Short notes

Temperature differentially mediates species richness of birds of different biogeographic types

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This study explores the relationship between richness of bird species and climate in Spain, distinguishing groups of species according to biogeographic type. Species richness proved to be related to temperature but in a different way for each of the biogeographic groups. While controlling for other variables, species richness initially increased with temperature, but dropped when temperature increased further. As this drop was less strong in southern species than in northern species, a positive relationship between the percentage of southern species and temperature emerged. Moreover, the percentage of southern species varied with human population density, altitude range and precipitation in a quadratic way.

Key words: climatic change, habitat heterogeneity, human population, land use, Spain

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Introduction

Climate is one of the most important factors determining the distribution of avian species richness (e.g. Rahbek & Graves 2001) by its effect on primary production (van Rensburg et al. 2002, Chown *et al.* 2003, Hurlbert & Haskell 2003), and by its interaction with physiological requirements and tolerances of species (Turner *et al.* 1988, Woodward & Kelly 2003). Factors determining species richness are not universal, but vary among taxa (e.g. Miller *et al.* 2003). This is because the distribution of species is mediated by their ecological niche (Pulliam 2000, Wiens & Donoghue 2004), and groups of species differentiated by their taxonomy, behaviour, or physiology can have a shared or convergent evolution, responding differentially to certain factors which interact with the necessities imposed by their niche. Knowledge on the way how climate affects the distribution of avian species richness is of prime importance as the Earth is under a climatic warming (IPCC 2001). This climatic change is already affecting bird distribution (Thomas & Lennon 1999), and dramatic changes in the distribution of birds are predicted (Huntley *et al.* 2006).

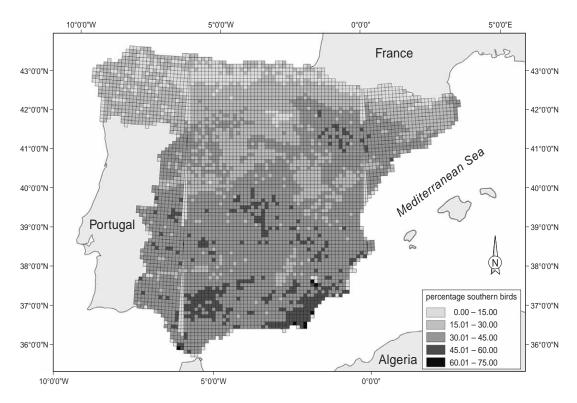


Figure 1. Distribution map for the percentage of southern species in Spain in 10 x 10 km squares.

Species in different climate zones of the Earth must be adapted to different environmental conditions, which spawned the distinction between biogeographic types (Voous 1960, Newton 2003). As species of different biogeographic types are adapted to different climates, climate might differentially affect species richness of birds of different biogeographic types. We tested this hypothesis on the basis of the distribution of birds in Spain. We predict that the richness of northern species should be negatively correlated with temperature, and positively with precipitation, while the reverse should occur in the richness of southern species (also see Santos & Tellería 1995).

Methods

The study area was peninsular Spain, which has a variety of environments ranging from Mediterranean aspects to an oceanic climate along the Cantabrian coast. The study area was divided in 5331 UTM squares of about 10 x 10 km (Fig. 1). Cartographic distortions caused some squares to be less than 100 km², and these were removed from the analyses. Squares without environmental information were also dropped from analyses, resulting in a final sample size of 5070 squares.

Species richness was defined as the number of bird species in each cell. We used all species of breeding birds listed in the national atlas (Martí & del Moral 2003, Ministerio de Medio Ambiente 2003). We assigned each species to the category 'northern' or 'southern', according to its biogeographic type (listed in Online appendix 1). Biogeographic types for which distribution was ubiquitous (e.g. Cosmopolitan or Old World) were discarded (Online appendix 1). With these data, we calculated the percentage of southern species in each square. The percentage of southern species was positively correlated with the richness of southern species (r = 0.66; P < 0.001; n = 5070 squares) and negatively with the richness of northern species (r = -0.64; P < 0.001).

Independent variables were acquired from the European Environment Agency (www.eea.europa. eu), using a geographic information system (SAGA; Conrad 2005). To test effects of climate, we considered two variables for each of the squares: (1) mean annual temperature, and (2) total annual precipitation. Mean annual temperature was strongly correlated with mean temperature in the coldest and hottest months (r > 0.88). Moreover, we considered (3) altitude range, (4) habitat diversity, as the sum of types of land use, taken from Corine Land Cover (www.eea.europa. eu), (5) human population density (log-transformed), (6) humanized surface area, as the percentage of area used by humans (croplands and urban zones; arcsine-transformed), which served as a negative indicator of natural land available. Lastly, in order to minimize possible effects of spatial autocorrelation, we introduced the geographic variables longitude (Lon) and latitude (Lat) of the centre of the squares, as well as the composite variables Lon², Lat², Lat³, Lon²xLat and LonxLat², according to Legendre (1993). We did not use Lon³ and LatitudexLongitude because this destabilized the matrix and least squares could not be calculated. The inclusion of these terms successfully removed most of the spatial autocorrelation, indicated by Moran's I of the residual models, always lower than 0.15 (Diniz-Filho et al. 2003).

Variables had an almost normal distribution, otherwise they were transformed to fit a normal distribution. Variables were standardized with a mean of 0 ± 1 SD (Sokal & Rohlf 1995). To test the relationship between independent variables and species richness, we used a Generalized Linear Model (GLM) of Ordinal Least Squares (OLS). This analysis statistically controls for the effects of other independent variables. Multicollinearity was not high, as absolute values of correlations between independent variables were 0.66 or less, and tolerance was always higher than 0.3 (Quinn & Keough 2002). To test for curvilinear relationships, we introduced polynomial terms of variables 1–6 into the model. Variables in the final models were selected by a stepwise backward process.

Results and discussion

Figure 1 shows the distribution of the percentage of southern species in Spain. As expected, the percentage of southern species per square correlated with temperature in a positive way (r = 0.65; P < 0.001; n = 5070 squares; Fig. 2). When controlling for effects of other variables, the GLM showed a significant positive relationship between percentage of southern species and temperature (Table 1). This model explained 76% of variation in percentage of the southern species. We repeated the GLMs in order to examine the relationship between temperature and species richness of southern and northern species. After controlling for the other independent variables in this study, species richness of southern and northern species were related to temperature in a quadratic way (Table 1). In both cases, species richness dropped with increasing temperature, but less so in southern species, thus explaining the results found for the percentage of southern species. Other studies have shown that the distribution or abundance of

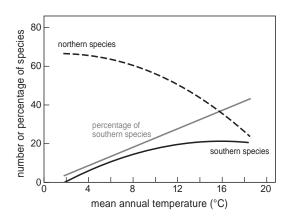


Figure 2. Relationship (without controlling for other variables) between temperature and number of southern species $(y=-7+0.24x-0.18x^2)$, number of northern species $(y=66-0.66x-0.12x^2)$, and percentage of southern species (y=0.65x). Data points are not shown for clarity.

Dependent variable	Percentage of southern species	Southern species richness	Northern species richness
	0.76	0.50	0.58
F-statistic	1079.12	282.36	403.52
df	15,5054	18,5051	17,5052
Longitude (Lon)	4.980	6.29	-2.47
Lon ²	-8.73	-13.86	2.63
Latitude (Lat)	-211.80	-396.05	-133.15
Lat ²	429.34	800.81	264.82
Lat ³	-217.67	-404.67	-131.66
Lon ² xLat	8.35	13.10	-3.23
LonxLat ²	-4.33	-5.46	3.11
Human population (HP)	0.21	0.22	0.05
HP^2	-0.28	-0.30	-
Humanized area (HA)	-	0.19	0.09
HA^2	-	-0.24	-0.24
Altitude range (AR)	0.42	0.36	-0.17
AR^2	-0.49	-0.30	0.26
Habitat diversity (HD)	-0.03	0.10	0.11
HD^2	-	-	-
Temperature (T)	0.39	0.69	0.13
T^2	-	-0.37	-0.36
Precipitation (P)	0.14	0.91	0.83
\mathbb{P}^2	-0.28	-1.09	-0.79

Table 1. Results of GLM's analysing dependence of percentage of southern species, richness of southern species, and richness of northern species on various variables. The b coefficients of the multiple-regression model are given, as well as values of R^2 and *F*-statistic. In bold, slopes that significantly differ from zero at P < 0.0025 (corrected by Bonferroni). - indicates that variable was removed by backward stepwise selection.

avian species, in general, is affected by temperature (Root 1988, Turner *et al.* 1988, Lennon *et al.* 2000), our study extending on this by showing that the effect of temperature depends on the biogeographic type considered.

While, percentage of southern species correlated negatively with precipitation (r = -0.64; P < 0.001). However, when the relationship with precipitation was controlled for other variables, a quadratic relationship emerged, with higher percentages of southern species for intermediate values of precipitation. Analysing richness of northern and southern species separately, the two biogeographic types showed a similar quadratic relationship with precipitation (Table 1). Probably, precipitation favours species richness through primary productivity (Waide *et al.* 1999, Hawkins *et al.* 2003, Whittaker *et al.* 2007), but high levels of precipitation harm species survival and breeding, affecting plumage impermeability and foraging opportunities (Lennon *et al.* 2000).

The GLM also showed a significant quadratic relationship between percentage of southern species and human population density, indicating a decline of percentage for high values of this variable (Table 1). Many southern species are associated with farmland (Suáres-Seoane *et al.* 2002), which could explain this relationship. On the other

hand, the relationship between human population density and species richness of the two southern and northern species differed, being quadratic for southern species, while linear for northern species (Table 1). Therefore, although avian species richness usually correlates with human population (e.g. Araújo 2003), this study shows differences in this relationship according the biogeographic type considered. This may have implications for avian conservation, as southern species seem to be more sensitive to high levels of human disturbance.

The percentage of southern species showed a significant quadratic relationship with altitude range, with a decline of percentage for highest values of altitude range (Table 1). The concave-up relationship between richness of northern species and altitude range (Table 1) is probably caused by the inclusion of different faunas in the 'northern species' category, with some species inhabiting mountains, while other dwelling in plains.

In sum, this study shows that ecological factors differentially correlate with richness of species of different biogeographic types, resulting in which factors such as temperature mediate differences in the composition of avian species throughout Iberian Peninsula. Similarly, other studies have shown that ecological factors differentially affect avian species richness according to the distribution range of species considered (Jetz & Rahbek 2002); species richness of birds of different foraging guilds is also affected by different environmental variables (Miller et al. 2003). The ecological determinants of avian species richness also vary geographically (Davies et al. 2007), which might be a consequence of different avian communities in which species richness is affected by different factors.

Lastly, temperature has increased in Spain in the last century (Hulme & Sheard 1999), and it is predicted to continue increasing in the coming years (IPCC 2001). According to the findings of this study, this will provoke a change in the composition of avian communities in the Mediterranean region by increasing the percentage of southern species. Apparently, northern species are more threatened by climatic change in the region, while in relatively cold zones southern species would be favoured by a rise of temperatures. However, our analysis provides evidence that in relatively hot zones southern species would be harmed as well. Thus, considerable increases of temperature may cause a decline in avian species richness in Mediterranean regions.

Comments by anonymous referees, Juan Manuel Pleguezuelos, David Nesbitt and Jouke Prop improved the manuscript.

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SAMENVATTING

Rijkdom van vogels wordt voor een groot deel door het klimaat bepaald. Deze studie onderzocht het verband tussen het aantal soorten vogels en het klimaat in Spanje op grond van blokken van 10 x 10 km. Hierbij werd onderscheid gemaakt tussen 'noordelijke' en 'zuidelijke' soorten. Het aantal noordelijke soorten per blok nam af naarmate de gemiddelde jaartemperatuur hoger was, terwijl zuidelijk soorten een omgekeerde trend lieten zien. In de warmste blokken nam ook het aantal zuidelijke soorten enigszins af. Het percentage zuidelijke soorten per blok nam daardoor sterk toe naarmate de temperatuur hoger was. Het percentage zuidelijke soorten nam bovendien toe met bevolkingsdichtheid, hoogteverschillen en neerslag per blok, maar het verband was tegengesteld in het hoogste bereik van deze parameters. (JP)

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Short notes

Appendix 1. Alphabetic list of bird species in Spain (scientific and common name), their biogeographic type according to Voous (1960) and that assigned by us. We assigned as 'northern' the types: Arctic, Northern Atlantic, European, Euroturquestan, Holarctic, Paleomontane, Palearctic, and Siberian-Canadian; as 'southern species' we assigned the types: Etiopic, Indoafrican, Mediterranean, Paleoxeric, Paleoxericmontane, and Turquestan-Mediterranean. The types Old World, Cosmopolitan, 'unknown', Mongoltibetan, and Sarmatic were disregarded, as they are amply distributed or their classification was unclear to us. Distribution maps of each group are available from the authors upon request.

Scientific name	Common name	Voous' type	Assigned type
Accipiter gentilis	Northern Goshawk	Holarctic	Northern
Accipiter nisus	Eurasian Sparrowhawk	Palearctic	Northern
Acrocephalus arundinaceus	Great Reed Warbler	Euroturquestan	Northern
Acrocephalus melanopogon	Moustached Warbler	Turquestan-Mediterranean	Southern
Acrocephalus schoenobaenus	Sedge Warbler	Euroturquestan	Northern
Acrocephalus scirpaceus	Reed Warbler	Euroturquestan	Northern
Actitis hypoleucos	Common Sandpiper	Holarctic	Northern
Aegithalos caudatus	Long-tailed Tit	Palearctic	Northern
Aegolius funereus	Tengmalm's Owl	Siberian-Canadian	Northern
Aegypius monachus	Monk Vulture	Mongoltibetan	Discarded
Alauda arvensis	Sky Lark	Palearctic	Northern
Alcedo atthis	Common Kingfisher	Old World	Discarded
Alectoris barbara	Barbary Partridge	Mediterranean	Southern
Alectoris rufa	Red-legged Partridge	Mediterranean	Southern
Amandava amandava	Avadavat	Unknown	Discarded
Anas acuta	Pintail	Palearctic	Northern
Anas clypeata	Northern Shoveler	Holarctic	Northern
Anas crecca	Common Teal	Holarctic	Northern
Anas platyrhynchos	Mallard	Holarctic	Northern
Anas querquedula	Garganey	Palearctic	Northern
Anas strepera	Gadwall	Holarctic	Northern
Anthus campestris	Tawny Pipit	Palearctic	Northern
Anthus pratensis	Meadow Pipit	European	Northern
Anthus spinoletta	Water Pipit	Palearctic	Northern
Anthus trivialis	Tree Pipit	Euroturquestan	Northern
Apus affinis	Little Swift	Unknown	Discarded
Apus apus	Common Swift	Palearctic	Northern
Apus caffer	White-rumped Swift	Etiopic	Southern
Apus melba	Alpine Swift	Indoafrican	Southern
Apus pallidus	Pallid Swift	Mediterranean	Southern
Aquila adalberti	Spanish Imperial Eagle	Palearctic	Northern
Aquila chrysaetos	Golden Eagle	Holarctic	Northern
Ardea cinerea	Grey Heron	Palearctic	Northern
Ardea purpurea	Purple Heron	Indoafrican	Southern
Ardeola ralloides	Squacco Heron	Etiopic	Southern
Asio flammeus	Short-eared Owl	Holarctic	Northern
Asio otus	Long-eared Owl	Holarctic	Northern
Athene noctua	Little Owl	Turquestan-Mediterranean	Southern
Aythya ferina	Common Pochard	Palearctic	Northern

Aythya fuligula Aythya nyroca Botaurus stellaris Bubo bubo Bubulcus ibis Bucanetes githagineus Burhinus oedicnemus Buteo buteo Calandrella brachydactyla Calandrella rufescens Calonectris diomedea Caprimulgus europaeus Caprimulgus ruficollis Carduelis cannabina Carduelis carduelis Carduelis chloris Carduelis spinus Cercotrichas galactotes Certhia brachydactyla Certhia familiaris Cettia cetti Charadrius alexandrinus Charadrius dubius Charadrius morinellus Chersophilus duponti Chlidonias hybrida Chlidonias niger Ciconia ciconia Ciconia nigra Cinclus cinclus Circaetus gallicus Circus aeruginosus Circus cyaneus Circus pygargus Cisticola juncidis Clamator glandarius Coccothraustes coccothraustes Columba livia Columba oenas Columba palumbus Coracias garrulus Corvus corax Corvus corone Corvus frugilegus Corvus monedula Coturnix coturnix Cuculus canorus

Tufted Duck Ferruginous Duck Great Bittern Eagle Owl Cattle Egret Trumpeter Finch Stone-curlew Common Buzzard Short-toed Lark Lesser Short-toed Lark Cory's Shearwater European Nightjar Red-necked Nightjar Linnet Goldfinch Greenfinch Siskin Rufous-tailed Scrub-robin Short-toed Treecreeper Eurasian Treecreeper Cetti's Warbler Kentish Plover Little Ringed Plover Dotterel Dupont's Lark Whiskered Tern Black Tern White Stork Black Stork Dipper Short-toed Eagle Marsh Harrier Hen Harrier Montagu's Harrier Zitting Cisticola Great Spotted Cuckoo Hawfinch Rock Dove Stock Dove Common Woodpigeon European Roller Common Raven Carrion Crow Rook Eurasian Jackdaw Common Ouail Common Cuckoo

Northern Palearctic Turquestan-Mediterranean Palearctic Palearctic Indoafrican Palearctic Turquestan-Mediterranean Palearctic Turquestan-Mediterranean Turquestan-Mediterranean Unknown Palearctic Mediterranean Euroturguestan Euroturquestan Euroturquestan Palearctic Mediterranean European Holarctic Turquestan-Mediterranean Cosmopolitan Palearctic Arctic Mediterranean Old World Holarctic Palearctic Palearctic Paleomontane Indoafrican Palearctic Holarctic Euroturquestan Indoafrican Etiopic Palearctic Turquestan-Mediterranean Euroturquestan Euroturquestan Euroturquestan Holarctic Palearctic Palearctic Palearctic Old World Discarded Palearctic Northern

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Cream-coloured Courser Azure-winged Magpie Mute Swan House Martin White-backed Woodpecker Great Spotted Woodpecker Middle Spotted Woodpecker Lesser Spotted Woodpecker Black Woodpecker Great White Egret Little Egret Black-shouldered Kite Corn Bunting **Rock Bunting Cirl Bunting** Yellowhammer Ortolan Bunting Reed Bunting Robin Common Waxbill Lesser Kestrel Peregrine Falcon Hobby Common Kestrel Pied Flycatcher Common Chaffinch Common Coot Red-knobbed Coot Crested Lark Thekla Lark Common Snipe Moorhen Eurasian Jay Collared Pratincole Lammergeier Griffon Vulture Oystercatcher Bonelli's Eagle Booted Eagle Black-winged Stilt Western Olivaceous Warbler Melodious Warbler Red-rumped Swallow Barn Swallow European Storm-petrel Little Bittern Wryneck

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Lagopus muta Lanius collurio Lanius meridionalis Lanius minor Lanius senator Larus argentatus Larus audouinii Larus fuscus Larus genei Larus melanocephalus Larus michahellis Larus ridibundus Limosa limosa Locustella luscinioides Locustella naevia Loxia curvirostra Lullula arborea Luscinia megarhynchos Luscinia svecica Marmaronetta angustirostris Melanocorypha calandra Merops apiaster Milvus migrans Milvus milvus Monticola saxatilis Monticola solitarius Montifringilla nivalis Motacilla alba Motacilla cinerea Motacilla flava Muscicapa striata Myiopsitta monachus Neophron percnopterus Netta rufina Numenius arquata Nycticorax nycticorax Oenanthe hispanica Oenanthe leucura Oenanthe oenanthe Oriolus oriolus Otis tarda Otus scops Oxyura jamaicensis Oxyura leucocephala Pandion haliaetus Panurus hiarmicus Parus ater

Ptarmigan Red-backed Shrike Southern Grey Shrike Lesser Grev Shrike Woodchat Shrike Herring Gull Audouin's Gull Black-backed Gull Slender-billed Gull Mediterranean Gull Yellow-legged Gull Black-headed Gull Black-tailed Godwit Savi's Warbler Grasshopper Warbler Common Crossbill Wood Lark Rufous Nightingale Bluethroat Marbled Duck Calandra Lark European Bee-eater Black Kite Red Kite Rock Thrush Blue Rock Thrush Snowfinch White Wagtail Grey Wagtail Yellow Wagtail Spotted Flycatcher Monk Parakeet Egyptian Vulture Red-crested Pochard Eurasian Curlew Night Heron Black-eared Wheatear Black Wheatear Northern Wheatear Golden Oriole Great Bustard Scops Owl Ruddy Duck White-headed Duck Osprey Bearded Tit Coal Tit

Arctic Palearctic Mediterranean Euroturquestan Mediterranean Holarctic Mediterranean Palearctic Sarmatic Sarmatic Holarctic Palearctic Palearctic Euroturguestan Euroturquestan Holarctic European European Palearctic Sarmatic Mediterranean Turquestan-Mediterranean Old World European Paleoxericmontane Paleoxericmontane Paleomontane Palearctic Palearctic Palearctic Euroturguestan Unknown Indoafrican Sarmatic Palearctic Cosmopolitan Mediterranean Mediterranean Palearctic Old World Palearctic Old World Unknown Sarmatic Cosmopolitan Palearctic Palearctic

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Parus caeruleus Parus cristatus Parus major Parus palustris Passer domesticus Passer hispaniolensis Passer montanus Perdix perdix Pernis apivorus Petronia petronia Phalacrocorax aristotelis Phalacrocorax carbo Phasianus colchicus Phoenicopterus roseus Phoenicurus ochruros Phoenicurus phoenicurus Phylloscopus bonelli Phylloscopus collybita Phylloscopus sibilatrix Phylloscopus trochilus Pica pica Picus viridis Platalea leucorodia Plegadis falcinellus Podiceps cristatus Podiceps nigricollis Porphyrio porphyrio Porzana parva Porzana porzana Porzana pusilla Prunella collaris Prunella modularis Psittacula krameri Pterocles alchata Pterocles orientalis Ptyonoprogne rupestris Pyrrhocorax graculus Pyrrhocorax pyrrhocorax Pyrrhula pyrrhula Rallus aquaticus Recurvirostra avosetta Regulus ignicapilla Regulus regulus Remiz pendulinus Riparia riparia Rissa tridactvla Saxicola rubetra

Blue Tit Crested Tit Great Tit Marsh Tit House Sparrow Spanish Sparrow Tree Sparrow Grey Partridge European Honey-buzzard Rock Sparrow Shag Great Cormorant Common Pheasant Greater Flamingo Black Redstart Common Redstart Bonelli's Warbler Common Chiffchaff Wood Warbler Willow Warbler Magpie Green Woodpecker Eurasian Spoonbill Glossy Ibis Great Crested Grebe Black-necked Grebe Purple Swamp-hen Little Crake Spotted Crake Baillon's Crake Alpine Accentor Dunnock Rose-ringed Parakeet Pin-tailed Sandgrouse Black-bellied Sandgrouse Crag Martin Yellow-billed Chough Red-billed Chough Common Bullfinch Water Rail Avocet Firecrest Goldcrest Penduline Tit Sand Martin Kittiwake Whinchat

European European Palearctic Palearctic Palearctic Turquestan-Mediterranean Palearctic Euroturquestan European Paleoxeric Northern Atlantic Old World Paleoxeric Mediterranean Paleoxericmontane European European Palearctic European Palearctic Palearctic European Old World Old World Old World Old World Indoafrican Palearctic European Old World Paleomontane European Unknown Paleoxeric Paleoxeric Paleoxericmontane Paleomontane Paleomontane Palearctic Palearctic Turquestan-Mediterranean European European Palearctic Holarctic Arctic European

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Saxicola torquatus Scolopax rusticola Serinus citrinella Serinus serinus Sitta europaea Sterna albifrons Sterna bengalensis Sterna hirundo Sterna nilotica Sterna sandvicensis Streptopelia decaocto Streptopelia turtur Strix aluco Sturnus unicolor Sturnus vulgaris Sylvia atricapilla Sylvia borin Sylvia cantillans Sylvia communis Sylvia conspicillata Sylvia hortensis Sylvia melanocephala Sylvia undata Tachybaptus ruficollis Tadorna tadorna Tetrao urogallus Tetrax tetrax Tichodroma muraria Tringa totanus Troglodytes troglodytes Turdus merula Turdus philomelos Turdus torquatus Turdus viscivorus Tyto alba Upupa epops Uria aalge Vanellus vanellus

Common Stonechat Woodcock Citril Finch European Serin European Nuthatch Little Tern Lesser Crested Tern Common Tern Gull-billed Tern Sandwich Tern Eurasian Collared Dove European Turtle Dove Tawny Owl Spotless Starling Common Starling Blackcap Garden Warbler Subalpine Warbler Common Whitethroat Spectacled Warbler Western Orphean Warbler Sardinian Warbler Dartford Warbler Little Grebe Common Shelduck Capercaillie Little Bustard Wallcreeper Common Redshank Wren Blackbird Song Thrush Ring Ouzel Mistle Thrush Barn Owl Hoopoe Common Guillemot Northern Lapwing

Palearctic Palearctic Paleomontane Mediterranean Palearctic Cosmopolitan Unknown Holarctic Cosmopolitan Cosmopolitan Indoafrican Euroturguestan Palearctic Mediterranean Euroturquestan European European Mediterranean Euroturquestan Mediterranean Mediterranean Turquestan-Mediterranean Mediterranean Old World Sarmatic Palearctic Paleoxeric Paleomontane Palearctic Holarctic Palearctic European Paleomontane Euroturquestan Cosmopolitan Old World Holarctic Palearctic

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