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Seasonality affects avian species distribution but not diversity and nestedness patterns in the urban parks of Vitoria–Gasteiz (Spain)

I. de la Hera

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Abstract

Seasonality affects avian species distribution but not diversity and nestedness patterns in the urban parks of Vitoria–Gasteiz (Spain). Environmental seasonality leads to variation in the composition and structure of bird communities over the year that might alter biodiversity and nestedness patterns in urban parks and other fragmented habitats. These changes could have important implications in the management and conservation of urban green areas and their populations, but they are largely unexplored. In this study, the composition, diversity and nestedness of the breeding and wintering avian communities in 31 urban parks of Vitoria–Gasteiz (Spain) were analysed. Avian diversity was significantly greater during breeding than during the winter period, although the most diverse parks during breeding were also the most diverse during winter. Most of the among–park variation in diversity was explained by park size, while tree density had a marginal contribution that was only significant during winter. Avian communities showed a significant nested subset pattern that was similar between seasons, with these patterns being mainly mediated by park size. Although the distribution of seven out of the 16 species occurring all–year–round changed significantly from one season to the other, the park ranks in the nestedness matrices were strongly correlated between seasons. This was caused by the reduction in the park distribution of some species from one season to the other that was compensated by the expansion of other species that were initially less common. These results support the idea that, in small and medium–sized cities, park size is the main constraint on avian diversity, and the presence of relatively large parks (> 10 ha) should be encouraged to promote a rich avifauna all year round.

Key words: Avian migration, Effective number of species, Environmental noise, European Green Capital, Mantel test.

Resumen

La estacionalidad afecta a la distribución de especies de aves, pero no a los patrones de diversidad y anidamiento en los parques urbanos de Vitoria–Gasteiz (España). La estacionalidad ambiental causa variaciones en la composición y estructura de las comunidades de aves a lo largo del año que podrían alterar los patrones de biodiversidad y anidamiento en los parques urbanos y otros hábitats fragmentados. Estos cambios podrían tener importantes implicaciones en la gestión y conservación de las áreas verdes urbanas y sus poblaciones de aves, que se han estudiado poco. En este estudio se analizaron la composición, la diversidad y el anidamiento de las comunidades de aves reproductoras e invernantes en 31 parques urbanos de Vitoria–Gasteiz (España). La diversidad de aves fue significativamente mayor durante la época reproductiva que en el período invernal, aunque los parques más diversos durante la reproducción también fueron los más diversos en invierno. La mayor parte de la variación de la diversidad entre parques se explicó por el tamaño del parque, mientras que la densidad del arbolado tuvo una contribución escasa que solo fue significativa en invierno. Las comunidades de aves mostraron un patrón de anidamiento significativo y similar en ambas estaciones, que estaba fundamentalmente determinado por el tamaño del parque. A pesar de que la distribución de siete de las 16 especies que están presentes todo el año cambió significativamente de una estación a otra, las posiciones de los parques en las matrices de anidamiento estuvieron estrechamente correlacionadas entre estaciones. Ello es debido a que la reducción de algunas especies en los parques de una estación a otra se vio compensada por el aumento de otras especies que inicialmente eran menos comunes. Estos resultados apoyan las ideas de que, en ciudades

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de pequeño y mediano tamaño, la superficie del parque es el principal factor limitante de la diversidad de aves, y que debería fomentarse la existencia de parques relativamente grandes (> 10 ha) para favorecer una rica avifauna durante todo el año.

Palabras clave: Migración de aves, Número efectivo de especies, Ruido Ambiental, Capital Verde Europea, Prueba de Mantel

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Introduction

Urbanisation is a major driver of environmental deterioration worldwide (McDonald et al., 2013). Apart from the direct damage to the land, urban areas are also primary consumers of energy and other external resources, producing pollutants that affect natural habitats elsewhere (Rickwood et al., 2008) and contributing significantly to what is known as Earth's sixth mass extinction (Ceballos et al., 2017). Urbanisation has also changed people's lifestyles dramatically. It is expected that the increasing number of people living in cities (around 70 % of world's population by 2050; United Nations, 2018) will also spend most of their time indoors. For example, North Americans spend more than 90 per cent of their time in buildings (87 %) or cars (6 %; Klepeis et al., 2001), drastically reducing their chances of interacting with nature. This is not of minor importance from a conservation perspective because direct experiences with the natural world trigger environmental awareness and conservation actions (Dearborn and Kark, 2010). In this scenario, urban ecosystems play a key role as a last–resort bond between urban human population and nature, contributing indirectly to global biodiversity conservation (see pigeon paradox; Dunn et al., 2006).

Cities are actively developing strategies to attenuate their many environmental challenges (e.g. air pollution, noise, waste management; Price and Tsouros, 1996). The protection and enhancement of their green spaces and natural capital is a main area of environmental performance that is highly recognised within some leading initiatives, such as the European Green Capital Award (EGCA; Gudmundsson, 2015). However, and although urban ecology is a growing field in research, our knowledge of urban biodiversity remains limited in most cities, generally being descriptive and mainly focused on specific taxonomic groups during restricted periods of the year.

Urban parks are hot–spots of biodiversity within the concrete matrix, and birds are among the most visible components (Caula et al., 2014). Avian communities are highly dynamic as a consequence of the environmental changes that occur between seasons across the globe, particularly in biogeographic areas subjected to strong seasonal regimes (Newton, 2008). Thus, avian communities in any geographic location can vary to some extent in species composition and structure throughout the year, with some species exclusively occurring during the breeding season, migration periods, and/or winter. Although less noticeable, the distributional patterns of some common species that are present year round in a region can also be dramatically altered between seasons in fragmented landscapes. This might be caused by seasonal changes in the characteristics of the fragments of habitat, but also because the abundance and/or behaviour (e.g. territoriality during the breeding season vs. gregariousness out of the breeding season) of these species differ between seasons. In any case, these seasonal changes might have consequences for avian diversity (Caula et al., 2014) and the species–park nestedness patterns (i.e. animal communities form 'nested subsets' if the most diverse fragments contain species that are not present in the least diverse ones; Patterson and Atmar, 1986; Blake, 1991) in urban environments that have been poorly explored (Murgui, 2010; Wang et al., 2013).

Although birds are favourite study models in urban ecology (Marzluff, 2017), very few studies have analysed both the breeding and wintering avian communities in the same set of urban parks (Caula et al., 2014; Leveau and Leveau, 2016), let alone estimating and comparing their nestedness patterns between seasons (Murgui, 2010; Wang et al., 2013). This means that our knowledge of urban bird communities is biased towards one season (typically the breeding season). It also means that the factors that predict avian diversity patterns during breeding might not be valid during other periods of the year (e.g. winter), which would have important implications in the design of urban areas aiming to promote a rich avifauna all year–round (Nielsen et al., 2013). Likewise, it has been suggested that the nested patterns that avian breeding communities typically show during the breeding season could be eroded during winter (Murgui, 2010). These seasonal differences in nestedness could be caused by urban birds selecting alternative habitats and/or relaxing their ecological requirements during the non–breeding period (McClure et al., 2013). Identifying the existence of these patterns would be relevant for the long–term conservation of urban bird populations (Murgui, 2010).

In this study, I surveyed the breeding and wintering avian communities of 31 urban parks in Vitoria–Gasteiz (EGCA 2012 holder) in order to expand our understanding of the factors explaining between–park and between–season variation in the avian communities of this city. The main aims were to: (1) identify the features of parks from among a set of potential candidates (e.g. size, vegetation characteristics, noise) that contributed the most to avian diversity, and to determine whether the contribution of these factors differed between the breeding and wintering period; (2) test the existence of nestedness patterns in breeding and wintering bird communities and the features of the parks that were correlated with their nestedness ranks (Patterson, 1987); and (3) explore how seasonality affected nestedness (i.e. whether nestedness is indeed disrupted in winter compared to the breeding season) and the park and species nestedness ranks. For this third purpose, I considered only the resident species (i.e. avian species occurring in both breeding and wintering periods). This approach allowed us to assess whether species and parks tended to maintain (i.e. ranks are correlated between seasons) or not to maintain (uncorrelated ranks) their position in the nestedness matrix between seasons. I considered this assessment would provide insight into how seasonality affects the avian communities of the urban parks in Vitoria–Gasteiz.

Material and methods

Study area

Vitoria–Gasteiz (42º 50' 58.4" N 2º 40' 14.8" W; 525 m a.s.l.; c.a. 250,000 inhabitants) is located in Northern Iberia (Araba, Basque Country, Spain) on a sub–plateau dominated by a mosaic of agricultural fields and forest patches. The Portuguese oak *Quercus faginea* is the most representative tree species. This region lies in a transitional area between the Mediterranean and the Atlantic climate (continental supra–Mediterranean climatic territory; Font, 1983) that confers cool summers (maximum temperature of ± 24ºC and ± 90 mm of rain between June and August), and cold, wet winters (minimum temperatures of around 1ºC and ± 250 mm of rain between November and February; Ninyerola et al., 2005). The main body of the city (approximately 26 km^2) is surrounded by an almost complete green belt composed of several streams with their associated riverine vegetation and a few large peri–urban parks. Inside this peripheral green belt, the city hosts around 100,000 trees distributed in innumerable tree–lined streets and urban green areas of different size. This green framework allows the city to surpass the minimum tree and green area per capita recommendations made by the Health World Organization, established in one tree every three inhabitants and, at least, 9 m^2 of green public areas per citizen (Ayuntamiento de Vitoria–Gasteiz, 2010). Many of the urban parks of the city with an extension of over 0.5 ha were selected for this study, which rendered a sample size of 31 parks (fig. 1, table 1).

Bird surveys and avian diversity estimates

Each park was visited three times (three rounds) by the author throughout the study period. Completing a full 31–park round took four days. Two of the rounds were carried out in the traditional wintering season in the region (Gainzarain, 2006). The first winter round occurred on 10–13 I 14, and the second took place during the first fortnight of February (sampling days were 7, 12–14 II 14). The order of park visits was reversed in the February survey compared to the January survey to avoid unexpected time–of–the–day effects. The third visit to the parks took place in late spring, 5–8 VI 14, coinciding with the breeding season in this region (De la Hera et al., 2014).

Implementing the same avian sampling method in parks with marked differences in size and shape is not a straightforward task (e.g. Jokimäki, 1999; Carbó–Ramírez and Zuria, 2011). In this study, a complete count method was selected over others (e.g. transects of fixed size or point counts) to reach all the potential microhabitats available within the parks, thereby maximizing the chances of detecting all the species occurring in each park, while obtaining estimates of the relative abundance of each species (Murgui, 2010). Thus, each park was surveyed by walking routes covering the whole park area. Winter surveys were carried out between 9:00 h and 14:00 h, while spring surveys took place between 6:30 h and 10:30 h, avoiding periods of rain and strong wind during the sampling. While detectability of birds during the breeding season is highest in the first hours of the day and surveys should be restricted to this period, avian detectability is more homogeneous during winter and surveys can be safely extended until early afternoon (Rollfinke and Yahner, 1990). Avian diversity was strongly intercorrelated between the two winter surveys (see Results), suggesting a relatively minor effect of sampling time on avian diversity estimates. It was also considered that the differences in detectability between species did not change significantly between the breeding and the winter period (e.g. large birds are more easy to detect than small ones; Johnston et al., 2014), a realistic assumption that would make the seasonal bias in detectability relatively homogenous between species (Anderson et al., 2015). The sampling time at each park varied between four and 70 minutes, with high and significant between–park repeatability in the sampling time invested (intraclass correlation coefficient (r_i) for the logarithmically transformed sampling time: $r_i = 0.93$, $F_{30,62} = 41.8$, $P < 0.001$). Following this procedure, it was noticed that the sampling effort (time/hectare) was comparatively greater in small parks than in large parks (log[sampling time] = 0.59 + 1.01*log[park area]; r = 0.96, $P < 0.001$) but this potential bias made the results of this study conservative (see Discussion).

During the surveys, all the visual and aural contacts with birds making an effective use of the park were annotated, trying to avoid double counting. Thus, birds flying over the tree canopy were excluded, which explains the complete absence of hirundinid and swift records in the database during the breeding period. Three anthropogenic avian species (house sparrow *Passer domesticus*, feral pigeon *Columba livia* and spotless starling *Sturnus unicolor*) and waterfowl were also ruled out from the final dataset given that their numbers strongly depend on stochastic supplementary feeding by the public and on the presence of permanent waterbodies to roost, respectively, which would have disrupted the avian diversity estimates.

Avian diversity was estimated for each park and visit using the effective number of species (*D*), which is a more meaningful and correct index to express diversity. This metric is defined as the number of equally–common species needed to obtain a specific score of entropy or other traditional diversity surrogates (Jost, 2006). In the case of this study, the Shannon–Weiner entropy index was initially calculated and its values were transformed into *D* using the formula suggested by Jost (2006): $D = \exp(x)$, where x is the Shannon index value of each visit to a park. Given the relatively low number of bird records obtained in the smallest parks, their intrapolation/extrapolation curves could not be calculated reliably, making rarefaction methods impossible to apply under the sampling method used in this study (Chao and Jost, 2012).

Urban park characteristics

QGIS was used to digitalize the limits of the parks and to obtain their area and shape (i.e. park area divided

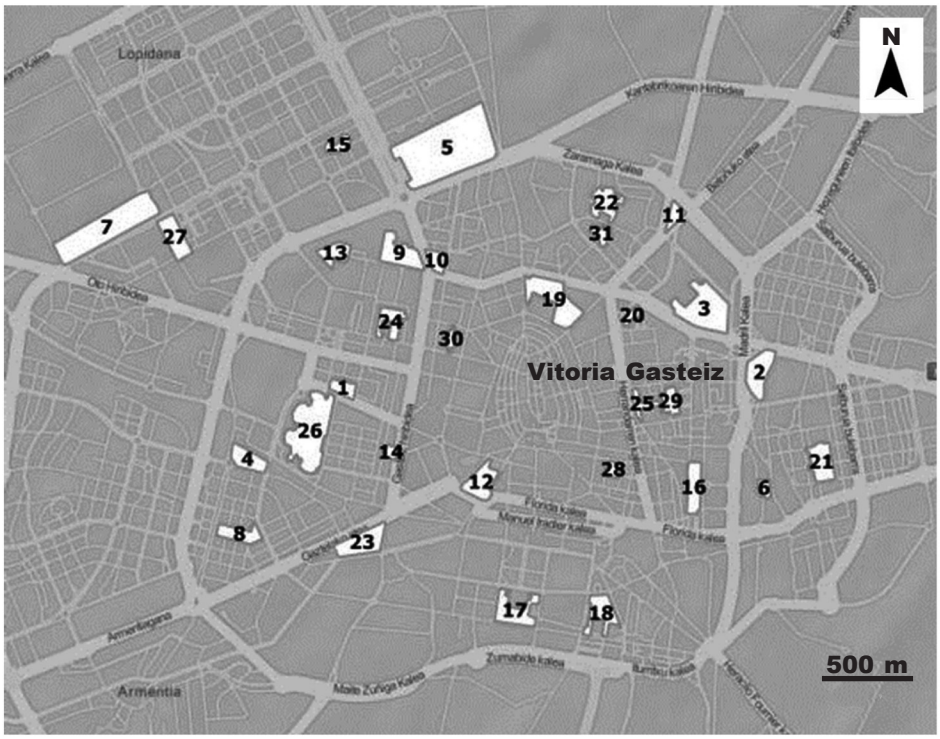


Fig. 1. Spatial distribution of the 31 urban parks selected for studying their breeding and wintering avian communities. See table 1 for the park names.

Fig. 1. Distribución espacial de los 31 parques urbanos seleccionados para estudiar las comunidades de aves que albergan en la época reproductiva y el período invernal. Véase la tabla 1 para consultar el nombre de los parques.

by its perimeter). Vitoria–Gasteiz council provided (fully transferred on the 16 I 15) the most updated digital information on urban vegetation. This enabled accurate estimates following the variables of the parks (table 1): grass cover, shrub cover, tree density, and tree diversity (measured as the effective number of tree species). Between 2 and 6 geographic locations within each park were selected randomly to visually estimate the tree height and trunk diameter at breast height of the 15 closest trees, since this information was not operational in the digital data provided by the city council. The calculation of the intraclass correlation coefficients for these two variables showed reasonably high and significant between–park repeatability (tree height: $r_i = 0.58$, $F_{30,41} = 4.24$, $P < 0.001$; trunk diameter: $r_i = 0.70$, $F_{30,41} = 6.27$, $P < 0.001$), suggesting that the mean values of these estimates of tree height and trunk diameter were representative of each park. From the noise maps of Vitoria–Gasteiz published in 2012 (Ayuntamiento de Vitoria–Gasteiz, 2012), mean environmental noise was also obtained for each park as an indicator of human–induced disturbance that might affect avian communities (González–Oreja et al., 2012). For this purpose, the grids of the full–day environmental noise map that intersected with each park were extracted digitally, and the mean value of those grids was used as a surrogate of the human disturbance experienced by each park.

Statistical analyses

First, whether the occurrence of each avian species differed between seasons was tested for those species that were present in at least one park/visit in each season (table 2). For this purpose, generalized linear mixed models with binomial error distribution (0, absence; 1, presence, for each park and visit) were carried out including season (n = 62 for winter; n = 31 for breeding) as fixed effects and park as a random factor. Second, the way avian diversity varied between the two winter surveys and between seasons were explored using Pearson correlations and paired–t tests.

To explore the existence of spatial autocorrelation in the data, a set of Mantel tests were performed. After confirming the lack of spatial autocorrelation (see Results), winter and breeding avian diversities were analysed, using multiple regression, in relation to three principal components (PCs) obtained from a principal component analysis (PCA) that included all the descriptive characteristics of the parks

Table 1. Characteristics of the 31 urban parks studied in Vitoria–Gasteiz and their avian diversity estimates expressed as the effective number of species (*D*). See Methods section for more details on data collection: N, park number; P, park name; A, area (in ha); S, shape (in ha/km); Gc, grass cover (in %); Sc, shrub cover (in %); Td, tree density (nº/ha); Mth, mean tree height (in m); Mttd, mean tree trunk diameter (in cm); *D*, tree diversity; dB, mean noise; M*D*w, mean winter avian diversity; *D*b, breeding avian diversity.

*Tabla 1. Características de los 31 parques urbanos estudiados en Vitoria–Gasteiz y estimaciones de la diversidad de aves que contienen, expresadas como el número efectivo de especies (*D*). Véase el apartado "Material and methods" para obtener información detallada sobre la recopilación de datos: N, número de parque; P, nombre del parque; A, área (en ha); S, forma (en ha/km); Gc, cubierta de hierba (en %); Sc, cubierta de arbustos (en %); Td, densidad de árboles (nº/ha); Mth, altura media del árbol (en m); Mttd, diámetro medio del tronco del árbol (en cm); D, diversidad de árboles; dB, ruido medio; MDw, diversidad aviar media en invierno; Db, diversidad aviar durante la reproducción.*

		Urban park characteristics									Avian diversity	
N	P	A	S	Gc	Sc	Td	Mth	Mttd	*D*	dB	MDw	Db
1	Adriano VI	1.21	2.43	33	10.4	31	8.1	28	2.4	63.7	3.47	1.75
2	Arana	3.09	4.08	77.6	7.3	108	15.4	42.7	13.4	65.2	4.34	8.09
3	Aranbizkarra	6.1	4.91	78.9	2.7	118	13.7	34.4	19.2	64.7	7.48	9.44
4	Ariznavarra	2.16	3.48	78	2.9	131	10.4	24.5	12.5	69.3	4.66	3.89
5	Arriaga	17.01	9.35	75	4.6	105	13.3	36.4	28	63.4	9.89	10.43
6	Astronomos	0.74	2.15	74.4	5.8	199	12.6	29.3	12.2	62.8	3.17	2.83
7	Campa Sansomendi	9.63	6.15	81.6	1.6	164	12.9	26.8	26.9	63.3	8.41	10.04
8	Castillo de Zaitegui	1.94	2.66	41.5	8.4	84	11.5	34	11.4	60.3	3.36	5.53
9	Conservatorio	3.23	3.63	43.7	7.1	104	15.3	38.7	14.2	59.7	6.32	7.1
10	Constitucion	1.15	2.57	38.8	2.6	125	15.1	39.3	17.8	68.5	2.89	3.79
11	Deba	0.95	2.03	52.9	21.9	40	12.4	29.5	4.8	69.7	1.44	1
12	Florida	2.71	3.67	33.5	2.9	146	15.6	45.7	9.8	64	5.23	7.96
13	Gazalbide	1.77	2.88	69.1	4.1	143	14.3	40	6.7	59.5	6.03	5.74
14	Gerardo Armesto	0.5	1.77	49.7	0.3	143	13.1	37.7	11.6	68.7	1	1
15	Gran Sol	0.94	1.83	44.7	3.1	225	6.7	12.3	13.2	55.4	1	2.87
16	Judimendi	2.33	3.1	60.3	1.2	131	13.9	27	10.3	58.4	3.71	5.67
17	Maria de Maeztu	3.02	2.44	85	1.3	153	13.9	37	12.4	64.4	6.46	6.24
18	Maurice Ravel	2.69	2.49	53	2.3	68	14.2	36.3	16.2	61	5.38	5.33
19	Molinuevo	4.83	3.85	51.5	2	144	14.6	38.7	31.9	64.1	5.8	7.3
20	Obispo Ballester	0.61	1.65	70.3	7.9	107	11.7	31.3	7.2	69.8	4.23	3
21	Parque del Este	2.76	3.46	51	0	47	5.1	7.3	11.7	56.8	1.91	2
22	Plaza de Llodio	2.44	2.57	61.4	0.5	102	13.2	33.7	14.4	60.4	3.85	5.66
23	Prado	3.36	4.08	76.9	0	118	15.5	44.3	13.5	64.6	3.44	6.83
24	Rosaleda Bolivia	1.98	2.12	54.9	7.1	134	13.9	40.7	8.3	55	5.32	4.34
25	Salvador Allende	1.02	1.54	29	13.2	72	11.5	35.3	10.4	65.4	2.88	3.37
26	San Martin	8.41	5	60.6	4	134	9.9	27.8	15.3	56.9	8.07	5.34
27	Sansomendi	2.69	3.71	72.3	3.4	130	12.3	31.7	16	60.5	7.87	7.4
28	Santa Barbara	0.74	2.14	39.5	8.1	82	9.7	31.3	5.8	62.9	3.29	4.75
29	Simon Bolivar	1.33	2.5	17.8	2.1	104	12.2	30	8.1	52.5	1	1.75
30	Zaldiaran	0.53	1.28	27.1	0	85	9.1	18.2	5.9	51.7	1	1
31	Zaramaga	0.98	1.81	38.2	5	141	12.4	28	4.9	63	2.84	3.36

Table 2. Between–survey frequency of occurrence of the 21 avian species detected in the urban parks of Vitoria–Gasteiz and results of the generalized linear mixed models that tested the existence of differences between seasons in these frequencies for the 16 resident species, i.e. species occurring in at least one park/visit in both seasons: Jan, parks occupaied in January; Feb, parks occupied in February; Jun, parks occupied in June; V, variance ± SD; I, intercept (breeding); S, season (winter). (The statistical significance of the effects was simplified in the superscript: $^{n.s.}$ non–significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Tabla 2. Frecuencia entre estudios de la presencia de las 21 especies de aves detectadas en los parques urbanos de Vitoria–Gasteiz y resultados de los modelos mixtos lineales generalizados con los que se analizó la existencia de diferencias en estas frecuencias entre estaciones para las 16 especies residentes, es decir, las especies observadas por lo menos en un parque o visita en ambas estaciones: Jan, parques ocupados en enero; Feb, parques ocupados en febrero; Jun, parques ocupados en junio; V, variancia ± DE; I, interceptar (cría nza); S, estación (invierno). *(La significación estadística de los efectos se simplificó en el superíndice: $^{n.s.}$ no significativo;* * P < *0,05;* ** P < *0,01;* *** P < *0,001).*

				Random effects	Fixed effects	
	Jan	Feb	Jun	V	I	S
Avian species occurring in either winter or summer (linear mixed models)						
Long–tailed tit *Aegithalos caudatus*	1	4	5	1.78±1.34	–2.20±0.85**	–0.91±0.74$^{n.s.}$
European goldfinch *Carduelis carduelis*	1	4	14	0.37±0.61	–0.21±0.40$^{n.s.}$	–2.37±0.70***
European greenfinch *Chloris chloris*	3	4	12	1.80 ± 1.34	–0.63±0.52$^{n.s.}$	–2.05±0.71**
Short–toed treecreeper *Certhia brachydactyla*	10	10	8	152.4 ± 12.3	–9.24±2.38***	1.55±1.18$^{n.s.}$
Blue tit *Cyanistes caeruleus*	17	16	15	5.19±2.28	–0.11±0.62$^{n.s.}$	0.35±0.55$^{n.s.}$
European robin *Erithacus rubecula*	15	10	17	4.64±2.16	0.36±0.64$^{n.s.}$	–1.06±0.63$^{n.s.}$
Chaffinch *Fringilla coelebs*	15	8	1	3.78±1.95	–4.94±1.62**	4.04±1.46**
Pied wagtail *Motacilla alba*	9	7	2	130.4±11.4	–15.04±4.6**	7.45±3.12*
Great tit *Parus major*	22	19	8	2.59±1.61	–1.58±0.64*	2.59±0.76***
Black redstart *Phoenicurus ochruros*	1	0	3	0.00±0.00	–2.23±0.61***	–1.88±1.18$^{n.s.}$
Common magpie *Pica pica*	20	20	25	2.61±1.62	2.11±0.74**	–1.18±.66$^{n.s.}$
Firecrest *Regulus ignicapilla*	13	14	15	3.19±1.79	–0.11±0.55$^{n.s.}$	–0.31±0.54$^{n.s.}$
European serin *Serinus serinus*	2	0	21	372.1±19.2	8.36±2.20***	–20.1±5.51***
Eurasian collared dove *Streptopelia decaocto*	1	1	5	65.9±8.12	–6.77±2.34**	–4.67±2.25*
Eurasian blackcap *Sylvia atricapilla*	3	1	4	1.25±1.12	–2.35±0.90**	–0.83±0.78$^{n.s.}$
Blackbird *Turdus merula*	22	21	23	16.9±4.1	3.48±2.66$^{n.s.}$	–0.59±0.80$^{n.s.}$
Avian species occurring in only one season						
Melodious warbler *Hippolais polyglotta*	0	0	2	–	–	–
Common wheatear *Oenanthe oenanthe*	0	0	1	–	–	–
Common chiffchaff *Phylloscopus collybita*	11	10	0	–	–	–
Eurasian wren *Troglodytes troglodytes*	0	0	1	–	–	–
Song thrush *Turdus philomelos*	2	3	0	–	–	–

mentioned above. Some of these variables had to be transformed to meet the normality requirements (table 3).

Finally, it was examined whether the species–park matrices of Vitoria–Gasteiz showed a nested pattern (Blake, 1991). For this purpose, the NODF index (Almeida–Neto et al., 2008) was calculated for each of the three presence/absence matrices independently (two for winter and one for breeding), and the associated *P*–values were obtained from binary null

Table 3. Coefficients of correlation (factor loadings) between the three principal components (PC) derived from the principal component analysis and the urban park characteristics. Table also shows the eigenvalues, the percentage of variance explained by each component and the significance levels between each PC and the descriptive traits of the parks. ($^{n.s.}$ non–significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

*Tabla 3. Coeficientes de correlación (cargas factoriales) entre los tres componentes principales (CP) derivados del análisis de componentes principales y las características de los parques urbanos. En la tabla también se indican las raíces latentes, el porcentaje de varianza explicado por cada componente y los niveles de significación entre cada CP y los rasgos descriptivos de los parques. ($^{n.s.}$ no significativo; * P < 0,05; ** P < 0,01; *** P < 0,001).*

Variables	PC1	PC2	PC3
Area (log–transformed)	0.44***	–0.20$^{n.s.}$	–0.37*
Shape (log–transformed)	0.45***	–0.15$^{n.s.}$	–0.38*
Grass cover	0.38***	–0.02$^{n.s.}$	–0.02$^{n.s.}$
Shrub cover (arcsine–transformed)	–0.13$^{n.s.}$	0.44***	–0.38*
Tree density	0.20*	–0.16$^{n.s.}$	0.66***
Tree height	0.34***	0.42***	0.29$^{n.s.}$
Tree trunk diameter	0.27**	0.52***	0.16$^{n.s.}$
Tree diversity (log–transformed)	0.44***	–0.20$^{n.s.}$	0.09$^{n.s.}$.
Noise	0.14$^{n.s.}$	0.47***	–0.12$^{n.s.}$
Eigenvalue	3.44	2.00	1.20
Variance explained	0.38	0.22	0.13

models. Random matrices were generated, keeping the frequency of each species constant using the 'c0' method in order to control for the fact that some species are more common than others (Jonsson, 2001). The relationship between the nestedness ranks of the parks (i.e. the value of the richest park will be 31, while it will be one for the poorest park) and their PC scores were also assessed by Spearman correlation coefficients in order to identify candidate park characteristics that might promote the observed nested patterns.

Three restricted presence/absence matrices of equal size (31 parks and 16 species) were additionally analysed. The number of species in these matrices was limited to the 16 (resident) species that were present in at least one park/visit in both summer and winter (table 2), as a way to assess whether park (range: 1–31) and species ranks (range: 1–16; value 16 for the most widely–distributed species and one for the least common) were correlated between seasons using comparable matrices. This approach helped to indirectly assess how seasonality affects the species–park nestedness matrices in Vitoria–Gasteiz.

All analyses were performed with R version 3.4.3, using 'vegan' package for diversity calculations, Mantel tests and nestedness analyses (Oksanen et al., 2018). An α threshold of $P = 0.05$ was used in all statistical tests.

Results

Avian composition and diversity between the breeding and winter period

After excluding aquatic and anthropogenic avian species (see Material and methods), records of 1,514 birds from 21 species were gathered during the surveys (table 2, see also table 1s in Supplementary material). The common chiffchaff *Phylloscopus collybita* and the song thrush *Turdus philomelos* were only detected in winter in the parks of Vitoria–Gasteiz while the Eurasian wren *Troglodytes troglodytes*, common Northern wheatear *Oenanthe oenanthe,* and the melodious warbler *Hippolais polyglotta* appeared only during breeding (table 2) and in very low numbers. For species occurring in both seasons in at least one park/visit, the common chaffinch *Fringilla coelebs*, pied wagtail *Motacilla alba* and great tit *Parus major* were significantly more common during winter than during the breeding season, while the European goldfinch *Carduelis carduelis*, the European greenfinch *Chloris chloris*, the European serin *Serinus serinus* and the Eurasian collared dove *Streptopelia decaocto* were more widely distributed during the breeding season than during winter (table 2). The remaining species (n = 9) showed no significant differences between seasons.

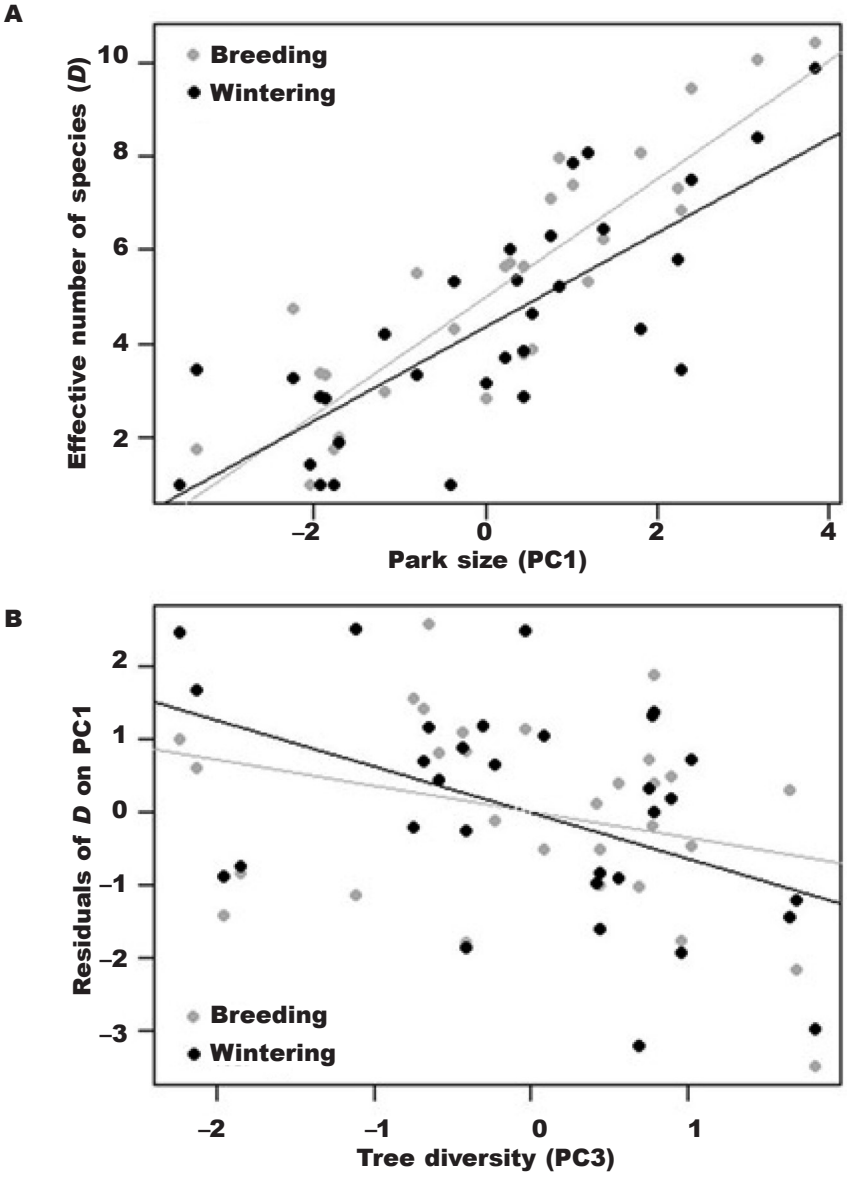


Fig. 2. Relationship between winter (in black) and breeding (in grey) avian diversity and (A) park size –PC1– (partial r^2 was 0.76 and 0.61 for breeding and winter diversity) and (B) tree density –PC3– (partial r^2 was 0.08 and 0.02, respectively).

Fig. 2. Relación entre la diversidad de aves en el período invernal (en negro) y la época reproductiva (en gris), por un lado, y (A) la superficie del parque (CP1) (el coeficiente r^2 parcial fue de 0,76 y 0,61 para la diversidad en la época reproductiva y en el período invernal) y (B) la densidad de los árboles (CP3) (el coeficiente r^2 parcial fue de 0,08 y 0,02, respectivamente).

The diversity of the parks was estimated as the effective number of species and varied between one and 11 species (table 1). Winter diversity estimated in January was strongly correlated with the values obtained in February (Pearson r = 0.72, $P < 0.001$), with no significant differences between them (paired *t*–test: $t = 1.48$, $P = 0.149$), so the average values of these two surveys were used as an estimate of winter diversity at each park (table 1). Parks with higher diversity in winter also had a higher effective number of species during the breeding period (Pearson r = 0.84, $P < 0.001$), although, on average, avian diversity during the breeding period ($D = 4.99 \pm 2.68$ SD) was significantly higher than during the winter ($D = 4.38 \pm 2.39$ SD; paired *t*–test: $t = 2.34$, $P = 0.026$).

Avian diversity and spatial autocorrelation

The Mantel tests did not show a significant association between the spatial distribution of the parks and their winter (Mantel statistic r = 0.10, *P* = 0.074) or breeding avian diversity (Mantel statistic r = 0.01, *P* = 0.405). Neither did the size of the studied parks show a spatial autocorrelation in Vitoria–Gasteiz (Mantel statistic r = 0.02, *P* = 0.382). For this reason, I did not apply any correction for spatial autocorrelation in the following analyses, and each park was treated as an independent data point.

Relationships between avian diversity and urban park characteristics

The PCA on the nine abovementioned characteristics of the urban parks provided three principal components (PCs) with eigenvalues higher than one (table 3). PC1 was interpreted as an index of park size, where high factor scores represented parks with a larger area, higher area–perimeter ratio, and more tree diversity than parks with low factor scores of PC1. Tree height, tree trunk diameter, shrub cover and noise were strongly and positively correlated with PC2 values, so that this component was considered a surrogate of the degree of vegetation development. Finally, tree density was the only variable strongly associated with PC3 (table 3).

PC1 was the main component explaining the observed variation in both winter (partial r^2 = 0.61) and breeding avian diversity (partial r^2= 0.76; fig. 2A, see table 4 for the overall r^2 of the models) with no between–season differences in the slope of this relationship (*season* × *PC1* interaction: *t* = 1.84, *P* = 0.077). PC3 also had a minor significant contribution to winter avian diversity (partial r^2 = 0.08), where more densely wooded parks had lower diversity indexes (fig. 2B). This effect was not significant for breeding avian diversity (partial r^2 = 0.02), although the diversity–PC3 slopes did not differ significantly between seasons (effects of *season* × *PC3* interaction: *t* = 1.13, *P* = 0.268). On the other hand, PC2 was not significantly associated with avian diversity in either the breeding or winter period (partial $r^2 \approx 0$, in both cases; table 4).

Nestedness patterns and urban park characteristics

Avian communities showed a significant nested subset pattern in the urban parks of Vitoria–Gasteiz under the null model selected, and the nestedness values were similar during the winter (January survey: NODF = 55.6, *P* < 0.001, NODF simulated values = 32.3–37.1 [95% CI]; February survey: NODF = 57.0, *P* < 0.001, NODF simulated values = 34.9–40.7 [95 % CI]) and the breeding period (NODF = 61.9, *P* < 0.001, NODF simulated values = 35.7–40.8 [9 5% CI]). For the three full presence/absence matrices, park nestedness ranks were positively associated with PC1 (richer parks had higher PC1 scores; January survey: Spearman r = 0.67; February survey: r = 0.68; breeding survey: Spearman r = 0.82; all *P* < 0.001), but in no case park ranks were correlated with PC2. Finally, PC3 only showed a significant negative association with the ranks for the February survey (Spearman r = –0.40, *P* = 0.025), but not for January (Spearman r = –0.18, *P* = 0.337) or June (Spearman r = –0.19, *P* = 0.308).

The presence–absence matrices that only considered the 16 species occurring in both seasons also showed a significant nested pattern (January survey: NODF = 56.7, *P* < 0.001, NODF simulated values = 33.1–37.8 [95 % CI]; February survey: NODF = 54.5, *P* < 0.001, NODF simulated values = 31.3–36.7 [95 % CI]; June survey: NODF = 63.9, *P* < 0.001, NODF simulated values = 41.4–46.7 [9 % CI]). Species ranks of the two restricted winter matrices were correlated with each other (Spearman [January–February] r = 0.89, *P* < 0.001), but this association was not significant between seasons (Spearman [January–June] r = 0.32, *P* = 0.222; Spearman [February–June] r = 0.48, *P* = 0.062). In spite of this lack of association in the species ranks between seasons, the park ranks of the three matrices were significantly, and positively, inter–correlated (Spearman [January–February] r = 0.82, *P* < 0.001; Spearman [January–June] r = 0.79, *P* < 0.001; Spearman [February–June] r = 0.76, *P* < 0.001) and their associations with the PCs of the parks were qualitatively the same as those observed for the full matrices.

Discussion

In accordance with expectations in a city in a temperate zone with a marked seasonal regime, the distribution patterns of some species changed dramatically between the breeding and wintering seasons, the two most stable seasons of the year for avian assemblages. For example, seven out of the 16 species that occurred all–year round (resident species) showed significant differences in their park occupancy rates between the breeding and the wintering period: four of them were more common during the breeding season and three were more common during the winter (table 2). This led to a lack of association in the resident species nestedness ranks between seasons, which confirmed that the structure and composition of the avian community differed markedly in summer compared to winter. These dynamics were probably mainly determined by the seasonal changes in abundance that the migratory dynamics of each species promote in this region (Gainzarain, 2006; De la Hera et al., 2014), although other factors, such as changes in behaviour (gregariousness versus territoriality) or habitat selection, might also contribute, but to a lesser extent (Murgui, 2010).

In an area where winter conditions are harsh and spring–summers are relatively mild (Ninyerola et al., 2005), avian communities are also expected to be more diverse during the more favourable season (Newton, 2008). Avian diversity was slightly higher during the breeding season than during the wintering period in the urban parks of Vitoria–Gasteiz. However, these differences were relatively small. This could be

Table 4. Results of the multiple regression analyses exploring the contribution of park characteristics (PC1–3) to the variation in winter and breeding avian diversity, expressed as the effective number of species (*D*).

*Tabla 4. Resultados de los análisis de regresión múltiple para estudiar la contribución de las características de los parques (CP1–3) a la variación de la diversidad de aves entre el período invernal y la época reproductiva, expresada como el número efectivo de especies (*D*).*

	Winter avian diversity (R^2 = 0.69)			Breeding avian diversity (R^2 = 0.78)		
	Estimate ± SE	*t*–value	*P*	Estimate ± SE	*t*–value	*P*
Intercept	4.38 ± 0.25	17.38	< 0.001	4.99 ± 0.24	20.92	< 0.001
PC1	1.00 ± 0.14	7.25	< 0.001	1.26 ± 0.13	9.61	< 0.001
PC2	–0.05 ± 0.18	–0.25	0.805	–0.01 ± 0.17	–0.04	0.970
PC3	–0.63 ± 0.23	–2.69	0.012	–0.35 ± 0.22	–1.60	0.121

caused by two main reasons. Firstly, from the pool of approximately 18 migratory species that occur in the region exclusively for breeding but spend the winter in tropical Africa (Martí and Del Moral, 2003; Unanue–Goikoetxea, 2017), only two species were observed in spring within the city boundaries (i.e. melodious Warbler and Northern wheatear), and their occurrence was very low, if not anecdotal (table 2). These two species are insectivore specialists that, like other representatives of this group that are lacking from the urban matrix but are common outside of it (e.g. Iberian chiffchaff *Phylloscopus ibericus*), probably have serious difficulties to find suitable conditions and enough food resources (invertebrates) for breeding in urban green areas as a consequence of causes such as pollution, greater presence of exotic plants, and intensive management of urban vegetation (e.g. regular lawn mowing, tree/bush pruning; Jones and Leather, 2012; Leveau and Leveau, 2016). Secondly, diversity was balanced between seasons by the more frequent winter occurrence in the parks of several species that are present year–round at a regional scale, such as the chaffinch, the pied wagtail, the song thrush and the common chiffchaff. The population sizes of these four species are boosted in winter by the arrival of many migratory conspecifics from higher latitudes (Asensio, 1985; Pérez–Tris and Asensio, 1997; SEO/Birdlife, 2012). Additionally, anthropogenic food resources and higher temperatures have also been suggested as factors that would allow these species to use the urban parks for overwintering (Gainzarain, 2006). Ultimately, what makes breeding communities slightly more diverse is the usual presence of some finch species (i.e. European greenfinch, European goldfinch, and European serin) during the breeding period that are rare during winter. This is probably a consequence of the tendency of many finches to group together in alternative habitats of the periphery of the city during the non–breeding period, becoming less frequent in the urban matrix (Gainzarain, 2006). Murgui (2010) found this same pattern in the city of Valencia (southeastern Spain), although the harsh winter conditions in Vitoria–Gasteiz suggest that the regional abundance of finches will be much lower than in Southern Iberia during winter (Gainzarain, 2006; SEO/Birdlife, 2012). Interestingly, the consequences for the nestedness patterns of the seasonal rearrangements of finch populations were completely different between these two cities (Murgui, 2010). Thus, while winter avian communities did not show a nested pattern in the urban parks of Valencia, nestedness was significant and similar in both seasons in Vitoria–Gasteiz. In any case, the seasonal variation in abundance of many breeding and wintering birds in the urban parks of Vitoria–Gasteiz (see above) suggests that, during some parts of their annual cycle, many of them rely on habitats located outside the city. Expanding our knowledge of the spatiotemporal distribution of these urban birds is essential to understand their population dynamics and implement management practices that could favour their occurrence and abundance within the city boundaries.

In spite of the structural and composition differences between the breeding and wintering avian communities, avian diversity and nestedness ranks were consistent between seasons, with the urban parks that were the most diverse during breeding also being the most diverse during winter. This supports the idea that the reduction in the park distribution of some species from one season to the other is compensated by the expansion of other species. Although previous research has explored the potential determinants of the richness of avian breeding species in the urban parks of Vitoria–Gasteiz (De la Hera et al., 2009), this is the first study associating avian diversity with park features using more suitable measures of diversity and orthogonal explanatory variables by means of PCA for both breeding and wintering assemblages, and the first to describe park–species nested patterns.

The results of this study highlight park size (PC1) as the indisputably best predictor explaining between–park variation in avian diversity (r^2 > 0.61) and the nested-

ness patterns in both seasons. Tree density (PC3) also contributed to avian diversity, although to a lesser extent: parks with less density of trees exhibited higher diversity values. As observed in Valencia, the nested patterns observed in the urban parks of Vitoria–Gasteiz might be mainly determined by selective extinction (Patterson and Atmar, 1986) and/or colonization (Cook and Quinn, 1995). This would be supported by the observed pervasive influence of park size and the fact that the parks studied have similar designs and management practices (Murgui, 2010). Thus, larger parks will be able to host most of the generalist urban species and a few specialists that are probably not able to persist in smaller parks in the long–term. It is important to note that the fact that small parks were relatively oversampled per unit area compared to large parks (see Material and methods) makes the patterns observed in this study more robust, because, in spite of these differences, large parks were still richer and more diverse than small parks.

This study also showed that nestedness and avian diversity patterns were not greatly affected by seasonality in the urban parks of Vitoria–Gasteiz. This is probably a common pattern in relatively small cities, where the size of the parks rarely exceeds the threshold in which the species–area relationship maintains its positive slope, which has been established at approximately 10 hectares for urban parks (Nielsen et al., 2013). Promoting habitat heterogeneity within and between urban parks (e.g. implementing different management practices of the vegetation) could increase the number of urban species in the city and expand the distribution of some rare ones, but the benefits of these measures would be cushioned in small parks by edge effects and other factors (Fernández–Juricic, 2001). Thus, these results suggest that park size is the main constraint for avian diversity in small and medium–sized cities, so that favouring the existence of a few relatively large parks (i.e. over 10 ha) instead of many small ones would be a much more effective measure to maintain a diverse urban avifauna all year round.

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