleus</i>	23.3	89.7	20.7	%BUILT < 43; %PAVED < 26; %TREES > 19
<i>P. cristatus</i>	45.8	96.4	29.4	TREESCON > 7; TREES10 < 13; %BUILT < 21
<i>P. major</i>	32.3	83.0	83.3	%PAVED < 13; TREES30 > 15; hTREES < 7
<i>Passer domesticus</i>	52.8	94.8	100.0	TREES10 < 17; %BUILT > 31
<i>Phoenicurus ochruros</i>	32.8	79.9	70.4	VEHICL > 5; %BUILT > 66
<i>Pica pica</i>	26.3	79.9	100.0	TREES30 > 8; hTREES < 6
<i>Picus viridis</i>	33.4	93.8	20.9	%PAVED < 13; %TREES > 11
<i>Regulus ignicapillus</i>	53.8	88.7	74.4	%BUILT < 47; TREESCON > 5; %SHRUB > 1
<i>Serinus serinus</i>	71.3	92.3	100.0	TREESCON > 5
<i>Streptopelia decaocto</i>	36.6	86.1	54.6	TREES30 > 6; hBUILT < 5.5
<i>Sturnus unicolor</i>	43.0	85.6	96.8	%BUILT < 73; VEHICL < 18; %LAWN > 32
<i>Sylvia atricapilla</i>	36.7	83.0	70.6	TREES30 > 10; %LAWN < 6
<i>Troglodytes troglodytes</i>	32.5	85.6	44.0	TREESCON > 1.5; hBUILT < 9.3; %SHRUB > 2
<i>Turdus merula</i>	36.9	82.0	96.4	%LAWN > 3; hBUILT < 6.3

Dev²: amount of original deviance accounted for the whole tree model obtained; %CorrClas: amount of cases correctly classified by each tree model. %Prob: probability of occurrence when the selected conditions met. See Table 1 for variable names.

urbanization pressures (McKinney and Lockwood, 1999). Conversely, species richness and bird diversity clearly showed a negative effect of urbanization on bird fauna, even in the most transformed natural habitats (open-country habitats and ash-groves). Moreover, although species richness per census plots was higher in urban environments than in pineforests, species-specific comparisons between natural and urban habitats clearly show a global negative influence of urbanization in the regional bird fauna (37 species being negatively affected versus eight species favoured).

Nevertheless, the negative outcome of urbanization on regional avifauna is far from being homogeneous because it depends upon the particular types

of developments (see also Blair, 1996; Haddidian et al., 1997; Clergeau et al., 1998; Sandström et al., 2006). Older, uncrowded and well-gardened typologies clearly enhance avian biodiversity, while the more densely built-up typologies with higher human disturbance heavily diminish it, promoting similarity in bird species composition (Fernández-Juricic, 2002). Only a few species thrived in the heavily built-up sites where habitat requirements, particularly with regard to nesting supplies, must rely on building cavities rather than on amount of vegetation cover (Blair, 1996; Savard and Falls, 2001; Melles et al., 2003; Lim and Sodhi, 2004). For instance, the five dominant species in urban habitats reach their highest abundances in this unvegetated typology, accounting for 78% of total bird numbers.

Four of these species are characteristic cavity-nesters. Nevertheless, maximum bird density was attained at the opposite end of the urban gradient, in the less impacted, more gardened, sites. This can be explained considering the large variety of structural and trophic resources provided by the less crowded urban areas, specially lawn, which is the main determinant of urban bird density and reaches the maximum cover in the more vegetated, less built-up, typology. Some dominant species in urban habitats, such as ground or aerial feeders, benefit from this substrate because open areas of irrigated and mowed lawn provide plenty of invertebrates, and facilitate scanning for predators and walking locomotion and maneuverability (Emlen, 1974; Brownsmith, 1977; Beissinger and Osborne, 1982).

Regression trees have been more successful in explaining the observed variability in bird species density and richness than linear regression models (see Boone and Krohn, 2000 for similar results comparing both statistical approaches). This is because statistical trees identify subsets of environmental conditions where relatively homogeneous values of the response variables are observed, instead of defining common linear patterns affecting the whole pool of samples (De'ath and Fabricius, 2000), thus accounting for non-linear relationships and complex interactions among predictor variables. For example, both statistical techniques reveal the prominent role of lawn cover in bird density. Nevertheless, multiple regression fails to discover other structural variables defining the subset of environmental conditions responsible for a large proportion in the explainable variability (26.4% resulting from the difference between 32.3% of deviance accounted for by the tree regression and 5.9% of the variance explained by the multiple regression model; see Fig. 5). In addition, analyses obtained with regression trees are easily converted into management principles having a practical value in landscape planning. These models are based on a few, easily measurable variables, identifying clear threshold values that define urban habitat suitability for each species (see also Germaine et al., 1998; Melles et al., 2003).

The increase in species richness with progressively more vegetated typologies emphasizes the critical importance of a diverse tree layer (in height and floristic composition) to attract species. A denser, older and higher tree canopy leads to increased foliage height

diversity which positively affects diversity and species richness (see Wiens, 1989 and references therein), providing nesting and foraging opportunities to several common woodland species in cities (e.g., *Aegithalos caudatus*, *Certhia brachydactyla*, *Erithacus rubecula*, or *Troglodytes troglodytes*). Urban habitat diversity is also enhanced by the addition of coniferous trees (mainly exotic species; e.g., *Cedrus atlantica*, *Abies* spp., *Picea* spp., *Cupressus* spp.) to the broad-leaved floristic basis of the region (holm and pyrenean oaks, ashes and poplars). Thus, some species inhabiting the mountain pinewoods of the study region, that are very scarce in the valleys (e.g., *Loxia curvirostra*, *Parus ater*, *P. cristatus* or *Regulus ignicapillus*) can colonize urban sites because there are enough coniferous trees to thrive. The relatively high urban abundance of *Loxia curvirostra* probably is related to the high diversity of coniferous trees in well-gardened urban environments (the preferred habitat of this species are the subalpine pinewoods far from cities). This species may benefit from a longer harvesting period and an enlarged seed mast in urban areas due to the very different ripening periods of the several coniferous species available. We conclude that even forest species can colonize the urban environment for breeding if typologies with extensive and mature tree cover are provided (Kluza et al., 2000; Fernández-Juricic, 2004; Lim and Sodhi, 2004), reversing the global negative effect of urbanization in the study area.

Nevertheless, urban environments remain suboptimal for most species of the regional pool (i.e., lower densities in urban than in the surrounding natural habitats). Only a few number of species were denser in urban environments than in natural habitats, but a large proportion of species, although present in this artificial environment, were considerably less abundant even in the most vegetated urban typology. This could be explained considering that resources supplied by urban habitats provide valuable and novel resources, but are not able to support high populations (i.e., they are patchy and small). This is a common phenomenon in other ecotonic environments in the mediterranean region (e.g., holm-oak *Quercus ilex* parklands: Díaz and Pulido, 1995; Tellería, 2001). Moreover, highly anthropogenic habitats could act as sinks for several species, because of high predation rates in urban environments (e.g., high density of feral and domestic cats; Churcher and Lawton, 1987; Jokimäki and Huhta,

2000; Vierling, 2000; Thorington and Bowman, 2003; Woods et al., 2003). These cities are almost completely unable to provide minimal habitat requirements for 14 scarce species in the region (maximum densities below 0.05 birds/plot, Table 2). Although this is specially obvious for bird species typical of mature forests (e.g., *Dendrocopos major*, *Ficedula hypoleuca*, *Garulus glandarius* and *Sitta europaea*), it also applies to birds inhabiting moderately wooded habitats (e.g., *Emberiza circlus* or *Sylvia cantillans*). On the other hand, open-country habitats of the study area support several species of European conservation concern, which are not capable of using urban environments as alternative habitats (e.g., *Lullula arborea*, *Saxicola torquata* or *Streptopelia turtur*).

Thus, we conclude that the studied regional pool of species are predominantly urban-avoiders. Nevertheless, this urban avoidance can be mitigated in some urban typologies. Well-gardened, single-family detached houses are colonized with relatively high densities (e.g., at least one half of that observed in natural habitats) by many species, and other scarce birds such as raptors (e.g., *Athene noctua*, *Milvus milvus*, *M. migrans*, *Hieraetus pennatus*; pers. obs.) have begun to occupy these environments.

Future land-planning should stress the negative effect of dense, low-gardened housing developments. The different natural habitats surrounding the cities should also be evaluated before selected for urban encroachment. Open wooded valley areas devoted to cattle-grazing merit a special attention (mainly ashgroves) because they have large values of species richness and bird density. We recommend the exclusion of urban developments from this habitat. We suggest the following general proposals for improving the quality of the urban environments for the bird fauna of the study region:

- (1) Species richness of highly impacted sites should be enhanced by means of tree plantation, including diverse coniferous species (we empirically found a minimum threshold of 43 medium-sized trees/ha with 14% of canopy cover). Built-up cover above 70% should be avoided, while an average 40% of lawn cover is useful for maximizing total bird density.
- (2) The most vegetated neighborhoods should be preserved through regulation of private green-

ery, and the most mature gardens should be inter-connected, to support populations of forest species.

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