ORIGINAL ARTICLE

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Birds on novel island environments. A case study with the urban avifauna of Tenerife (Canary Islands)

Abstract We analyzed the variation in island bird communities of urban environments related to habitat characteristics, using regression/classification tree analyses. Data from field censuses in cities/towns representing the urban heterogeneity of the whole island were obtained in Tenerife (Canary Islands, Spain). Urban bird abundance in Tenerife was negatively affected by altitude and the cover of dry *Euphorbia* shrubs and positively influenced by the height and cover of the tree layer. Species richness was negatively associated with building cover and positively related to tree height and altitude. Data from field censuses in Tenerife were compared with that of similar urban environments in the mainland (Madrid Province, central Spain). Species diversity was higher in the urban sample of Tenerife than in that of Madrid and the proportion of bird species from the regional pool 'captured' by urban environments was higher in the island than in the mainland. Nine native species and three alien species were more abundant in island urban environments than in the continent (densities, at least, 100% higher), the converse occurring for only five species. At a biogeographic scale, we conclude that the avifauna of Tenerife Island is more prone to occupy a new artificial environment than the mainland bird fauna of central Spain.

Keywords Avian biogeography · Distribution patterns · Habitat preferences · Island–mainland comparisons · Urban habitats

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Introduction

Comparisons between biotas of islands and their corresponding mainland sources have led to the proposal of suggestive biogeographical, ecological and evolutionary theories. Most of them predict that island ecosystems, because of their geographical isolation, favor the appearance of novel community and population patterns different from those observed in nearby mainland communities (for reviews, see Brown and Lomolino 1998; Whittaker 1998; see references therein for species–area relationships, taxon cycle, density inflation, niche expansion). However, environmental characteristics and evolutionary histories of islands and continental sources also diverge, and a reliable equivalence between them becomes more problematic. Urban environments offer a good opportunity to deal with this limitation, as they are recent, artificial habitats and are structurally similar among distant regions.

Although birds are a favorite taxon for testing community patterns either on islands (e.g. Abbott 1980; Terborgh and Faaborg 1980; Blondel et al. 1988; Martin et al. 1995; Adler 1994; Ricklefs and Bermingham 1999) or in urban environments (e.g. Beissinger and Osborne 1982; Blair 1996; Clergeau et al. 1998; Marzluff et al. 2001; Green and Baker 2003), only a few references join both research fields (e.g. Lim and Sodhi 2004; Lee et al. 2004). Island avifaunas have been traditionally considered very susceptible to extinction risks because of human influence (Pimm et al. 1988; Milberg and Tyrberg 1993; Collar et al. 1994; McKinney 2001; though see also Manne et al. 1999). In addition, urbanization is repeatedly reported as a key factor threatening bird diversity (Marzluff and Erwing 2001; Marzluff et al. 2001). Thus, from a conservational perspective, contributions to the study of urban habitats in islands are valuable, because islands worldwide usually support high levels of avian endemicity, potentially menaced by urban sprawl (Johnson and Stattersfield 1990; Stattersfield et al. 1998). This paper focuses on these aspects, studying the effects

of urbanization on the breeding avifauna of an oceanic island. Our specific goals are: (a) to compare the community patterns and species-specific abundances between urban habitats of Tenerife island and a mainland region biogeographically representative of the ornithological source of the Canary archipelago (Central Iberia), (b) to analyze variations in bird density, species richness and species occurrences related to variables describing structure and geographical location of the urban habitats of Tenerife Island.

Materials and methods

Tenerife (Canary Islands, 28°15′ N, 16°35′ W; 2,059 km^2) is an ancient (11.6 million years old) oceanic island located 288 km from the African coast. Twenty-four percent of its area is covered by coniferous and evergreen forests, while 0.9% was covered by urban areas. For more details on environmental characteristics of Tenerife Island see Anonymous (1980).

Bird censuses in urban habitats of Tenerife Island were carried out during the breeding season (April 2002, 2003). We excluded from analyses vagrant species and regular migrants not breeding in the island (Martín and Lorenzo 2001). The census method was the line transect, including all the birds heard or seen within survey belts of 25 m at each side of the progression line (Bibby et al. 2000). All censuses were carried out on windless and rainless days, at a low speed (ca. 1–3 km/h), early in the morning (7:00–11:00 GMT) and late in the evening (16:00–17:30 GMT). Due to these sampling periods, two nocturnal birds present in urban environments of Tenerife were excluded from the study (*Tyto alba* and *Asio otus*). Each transect was divided into 500-m units of homogeneous urban structure (500×50 m = 2.5 ha censused) and georeferenced with GPS ('Garmin 12'; precision of 1 m by means of the average location function). Seventy-seven urban transects (38.5 km) were made throughout Tenerife in 19 different cities/villages, representing the entire gradient of urbanization on the island (mean altitude 341 m a.s.l.; range from sea level to 1,000 m). Each transect was characterized by sampling the following structural variables (estimated by eye, after training): percentage cover of buildings (mean 44%; range 2–85%), pavement (20%; 0–80%), lawn (13%; 0–85%), shrubs (12%; 0–50%) and tree canopy (3%; 0–30%) and average height of buildings (mean 9 m; range 4–30 m), shrubs (0.8 m; 0.1–2.0 m) and trees (7.3 m; 3–15 m). In addition, the size of the city where each transect was located was measured on 1:25,000 maps (mean 1.9 km^2; range from 1 ha to 5.3 km^2).

The avifauna inhabiting the urban environments of Tenerife Island was compared with that living in comparable urban environments in the mainland. This comparison was carried out with birds living in the western part of Madrid Province (Central Iberia, 40°30′ N, 3°50′ W; approximately 2,500 km^2). This area has a large variability in the size and structure of urban centers, ranging from large cities to small rural and residential towns. It was chosen as representative of the source mainland avifauna of the Canary Islands, considering the European and Mediterranean origin of the birds of Tenerife (Bacallado 1976). We carried out 28 km of transect counting during 2001, 2002 and 2003 (all censuses early in the morning during May). Habitat characteristics of the urban environments of Madrid extensively overlapped with those observed in Tenerife, as heavily built-up areas and garden-developments were included (see above): percentage cover of buildings (mean 43%; range 10–80%), pavement (30%; 8–80%), lawn (21%; 0–67%), shrubs (2%; 0–10%) and tree canopy (7%; 0–18%) and average height of buildings (mean 18 m; range 7–33 m), shrubs (0.6 m; 0.1–1.5 m) and trees (10.4 m; 3–18 m); altitude range was 500–1,100 m.

From the Spanish Atlas of Breeding Birds (Martí and del Moral 2003), we counted the number of species breeding in Tenerife (island) and Madrid (mainland) in areas where the maximum altitude was lower than 1,500 m a.s.l. (i.e. sectors where the urban transects were made; 26 UTM coordinates, 10×10 km squares in both Tenerife Island and Madrid Province). These numbers were compared with the total number of species recorded in the urban transects.

Regression trees were used to analyze the relationships of bird abundance and species richness, with variables characterizing the structure of the 77 urban transects. Classification trees were used to analyze the effect of urban structure on bird species occurrence in these transect samples. Only species that occurred seven or more times in the sample of 77 transects were considered. Regression and classification tree analyses allow interpretation of datasets where there were complex nonlinear relationships between response and predictor variables, and/or high-order interactions among predictor variables (Breiman et al. 1984; Venables and Ripley 1994; Boone and Krohn 2000; De'ath and Fabricius 2000). The stopping rules in tree growth applied in our data analyses were: (1) groups including at least ten cases and (2) significant reductions in residual deviance (a measure of group heterogeneity) attained by a splitting criteria (according to a χ^2 test).

Results

Comparison of urban environments of Tenerife Island and Central Iberia

Table 1 shows bird densities of species in urban areas of Tenerife Island and Madrid Province (mainland). The total bird density is higher in the mainland (120.9 birds/10 ha) than in the island (62.9 birds/10 ha). This difference is mainly attributable to the densities of *Passer* species (*P. domesticus* in Madrid, *P. hispaniolensis* in Tenerife), since subtotals excluding these species are 47.7 birds/10 ha and 45.4 birds/10 ha,

Table 1 Average densities (birds/10 ha) of species present in urban environments of Tenerife Island (192 ha censused) and Madrid Province (mainland; 140 ha censused). Endemic island species are listed paired with their nearest continental relative. *0.0* Absent from the urban censuses though present in the region, − not present in the region, + present in the urban censuses with a density lower than 0.05 birds/10 ha

Bird species	Madrid (mainland; birds/10 ha)	Tenerife (island; birds/10 ha)
Aegithalos caudatus	0.1	−
Anthus campestris/A. berthelotii	0.0	0.7
Carduelis cannabina	0.0	0.8
C. carduelis	0.1	0.1
C. chloris	5.4	0.3
Certhia brachydactyla	0.3	−
Columba livia	4.2	15.4
C. palumbus	2.1	−
Corvus monedula	+	−
Delichon urbica	4.7	−
Erithacus rubecula	0.5	0.5
Fringilla coelebs	0.2	0.1
Hirundo rustica	1.5	−
Luscinia megarhynchos	0.1	−
Motacilla alba	0.1	−
M. cinerea	0.0	1.2
Myiopsitta monachus	0.0	0.1
Parus ater	0.1	−
P. caeruleus	0.7	1.7
P. cristatus	0.1	−
P. major	0.6	−
Passer domesticus	75.5	−
P. hispaniolensis	0.0	15.2
P. montanus	0.1	−
Petronia petronia	0.1	+
Phoenicurus ochruros	0.2	−
Phylloscopus ibericus/P. canariensis	0.1	6.4
Pica pica	2.2	−
Picus viridis	0.1	−
Psittacula krameri	0.0	0.5
Regulus ignicapillus	0.6	−
Regulus regulus/R. teneriffae	0.0	0.1
Serinus serinus/S. canarius	5.5	2.8
Streptopelia decaocto	3.7	8.7
S. roseogrisea	0.0	1.9
S. turtur	0.0	0.5
Sturnus unicolor/S. vulgaris	3.5	+
Sylvia atricapilla	0.6	1.6
S. conspicillata	0.0	0.7
S. melanocephala	0.2	0.3
Troglodytes troglodytes	0.3	−
Turdus merula	7.2	3.1
Upupa epops	0.2	0.1

respectively, in the mainland and in the island. The diversity of urban bird communities is larger in Tenerife Island than in Madrid Province (Shannon index: 2.1 nats and 1.7 nats, respectively). Urban environments of Tenerife include 64% of species from the total island pool (25 out of 39), a figure two times higher than that reached in Madrid Province (28%; 33 out of 120 species from the Central Iberia pool; Yates corrected $\chi^2 = 15.5$, $P = 0.0001$). Species-specific densities in urban environments of Tenerife and Madrid are not significantly correlated ($r = -0.022$, $n = 43$ species, $P = 0.889$). Among common species in urban

habitats (arbitrarily established at 0.5 birds/10 ha, either on the island or on the continent), nine native species are, at least, 100% more abundant in urban environments on the island than in the continent (i.e. *Carduelis cannabina*, *Columba livia*, *Motacilla cinerea*, *Parus caeruleus*, *Streptopelia turtur*, *Sylvia atricapilla* and *Sylvia conspicillata*; *Anthus berthelotii* and *Phylloscopus canariensis* were also included considering their counterpart species *A. campestris* and *P. ibericus* in the mainland; Voelker 1999; Helbig et al. 1996). In addition, three alien and exclusively urban species, *Psittacula krameri*, *Streptopelia decaocto* and *S. roseogrisea*, have also achieved more successful urban colonizations in Tenerife than in Central Iberia. In contrast, five island species are clearly more scarce in urban Tenerife than in urban Madrid (i.e. *Carduelis chloris*, *Sturnus unicolor*, *Turdus merula*, the endemic laurel pigeon *Columba junoniae* paired with continental *C. palumbus* and the endemic *Serinus canarius* paired with the European *S. serinus*). The marked island overabundance of *Passer hispaniolensis* (15.2 birds/10 ha in urban Tenerife, but completely absent from urban Madrid) is ambiguous, because if compared with its most obvious ecological equivalent in Central Spain, *P. domesticus* (75.5 birds/10 ha), it becomes clearly more scarce.

Variation of bird density and species richness in urban areas of Tenerife

Structural variables characterizing urban transects accounted for 40.6% of the original deviance in total bird numbers (tree regression analysis: $\chi^2 = 110{,}9$, d.f. = 5, $P < 0.001$). Urban bird abundance was negatively affected by altitude and shrub cover (mainly *Euphorbia* scrubs) and positively influenced by the presence and
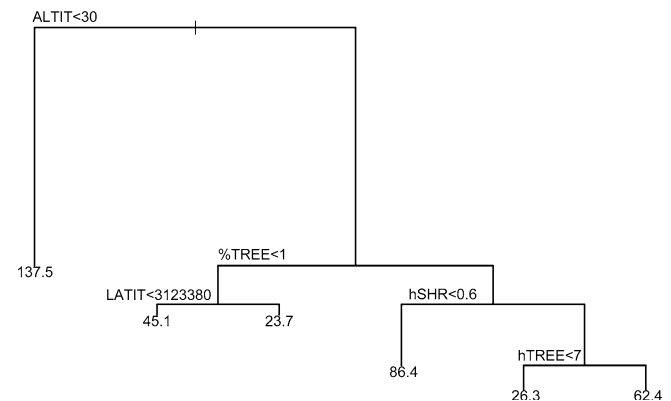
Fig. 1 Regression tree modeling bird density in urban environments of Tenerife. Splitting criteria indicate the conditions for the *left branches*. *Numbers* at terminal tips are average abundance figures (birds/10 ha). Length of branch is proportional to deviance explained by each split. *ALTIT* altitude a.s.l. (m), *hSHR* mean height of the shrub layer (m), *hTREE* mean tree height (m), *%TREE* tree canopy cover, *LATIT* latitude (UTM coordinates)
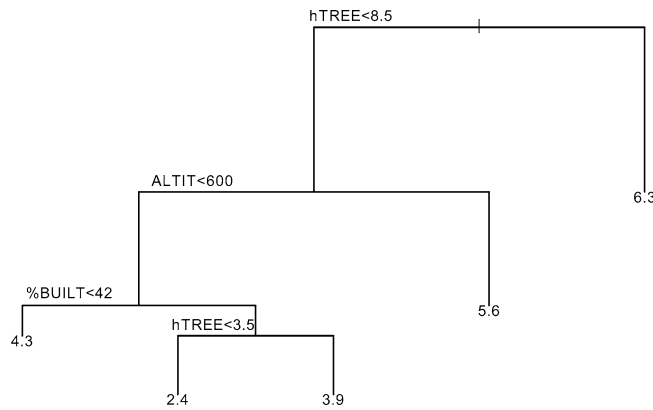
Fig. 2 Regression tree modeling the species richness per transect in urban environments of Tenerife. Splitting criteria indicate the conditions for the *left branches*. *Numbers* at terminal tips are average richness figures (species/2.5 ha). Length of branch is proportional to deviance explained by each split. *ALTIT* altitude above sea level (m), *%BUILT* built-up cover, *hTREE* mean tree height (m)

height of the tree layer. Urban sites with the highest total densities in the regression tree (138 birds/10 ha) were located near sea level (< 30 m a.s.l.), independently of their structural characteristics. Conversely, the lower total densities (24 birds/10 ha) were measured in treeless urban sites located in the north of the island (Fig. 1).

Species richness in transects was significantly explained by the regression tree in Fig. 2 (36.1% of original deviance explained; $\chi^2 = 103.6$, d.f. = 4, $P < 0.001$). Tree height and altitude positively related to species richness. In contrast, building cover negatively affected the number of species. The maximal species richness (6.3 species per transect of 2.5 ha) was reached in urban sites having trees taller than 8.5 m. The lowest richness (2.4 species/transect) was observed at locations below 600 m a.s.l. with built cover greater than 42% and tree height lower than 3.5 m.

Urban characteristics and species-specific occurrences

Significant classification trees were obtained for 13 species, modeling their presence/absence in urban transects at Tenerife Island. Table 2 provides the criteria defining the maximum probabilities of species occurrence. Tree models explained an average 43.1% of the observed variability (range: 19.1–60.7%), with high percentages of correct classification (mean = 85.9%, range: 76.6–93.5%). The most influential predictors of the presence/absence of species were altitude and size of town/city (involved in one half of the tree conditions describing maximum probabilities of occurrence), although there were no generalizable positive or negative effects linked to particular variables. Urban size positively affected *Passer hispaniolensis* and *Streptopelia roseogrisea* ('large city' exploiters) and negatively influenced *C. cannabina*, *A. berthelotii* and *M. cinerea* ('large city' avoiders). Low altitudes in Tenerife constrained the occurrence of *M. cinerea* and *P. caeruleus*, while favoring the presence of *P. hispaniolensis*, *S. canarius* and the two alien *Streptopelia* species.

Discussion

Biogeographic aspects

Species richness impoverishment is a common phenomenon on islands, because their ecological bases are related to the dispersion abilities of species from the continental pool, the availability of ecological resources and the stress of abiotic factors on island environments (Brown and Lomolino 1998; Whittaker 1998). The lower species richness in insular faunas has been detected in many island environments, although it is not generalizable to all of them. Thus, Blondel et al. (1988) found that mature woodland habitats are more impoverished on islands (Corsica) versus mainland (southern France),

Table 2 Summary of classification trees for species with greater sample sizes showing the main splits (in order of appearance in the tree) modeling the influence of urban descriptors on the probabilities of presence. *Occ.* Frequency of occurrence in census transects (n = 77), *Dev.* amount of original deviance for the whole tree model explained, *Corr.* amount of cases correctly classified by the

tree model, *Prob.* probability of occurrence when the selected conditions are met. *ALTIT* Altitude above sea level (m), *URBSIZE* size of town/city (km^2), *%BUILT* built-up cover, *%SHR* shrub layer cover, *hSHR* mean height of the shrub layer (m), *%TREE* tree canopy cover

	Occ. (%)	Dev. (%)	Corr. (%)	Prob. (%)	Main splits
A. berthelotii	9.1	50.9	90.9	41.2	URBSIZE < 0.12
C. cannabina	10.4	54.2	89.6	47.1	URBSIZE < 0.12
C. livia	45.5	38.4	79.2	87.5	hSHR < 0.15; %BUILT > 60
M. cinerea	26.0	22.8	87.6	54.2	URBSIZE < 1; ALTIT > 420
P. caeruleus	29.9	30.3	80.5	72.2	ALTIT > 220; hSHR > 0.15; %BUILT > 20
P. hispaniolensis	49.4	60.7	87.0	96.4	URBSIZE > 1; ALTIT < 520
P. canariensis	71.4	54.9	89.6	100.0	%BUILT < 35
S. canarius	19.5	39.2	88.3	71.4	ALTIT < 560; %BUILT < 50
S. decaocto	46.8	54.7	87.0	92.3	ALTIT < 60
S. roseogrisea	18.2	54.9	89.6	80.0	ALTIT < 135; URBSIZE > 4.5
S. atricapilla	32.5	31.1	77.9	76.9	hSHR > 0.55; %SHR > 22
S. conspicillata	9.1	49.2	93.5	60.0	%SHR > 36
T. merula	37.7	19.1	76.6	70.6	hSHR < 1; %TREE > 2

than open habitats like shrub lands or pasturelands. Nevertheless, these comparisons pose some problems because natural counterpart habitats are not strictly equivalent due to the different geological, climatological and evolutionary history of island and mainland environments (Blondel et al. 1988). To overcome this limitation on island/mainland comparisons we focused on urban environments, whose habitat structure, ecological constraints due to human impact and recency are relatively similar across different biogeographical regions.

Considering all the bird species present in the urban samples of Tenerife and Madrid, species richness was higher in the mainland (33 species) than in the island (25 species). Nevertheless, this striking difference is probably attributable to the correspondingly larger regional pool of species in the mainland (120 species in Madrid vs 39 species in Tenerife), rather than to limitations posed by urban habitats in the island. Thus, the larger species richness in the mainland urban environments is related to the presence of very scarce or accidental species (< 0.5 birds/10 ha), because richness is equal in both areas when only common species are considered (16 species with densities higher than 0.5 birds/10 ha in both areas). Moreover, species diversity is higher in the urban sample of Tenerife than in that of Madrid. This result reinforces the idea of not-generalizable impoverishment of insular (vs mainland) bird faunas across different habitats (Martin 1984; Blondel et al. 1988).

The proportion of bird species 'captured' by urban environments is higher in Tenerife than in Madrid Province, whether considering the total number of species observed (64% vs 28%, respectively), or only the common ones (i.e. > 0.5 birds/10 ha; 48% vs 13%). Therefore, the whole bird fauna of Tenerife (including the alien species) is more prone to occupy a new artificial environment than the mainland bird fauna of central Spain (but see Sol 2000). This observation is consistent with the niche expansion hypothesis (Blondel et al. 1988; Martin 1992; Prodon et al. 2002), predicting broader habitat preferences in island species because of reduced interspecific competition in impoverished faunas.

Influence of urban location and structure

An inverse relationship between biological diversity and altitude has been commonly predicted (for general revisions, see Brown and Lomolino 1998; Rahbek 1995; Lomolino 2001). The basis of this association could be both metabolic (temperature is inversely related to altitude and energy expenditure increases with decreasing environmental temperature; Calder and King 1974) or biogeographic (lower species richness at higher altitudes due to the reduction of area with increasing altitude and increasing isolation from other mountaintops; MacArthur 1972; Rahbek 1997; Kattan and Franco 2004). However, these explanations seem not to apply to birds in urban habitats on Tenerife. Although bird density associates negatively with altitude, the ambient temperature at the altitudes where cities and towns are spread in Tenerife is not a clear constraint for birds during the breeding season (average temperature in March–June > 15°C; Anonymous 1980). However, and contrary to expectations, species richness correlates positively with altitude.

The negative relationship between altitude and bird density could be understood considering the effect of altitude as a surrogate of other structural variables. In Tenerife, altitude parallels the degree of urbanization. Urban developments in coastal cities are more intense than those at higher elevations, because the huge touristic demand stresses urban sprawl as close as possible to beaches (accordingly, altitude and urban size is significantly correlated in the sample of 77 transects: $r = -0.515$, $P < 0.001$). Due to the negative effect of fragmentation and the small size of island-habitats on bird abundance (Blake and Karr 1987; Boulinier et al. 1998; Jokimäki 1999; Santos et al. 2002), big cities can support large populations of just a few urban-specialist species, capable of attaining very high local densities (e.g. the three most abundant species in urban Tenerife, *P. hispaniolensis*, *C. livia*, *S. decaocto*, account for 63% of all urban bird numbers).

The positive influence of altitude on the number of bird species in urban habitats could be explained considering that avian species richness increases with altitude from sea level in Tenerife (Carrascal and Palomino 2005), reaching the highest figure around 1,000 m a.s.l. Dry *Euphorbia* scrublands comprise the dominant habitats distributed in Tenerife from sea level up to 500–600 m in altitude (Anonymous 1980). These habitats are comparatively poorer in species richness than the more vegetated habitats located between 500 m and 1000 m a.s.l. (e.g. humid scrublands, evergreen laurel forests; Carrascal and Palomino 2005). Therefore, urban environments placed on lowland areas dominated by dry *Euphorbia* scrublands have a poorer avifaunistic pool of colonizers than cities and towns located at higher altitudes. Although with low densities, urban habitats located above 600 m are occupied by many species of the surrounding habitats, thus contributing to increase the species richness.

Our results also have implications for the management of the urban environments of Tenerife in order to increase avian diversity. Using species-specific habitat preference models, or avian community–habitat structure associations, it is possible to provide site-specific recommendations for the management of urban biodiversity (e.g. Germaine et al. 1998; Melles et al. 2003). Our data clearly show that bird impoverishment in large cities on Tenerife could be ameliorated through less-crowded models of urbanization, by simply including more garden areas. Although coastal, intensely urbanized cities support the greatest urban bird densities across the island, they also have a low species richness, especially when the tree layer is not mature enough or is absent. Several works have also shown a marked increase in total avian density at the expense of decreasing species richness in heavily urbanized locations, where

built-up and paved surfaces prevail over wooded and garden areas (e.g. Lancaster and Rees 1979; Beissinger and Osborne 1982; Blair 1996; Clergeau et al. 1998; Melles et al. 2003; Crooks et al. 2004). This idea is reinforced by the whole community model explaining variation in species richness, showing the importance of the maturity of the tree layer in the urban avifauna of Tenerife. Moreover, the homogenization of the bird community at these sites is still more marked when the built-up cover is large (>42%). Reduction of the densely built-up area and improvement of the tree layer in gardens would add more species to the community dominated by urban-specialists. This should benefit several species, like *P. caeruleus*, *S. atricapilla*, *S. conspicillata* and *T. merula*, as shown in models in Table 2; and it could probably also benefit other birds actually very uncommon in Tenerife cities (e.g. *S. turtur*, *Erithacus rubecula*, *Regulus teneriffae*). This habitat diversification management should exert a more marked effect on cities and towns located at lower altitudes.

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