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# Towards inclusion of genetic diversity measures into IUCN assessments: a case study on birds

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## Abstract

*Towards inclusion of genetic diversity measures into IUCN assessments: a case study on birds.* The IUCN Red List categorizes species based on their geographical distribution and population size. However, attributes such as genetic information are not yet considered. We compiled information on genetic diversity ( $H_E$ ,  $H_O$ ) and inbreeding coefficient ( $f$ ) along with their ecological attributes (IUCN category, migratory habit, forest dependence and habitat type) from a literature survey to assess whether bird species categorized as being of highest conservation concern display the lowest genetic diversity. We used generalized linear mixed models (GLMM) to test whether avian species with less inclusive characteristics (e.g., taxa with small geographical distributions or low dispersal capability) display lower genetic diversity than those classified as Least Concern (LC). We used phylogenetic generalized least squares (pGLS) to account for phylogenetic independence of predictor variables and to verify robustness of GLMMs (generalized linear mixed models). In general, GLMM revealed more significant relationships among ecological attributes and genetic diversity patterns. After accounting for phylogenetic independence, the highest average heterozygosity values were observed in species falling under the LC category; non–migratory birds showed lower  $H_O$  and  $H_E$  average values than migratory birds, while non–forest birds showed lower heterozygosity than forest birds. Hence, we corroborate our hypothesis that genetic diversity of birds is lower in species of high conservation concern. We hope our results promote further studies on genetic diversity of bird populations. Lastly, we propose the incorporation of genetic data as metrics in the assessment of bird conservation status.

Key words: International Union for Conservation of Nature, Red List, Expected heterozygosity, Observed heterozygosity, Inbreeding coefficient

## Resumen

*Lograr la inclusión de las medidas de diversidad genética en las evaluaciones de la Unión Internacional para la Conservación de la Naturaleza: un estudio monográfico sobre aves.* La Lista Roja de la Unión Internacional para la Conservación de la Naturaleza (IUCN) clasifica las especies según su distribución geográfica y el tamaño de población. Sin embargo, todavía no se tienen en cuenta algunos aspectos como la información genética. A fin de evaluar si las especies de aves clasificadas como de máximo interés para la conservación son las que presentan la menor diversidad genética, en este estudio compilamos información sobre la diversidad genética ( $H_E$ ,  $H_O$ ) y el coeficiente de endogamia ( $f$ ), junto con sus características ecológicas (categoría de la UICN, hábitos migratorios, dependencia de los bosques y tipo de hábitat) a partir de un estudio de las publicaciones científicas. Utilizamos modelos mixtos lineales generalizados (GLMM) para determinar si las especies de aves con menos características inclusivas (por ejemplo, los taxones con una distribución geográfica reducida o con escasa capacidad de dispersión) presentan menor diversidad genética que las clasificadas como de Preocupación Menor. Utilizamos mínimos cuadrados generalizados filogenéticos para representar la independencia filogenética de las variables predictivas y para comprobar la robustez de los modelos mixtos lineales generalizados. En general, los modelos mixtos lineales generalizados (pGLS) revelaron la existencia de relaciones más significativas entre las características ecológicas y los patrones de diversidad genética. Al tener en cuenta la independencia filogenética, los valores máximos de heterocigosidad media se obser-

varon en especies de la categoría Preocupación Menor; las aves no migratorias mostraron valores medios de  $H_O$  y  $H_E$  más bajos que los de las aves migratorias, mientras que las aves no forestales mostraron una heterocigosidad inferior a la de las aves forestales. Por consiguiente, corroboramos nuestra hipótesis de que la diversidad genética de las aves es inferior en especies de gran interés para la conservación. Esperamos que nuestros resultados promuevan nuevos estudios sobre la diversidad genética de las poblaciones de aves. Por último, proponemos que se incorporen datos genéticos como parámetros en la evaluación de la situación de la conservación de las aves.

Palabras clave: Unión Internacional para la Conservación de la Naturaleza, Lista Roja, Heterocigosidad esperada, Heterocigosidad observada, Coeficiente de endogamia

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## Introduction

The IUCN Red Lists of threatened species, hereafter Red Lists, is the source of best available information on the global conservation status of species worldwide, providing quantitative measures of extinction risks (Lamoreux et al., 2003) and associated drivers (Baillie et al., 2004). Red Lists are an important tool not only to prioritize species conservation and identification of key biodiversity areas, but also to guide conservation responses, provide support for planning or implementing biodiversity projects, and help understand potential impacts on biodiversity (Bennun et al., 2018). In this sense, Red List indicators bear the potential to quantify possible anthropogenic threats to species (e.g., Wraith and Pickering, 2018), and to strategically connect science and politics (Do et al., 2018; Rabaud et al., 2018).

Once species are identified as being at risk in the Red Lists, it might be easier to induce willingness-to-pay for nature conservation in the broader public (Tisdell et al., 2007; Jin et al., 2018). Threatened species are typically prioritized in conservation policies because of the risk of their vanishing even before we can describe their characteristics, or before we know them as important parts of ecosystems. However, non-threatened species should also receive attention, as population-level analyses may reveal the local influence of anthropogenic changes, such as habitat loss and/or fragmentation. Such changes can increase selection pressures and culminate in genetic erosion, thereby endangering population persistence in the longer term (Bijlsma and Loeschcke, 2012).

Assigning species to a given threat category is based on five data-driven criteria concerning: i) population size, ii) population fragmentation, iii) observed or projected declines in abundance, iv) geographic range size in combination with fragmentation, and v) a quantitative analysis of extinction probability (IUCN, 2001). However, there is still an important aspect of biodiversity that is largely ignored in conservation assessments of species: genetic diversity. Despite its importance for maintaining biological distinctiveness and evolutionary processes, measures of genetic diversity such as number of alleles, number of haplotypes and heterozygosity are not explicitly considered in the Red Lists. This is somewhat puzzling since there is consensus that conservation of endangered species requires deep knowledge of metapopulation dynamics and structure, which involves determining the degree of genetic diversity within and between populations.

Variability estimated using molecular markers not only helps to distinguish genetically distinct populations that may be vulnerable to environmental changes (e.g., Lee and Mitchell-Olds, 2011; Hansen et al., 2012; Limborg et al., 2012; Munday et al., 2013; Razgour et al., 2018) but also infers phylogenetic relationships between individuals both within and between species, reconstructing genealogies and gathering information on inbreeding rates (e.g., Zollinger et al., 2012; McCormack et al., 2013; Lyu et al., 2018). The current use of microsatellite markers in biodiversity conservation studies is particularly useful to address

issues related to the conservation genetics of various bird species (e.g., Moura et al., 2017; Houston et al., 2018; Moussy et al., 2018; Stojanovic et al., 2018). Conservation Genetics has been defined as the discipline that applies genetic concepts and tools, including molecular markers, to small populations to reduce their risk of extinction (Frankham et al., 2002; Allendorf et al., 2012). Among its many applications, it allows to detect potential bottlenecks, measure gene flow and hybridization between populations, assess paternity, assign individuals to their population of origin, and infer population structure (e.g., Contina et al., 2018; Coster et al., 2018; Haworth et al., 2018; Kangas et al., 2018).

Birds are often used as bioindicators for various reasons (Furness et al., 1993; Herrera-Dueñas et al., 2014; Padoa-Schioppa et al., 2006; Silva et al., 2018; Souto et al., 2018), including the fact that their populations are heavily affected by air pollutants and pesticides. This has put many bird populations at risk, increasing the need for studies addressing loss of genetic diversity in metapopulations. Spielman et al. (2004) compared the heterozygosity ( $H_e$ ) of species categorized as threatened vs non-threatened taxonomically related species and found that, on average,  $H_e$  was 35% lower in threatened species. Similarly, Evans and Sheldon (2008) used Phylogenetic Independent Contrast (Felsenstein, 1985) to correlate heterozygosity with the increased extinction risk, showing that genetic diversity is relatively poor in the threatened bird species category.

Here we chose to use a more robust statistical approach. Following Ballesteros-Mejia et al. (2016), we fitted GLMMs to test the influence of different ecological attributes and extinction risk on estimates of genetic diversity. GLMMs combines desirable properties of two statistical frameworks, namely linear mixed models, incorporating random effects, and GLM, which handles non-normal data (Bolker et al., 2009). Since phylogeny is known to influence ecological and morphological characteristics (Harvey and Pagel, 1991; Bennett and Owens, 2002), we used generalized least squares (pGLS) to account for phylogenetic relationships and verify the robustness of the results found by significant GLMMs. All species in a monophyletic group share a common ancestor and tend to resemble each other more than those randomly chosen across a phylogenetic tree. In light of their phylogenetic non-independence, the former cannot be considered as independent data points in statistical analyses (Garland et al., 1992)

We addressed the relationship between genetic diversity and conservation status and tested the effect of ecological attributes on patterns of genetic diversity based on data from a literature survey. Specifically, we used GLMM to test the effect of migratory habits (migratory or non-migratory), forest dependence (high, medium or low), type of habitat (terrestrial vs non-restricted to it), and extinction risk (as classified in the IUCN Red List) on the patterns of genetic diversity ( $H_o$ , observed heterozygosity;  $H_e$ , expected heterozygosity;  $f$ , inbreeding coefficient). Additionally, we fitted Phylogenetic Least Squares (pGLS) to

account for phylogenetic non-independence as well as to verify the robustness of GLMM predictions. Most taxa are adversely affected by genetic factors before being driven to extinction (Spielman et al., 2004), but since processes that compromise genetic diversity do not affect all bird species equally, habitat specialization may be a predictor of the demographic and genetic consequences of fragmentation (Khimoun et al., 2016). Thus, it is likely that species classified as endangered or critically endangered exhibit lower  $H_O/H_E$  and higher  $f$  values. Therefore, we assessed whether the genetic diversity in birds based on microsatellite data available in the literature can be used as a proxy to define their risk category and inform conservation policies.

## Material and methods

### Obtaining bird genetic data and ecological attributes

We conducted a survey of studies on avian population genetic based on microsatellite data. We used the Web of Science (<http://www.isiknowledge.com>) database with the following combinations of keywords: [birds\* AND microsatellite\* AND genetic diversity\*], [birds\* AND SSR\* AND genetic diversity\*], [bird\* AND microsatellite\* AND genetic diversity\*] and [bird\* AND SSR\* AND genetic diversity\*]. We excluded studies that used less than four microsatellite loci.

From the publications, we retrieved the following data: (i) title; (ii) year of publication; (iii) journal; (iv) study species; (v) number of individuals; (vi) number of loci; and (vii) mean values of genetic diversity;  $H_E$ ,  $H_O$  and  $f$ . In several studies,  $f$  was not estimated. Thus, we estimate it using the equation:

$$f = 1 - (H_O / H_E).$$

We used the database of the IUCN Red List of Threatened Species (<http://www.iucnredlist.org>) to extract information about the conservation status of target species. We considered the following categories: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct in the Wild (EW) and Extinct (EX) as of December 2015 to July 2016.

The Birdlife International database (<http://www.birdlife.org/datazone/species>) contains data on avian species worldwide, and we used it to obtain the following information for each bird species in the selected studies: (i) migratory habit (migratory or low dependence or not occurring in forests) and (iii) habitat type (terrestrial or other). This information, as well as the conservation status of the species (IUCN Category), was considered here as the ecological attributes.

### Data analysis

To evaluate the temporal trend in the number of articles published annually, and to correct the effect of the general increase in the number of articles over

time, we use the following equation (Eq. 1):

$$\frac{\text{Number of articles in year (x)}}{\text{Total number of articles in the Web of Science in year (x)}}$$

we initially used analysis of variance and  $t$ -student to explore genetic variation among populations. We included bird populations of the same species analysed with the same microsatellite markers (table 1) to test whether genetic parameters  $H_O$ ,  $H_E$  and  $f$  varied significantly between population pairs.

We fitted generalized linear mixed models (GLMMs) to investigate the effects of ecological attributes and conservation status on genetic diversity. IUCN category and forest dependence were treated as multistate categorical variables, whereas habitat type and migratory habit were treated as binary variables. Models were fitted for each genetic parameter ( $H_O$ ,  $H_E$  and  $f$ ) as response variables. Ecological attributes were fitted as fixed factors, and species identity was considered as a random factor because multiple variables were measured per species. Analyses were performed using MCMCglmm package (Hadfield, 2010) implemented in R version 3.4.4 (R Core Team, 2018).

To account for phylogenetic non-independence of the effects of ecological attributes on genetic diversity, we first obtained the reference phylogenetic hypothesis of the species included in each analysis. We gathered ten thousand phylogenies sampled from a pseudo-posterior distribution (Jetz et al., 2012) deposited in BirdTree.org website (<https://birdtree.org/>). We made a consensus tree using Tree annotator 1.8.2 (Drummond et al., 2012) and dropped all species without data using the 'drop.tip' function in the package 'ape' (Paradis, 2004) implemented in R version 3.4.4.

We then tested whether the studied ecological attributes showed a phylogenetic signal to account for phylogenetic relationships. We performed Abouheif's proximity test of serial independence (Abouheif, 1999; Pavoinea et al., 2008) using the function 'abouheif.moran' from the R-package 'adephylo' (Jombart et al., 2010). We then fitted Phylogenetic Generalized Least Square Models (pGLS; Martins and Hansen, 1997) to the genetic parameters to verify whether GLMM models had resulted in robust inferences and hence the pattern persisted when accounting for phylogenetic relationships. We tested the solitary effect of each ecological attribute, as well as the effect of combining all of these in a complete model, on the genetic diversity parameters. When the same molecular marker was applied more than once to study a species the mean of the genetic parameters was used. The analyses were carried out using the package 'caper' (Orme, 2013) of the R.

Finally, Pearson's correlation analysis was performed to assess the effect of the number of individuals and the number of loci on the genetic diversity values; the number of loci and individuals were log-transformed (base 10) to reduce the discrepancies between values. Statistical tests were performed using the R statistical package.

Table 1. Species investigated in multiple studies on different populations but using the same microsatellite panel.

Tabla 1. Especies objeto de múltiples estudios sobre poblaciones distintas, pero utilizando el mismo grupo de microsatélites.

Species	Microsatellite loci
<i>Aquila chrysaetos</i>	Aa15, Aa26, Aa27, Aa36, Aa39 and Aa43 (Martínez-Cruz et al., 2002)
<i>Bubo bubo</i>	B101, B111, B126 and B11 (Isaksson and Tegelstrom, 2002)
<i>Cyanistes caeruleus</i>	Pca3, Pca4, Pca7, Pca8 and Pca9 (Dawson et al., 2000)
	POCC1 and POCC6 (Bensch et al., 1997)
	PATMP2-43 (Otter et al., 1998)
	Ase18 (Richardson et al., 2000)
	Pdoμ5 (Griffith et al., 1999)
	Mcyμ (Double et al., 1998)
	CcaTgu7, CcaTgu8, CcaTgu11, CcaTgu14, CcaTgu15, CcaTgu19, CcaTgu25 and CcaTgu28 (Olano-Marin et al., 2010)
	TG05-046, TG05-053, TG13-013 (Dawson et al., 2010)
	Tgu07 (Slate et al., 2007)
<i>Nipponia nippon</i>	NnNF5 (Ji et al., 2004)
<i>Passer domesticus</i>	Pdoμ1 and Pdoμ4 (Neumann and Wetton, 1996)
	Pdoμ5 (Griffith et al., 2007)
	Pdoμ10 (Segelbacher et al., 2000)
<i>Tetrao urogallus</i>	TUD1, TUD3, TUD5 and BG15 (Segelbacher et al., 2000, Piertney and Høglund, 2001)

Because of the cumulative effect of domestication and subsequent artificial selection, *Gallus gallus* was excluded from GLMM and pGLS analysis.

## Results

### Scientometrics

The search revealed 359 published papers that met the criteria entered. They were published across 98 different journals between 1998 and 2015. Five of these journals (i.e., *Molecular Ecology Resources*, *Conservation Genetics Resources*, *Conservation Genetics*, *Molecular Ecology* and *PLOS One*) hosted 51.81% of the articles; 35 journals published between four and eight articles, and the remaining 58 journals published only one article.

The analysis of annual number of publications per journal revealed that 2014 was the year with the highest number of publications; 13 of the analysed journals published studies containing genetic diversity data of bird species. The second highest mean annual publication rate occurred in 2013 and in 2015; in each of these years, nine different journals published articles that analysed the genetic diversity of birds using microsatellite markers.

After correcting for the general trend with equation 1, the number of published papers with analyses of bird genetic diversity increased significantly over time ( $r = 0.740$ ;  $p \leq 0.01$ ), especially between 2013 and 2014.

Values of  $H_E$ ,  $H_O$  and  $f$  were reported for 297 species (table 1s), 63 of which were represented more than once in the data set. *Gallus gallus* (7.80% of the total species) was the most studied species followed by *Passer domesticus* (2.40%), *Aquila chrysaetos* (1.20%), and *Tetrao urogallus* (1.20%). The total number of studied species was distributed among 94 families (table 1s) and 27 orders. The most highly represented orders were Passeriformes (44.10%), Charadriiformes (8.10%) and Galliformes (6.10%) (fig. 1A).

Most of the studied species were predominantly terrestrial (54.20%) and exhibited no migratory behaviour (62.30%). The analysis of species classification according to forest dependence showed that most species did not usually occur in forests (42.10%), followed by species with low (23.20%), medium (18.20%) and high (16.50%) forest dependence. Lastly, regarding classification according to IUCN category, the analyses showed that most of the studied bird species were categorized as LC (69.40%) (fig. 1B).

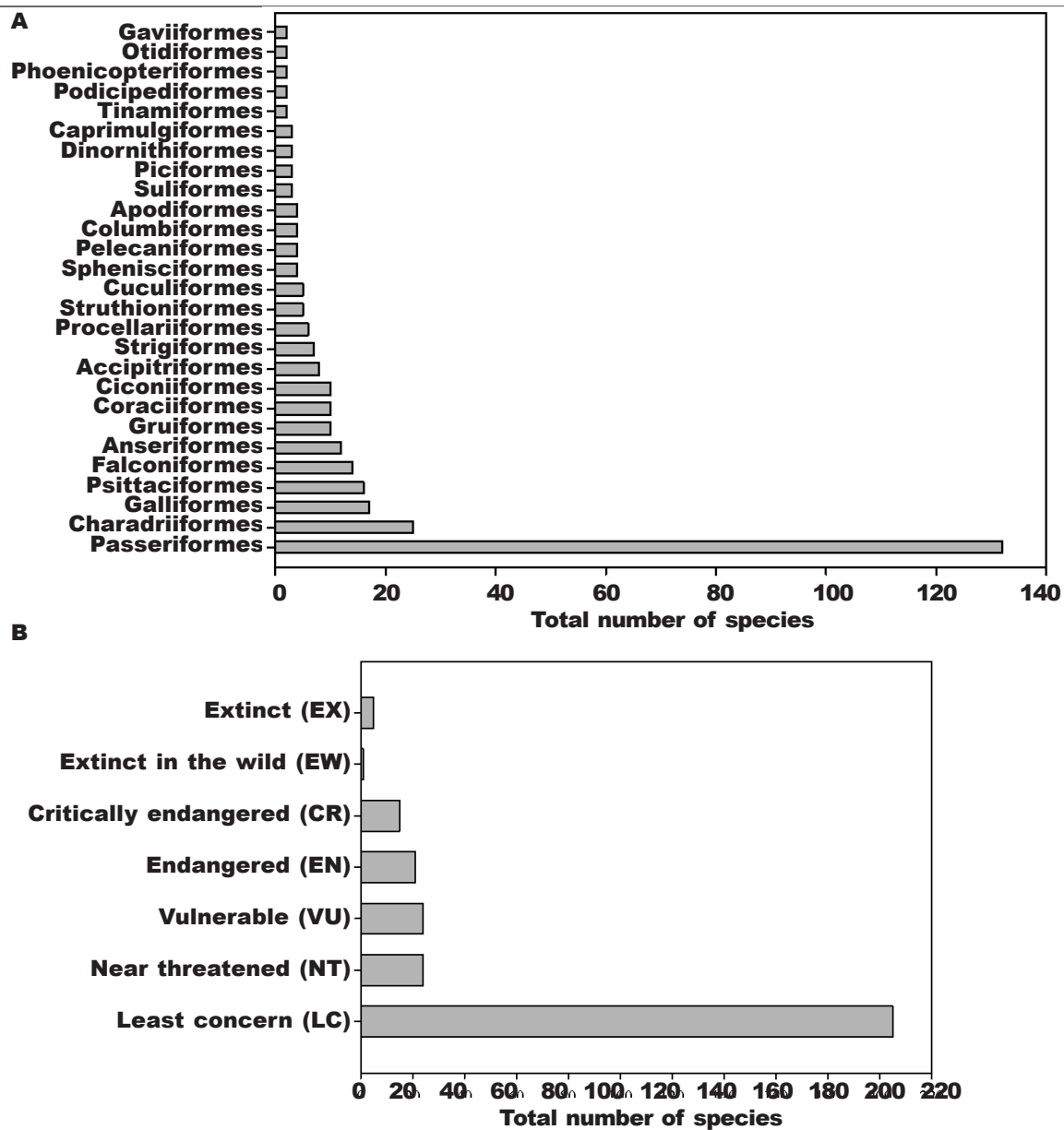


Fig. 1. A, bird orders evaluated in terms of articles addressing genetic diversity estimates and published between 1998 and 2015; B, classification of bird species that were the subject of articles published between 1998 and 2015 according to the IUCN category.

Fig. 1. A, órdenes de aves que se evaluaron en cuanto a los artículos en los que se abordaban las estimaciones de la diversidad genética y que se publicaron entre 1998 y 2015; B, clasificación de las especies de aves que fueron objeto de artículos publicados entre 1998 y 2015, según la categoría de la UICN.

#### Genetic diversity of bird populations

We compared the genetic diversity data obtained using the same microsatellite markers for three *Aquila chrysaetos* populations, two in Scotland and one in Slovakia, and found similar diversity patterns.  $H_o$  values (0.52, 0.50 and 0.40, respec-

tively) were always lower than  $H_e$  values (0.56, 0.54 and 0.43), whereas the  $f$  values were 0.34, 0.06 and 0.09 (fig. 2A). For the *Bubo bubo*, we compared data from four Spanish populations and one Norwegian population, and the highest average  $H_o$  was observed in the latter (0.63), while the Spanish populations presented values of 0.4, 0.48,

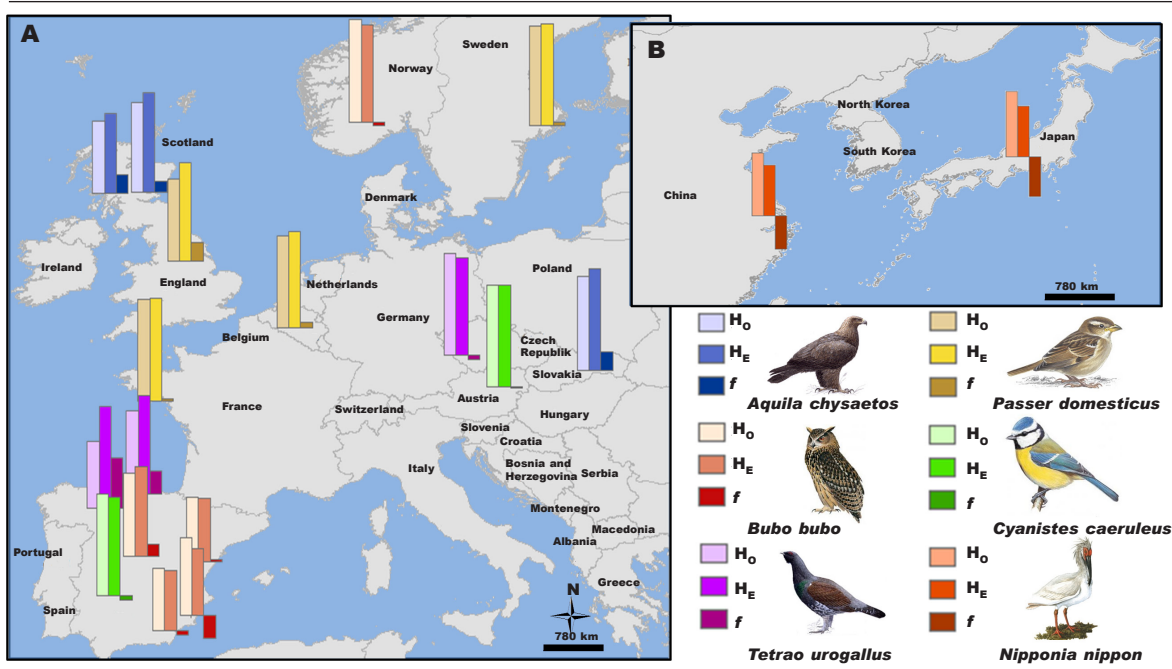


Fig. 2. Comparative map of the observed heterozygosity ( $H_O$ ), expected heterozygosity ( $H_E$ ) and inbreeding coefficient ( $f$ ) values for different bird populations in different countries of Europe (A), China and Japan (B). Data for the same species were obtained using the same microsatellite loci. In the legend, the metrics with their colors refer to the species indicated on the right.

Fig. 2. Mapa comparativo de los valores de heterocigosidad observada ( $H_O$ ), heterocigosidad esperada ( $H_E$ ) y coeficiente de endogamia ( $f$ ) para distintas poblaciones de aves en diferentes países de Europa (A), China y el Japón (B). Los datos de las mismas especies se obtuvieron utilizando los mismos loci de microsatélites. En la leyenda, los parámetros con sus colores se refieren a las especies indicadas a la derecha.

0.38 and 0.51. The same pattern was observed for the mean  $H_E$  with values of 0.6 in the Norwegian population and 0.39, 0.41, 0.37 and 0.55 for the Spanish populations. The  $f$  value was  $-0.02$  for the Norwegian population and 0.01, 0.07,  $-0.14$  and  $-0.03$  for the Spanish populations,

For *Tetrao urogallus*, we compared the average diversity values for three populations, one from the Czech Republic and two from Spain. The highest average  $H_O$  was observed in the Czech population (0.67), while the Spanish populations showed  $H_O$  values of 0.55 and 0.44. We observed the opposite pattern for the average  $H_E$  and  $f$  values, with the lowest occurring in the Czech population (0.64 and  $-0.03$ ) followed by 0.66 and 0.68 for  $H_E$  and 0.33 and 0.15 for  $f$  in the Spanish populations. When comparing the Spanish and Czech populations we found significant differences for  $H_O$  ( $t = 8.06$ ,  $p < 0.0001$ ) and  $H_E$  ( $t = 19.81$ ,  $p < 0.0001$ ) according to the  $t$ -test.

Significant differences were found between the average  $H_O$  ( $F = 53.15$ ,  $p < 0.001$ ),  $H_E$  ( $F = 11.57$ ,  $p = 0.002$ ) and  $f$  ( $F = 86.70$ ,  $p < 0.001$ ) values of four *Passer domesticus* populations from Scandina-

via, Belgium, France and England. The average  $H_O$  was highest in the French population (0.87) followed by Scandinavian (0.85), Belgian (0.79) and English populations (0.71). The highest average  $H_E$  values were found in the populations from France and Scandinavia (0.88 in both) followed by those from Britain (0.85) and Belgium (0.83). The  $f$  value was positive for all populations, and the lowest value was found in the population with the highest heterozygosity, the French population (0.01), followed by the Scandinavian (0.02), Belgian (0.05) and English populations (0.16).

The  $t$ -test also revealed a significant difference between the mean  $H_O$  ( $t = 11.49$ ,  $p < 0.0001$ ) and  $H_E$  ( $t = 11.84$ ,  $p < 0.0001$ ) values found in two populations of *Cyanistes caeruleus*, one Spanish ( $H_O = 0.80$  and  $H_E = 0.79$ ) and one Austrian ( $H_O = 0.78$  and  $H_E = 0.76$ ). The averages for  $f$ , however, were similar for the two populations with 0.03 in the Spanish population and  $-0.004$  in the Austrian population. However, for *Nipponia nippon*, we found similar values when comparing a Japanese and a Chinese population: 0.48 and 0.46 for  $H_O$ , 0.37 and 0.37 for  $H_E$ , and 0.83 and 0.88 for  $f$ , respectively (fig. 2B).



Table 2. Mean values of genetic diversity of microsatellite loci and ecological attributes of avian species: N, number of species analyzed;  $H_O$ , observed heterozygosity;  $H_E$ , expected heterozygosity;  $f$ , inbreeding coefficient.

*Tabla 2. Valores medios de la diversidad genética de los loci de microsatélites y características ecológicas de las especies de aves. N, número de especies analizadas;  $H_O$ , heterocigosidad observada;  $H_E$ , heterocigosidad esperada;  $f$ , coeficiente de endogamia.*

Ecological attribute	N	$H_O$	$H_E$	$f$
<b>IUCN category</b>				
LC	201	0.59 ± 0.16	0.63 ± 0.16	0.07 ± 0.10
NT	22	0.53 ± 0.17	0.54 ± 0.18	0.03 ± 0.20
VU	25	0.52 ± 0.13	0.54 ± 0.14	0.04 ± 0.10
EN	21	0.52 ± 0.19	0.54 ± 0.20	0.04 ± 0.07
CR	15	0.53 ± 0.12	0.55 ± 0.11	0.03 ± 0.07
EW	1	0.41 ± 0.00	0.40 ± 0.00	-0.02 ± 0.00
<b>Migratory habit</b>				
Migratory	109	0.59 ± 0.16	0.62 ± 0.16	0.06 ± 0.11
Non-migratory	176	0.56 ± 0.16	0.60 ± 0.16	0.06 ± 0.11
<b>Forest dependence</b>				
High	45	0.58 ± 0.16	0.61 ± 0.15	0.06 ± 0.12
Medium	52	0.60 ± 0.14	0.64 ± 0.14	0.05 ± 0.09
Low	68	0.56 ± 0.18	0.60 ± 0.18	0.06 ± 0.10
Not occurring in forests	120	0.56 ± 0.16	0.60 ± 0.16	0.06 ± 0.12
<b>Habitat type</b>				
Terrestrial	153	0.57 ± 0.17	0.60 ± 0.17	0.05 ± 0.11
Not restricted to the terrestrial environment	132	0.57 ± 0.15	0.61 ± 0.16	0.07 ± 0.11

#### Genetic diversity, ecological attributes and conservation status

In general, we observed a large variation in the values of genetic diversity sampled, with  $H_O$ ,  $H_E$  and  $f$  varying between 0.04 and 0.93, 0.08 and 0.91 and -0.61 and 0.64, respectively. When we evaluated the genetic diversity within orders, the lowest mean  $H_O$  and  $H_E$  values were observed in Otidiformes ( $H_O = 0.44$  and  $H_E = 0.49$ ), Accipitriformes ( $H_O = 0.49$  and  $H_E = 0.50$ ), Gaviiformes ( $H_O = 0.45$  and  $H_E = 0.46$ ) and Ciconiiformes ( $H_O = 0.44$  and  $H_E = 0.47$ ).

Regarding the conservation status, we found variation in the values of genetic diversity among the IUCN categories (table 2). The LC category showed the highest genetic diversity values ( $H_O = 0.59$  and  $H_E = 0.63$ ). However, values decreased substantially across the categories of greater concern, with 0.5 and 0.54 being the averages observed for  $H_O$  and  $H_E$  of all other categories combined.

Birds with migratory habits presented higher heterozygosity values ( $H_O = 0.59$  and  $H_E = 0.62$ ) than those observed in non-migratory birds ( $H_O = 0.56$  and  $H_E = 0.60$ ), but no significant variations were found in

terms of  $f$  ( $f = 0.06$  in both). Species that do not occur in forest environments or that have low dependence on forest fragments displayed the lowest averages of heterozygosity ( $H_O = 0.56$  and  $H_E = 0.60$  in both). In contrast, terrestrial birds or birds not restricted to terrestrial environments did not show differences in terms of heterozygosity ( $H_O = 0.57$  in both  $H_E = 0.60$  and  $H_E = 0.61$ , respectively), although  $f$  was slightly higher for birds not restricted to terrestrial environments (table 2).

When we accounted for phylogenetic relationships in the observed genetic patterns, the serial independence test showed that with the exception of the categorical variable IUCN category, all other attributes presented a significant phylogenetic signal (table 3). Phylogenetic generalized least squares performed on a complete model, with all variables combined, showed a significant relation between IUCN category and  $H_O$ ,  $H_E$  and  $f$  values. We observed the highest  $H_O$  values in the LC category ( $-0.021 \pm 0.028$ ) and the lowest for the EW category ( $-0.185 \pm 0.089$ ), which is the one of highest concern. The same pattern was observed for  $H_E$  and  $f$ : the highest  $H_E$  and  $f$  values were also observed in the LC category ( $0.079 \pm 0.027$

and  $0.172 \pm 0.023$ , respectively) and the lowest in the EW category ( $-0.194 \pm 0.086$  and  $-0.009 \pm 0.074$ ). The migratory habit significantly affected  $H_E$  and  $f$  values, equal to  $0.042 \pm 0.019$  and  $0.058 \pm 0.016$  for migratory and non-migratory birds, respectively. The forest dependence significantly affected only  $f$ , that turned out to be highest in birds with low dependence on forests ( $-0.021 \pm 0.029$ ) and lowest for species with medium forest dependence ( $-0.084 \pm 0.030$ ). Regarding habitat type, this significantly affected  $H_O$ ,  $H_E$  and  $f$ , with the highest values observed in terrestrial species ( $-0.059 \pm 0.023$ ;  $-0.079 \pm 0.022$  and  $-0.041 \pm 0.019$ ) (table 4).

When we evaluated the isolated effect of each variable, similar results were found for IUCN category and  $H_O$ ,  $H_E$  and  $f$ , so that species of the category EW had significantly lower values of  $H_O$  and  $H_E$  (tables 2, 5), but the results differed for the other categorical variables. Migratory habit, forest dependence and type of habitat affected  $H_O$  and  $H_E$ . The pGLS confirmed the hypothesis that non-migratory species have lower diversity values. Likewise,  $H_E$  values may be affected in non-forest bird species. We also observed that species in terrestrial habitat showed lower levels of  $H_O$  and  $H_E$  (table 5).

A significant correlation was found between the number of loci used and the  $H_O$  ( $r = -0.183$ ;  $p \leq 0.01$ ) and  $H_E$  ( $r = -0.191$ ;  $p \leq 0.01$ ) estimates, but the correlations were negative (fig. 3). Conversely, no correlations were observed between the number of loci and  $f$  or between the number of individuals sampled and any estimate of genetic diversity.

## Discussion

### Scientometrics

Microsatellite markers were developed in the 1980s (Tautz and Renz, 1984) and have since become increasingly popular in avian research. The observed annual increase in the number of published articles using estimates of genetic diversity for birds confirms this popularity. It should be noted that the accuracy of these indices is subject to the availability of study individuals, and is therefore favoured by larger sample sizes, which explains why most studies (69.40%) were conducted with species in the Least Concern (LC) IUCN category. However, the IUCN system categorizes species as LC based on attributes such as a wide geographical distribution and large population size (IUCN, 2015), but global conservation status may not be representative of local trends, as indicated by national Red Lists. Garcia and Marini (2006) evaluated 494 threatened or near-threatened taxa of Brazilian birds finding that the classifications of only 26% of these taxa were consistent with the global status, and revealing discrepancies between regional and global classifications. Such differences decrease the efficiency at which the IUCN list can be applied to establish national-scale conservation actions (Rodríguez et al., 2000), so studies should be conducted to evaluate the genetic diversity of bird species while

Table 3. Phylogenetic signal of ecological attributes for bird species included in the analyses of genetic diversity and differentiation using Abouheif's proximity test of serial independence:  $H_O$ , observed heterozygosity;  $H_E$ , expected heterozygosity;  $f$ , inbreeding coefficient. (Significant values are denoted in bold.)

Tabla 3. Señal filogenética de las características ecológicas de las especies de aves incluidas en los análisis de la diversidad genética y la diferenciación utilizando la prueba de proximidad de la independencia serial, elaborada por Abouheif:  $H_O$ , heterocigosidad observada;  $H_E$ , heterocigosidad esperada;  $f$ , coeficiente de endogamia. (Los valores significativos se indican en negrita.)

Ecological attribute	Observed Moran's I	p-value
IUCN category	-0.0457	0.9999
Migratory habit	0.0412	0.0010
Forest dependence	0.1519	0.0010
Habitat type	0.0590	0.0010

considering both state and national threat levels. In addition, the ability to perform studies involving estimates of genetic diversity is also apparently influenced by the behavioural traits of the study species. Indeed, such traits may either hinder or facilitate the sampling, which may explain why most studies have been performed on predominantly terrestrial (54.20%) and non-migratory (62.30%) species with low forest dependence (23.20%) or species for which sampling was not restricted to forest environments (42.10%).

Most bird species in the studies (44.10%) belonged to the order Passeriformes (passerines), the largest and most diverse avian order. The main Passeriformes lineages diversified on all continents and now occupy almost all terrestrial ecosystems (Barker et al., 2004), and they include approximately 5,700 species that account for nearly 60% of all living birds. Passeriformes have been the focus of many ecological, behavioural, anatomical and evolutionary studies because of their ubiquity and enormous diversity (Ericson et al., 2014), generally driven by the colonization of new biogeographical regions (Kennedy et al., 2017). This order encompasses domestic species such as *Poephila cincta* and *Serinus canaria* as well as to the globally distributed *Passer domesticus* (2.40%). The most predominant species in the literature was *Gallus gallus* (7.80%), which has a large number of lineages distributed across the globe and has been widely used as a model organism in biochemical, molecular (e.g., Piekarski et al., 2015; Guizard et al., 2016) and genetic studies such as those describing

Table 4. Phylogenetic generalized least squares for ecological attributes of bird species for each genetic parameter analysed. Data obtained considering the effect of the combination of all variables:  $H_O$ , observed heterozygosity;  $H_E$ , expected heterozygosity;  $f$ , inbreeding coefficient. T, T-value; P, P-value; C, coefficient  $\pm$  SE. (Significant values are denoted in bold)

Tabla 4. Mínimos cuadrados generalizados filogenéticos para las características ecológicas de las especies de aves para cada parámetro genético analizado. Datos obtenidos considerando el efecto de la combinación de todas las variables:  $H_O$ , heterocigosidad observada;  $H_E$ , heterocigosidad esperada;  $f$ , coeficiente de endogamia; T, valores T; P, valores P; C, coeficiente  $\pm$  EE. (Los valores significativos se indican en negrita).

Ecological attribute	$H_O$			$H_E$			$f$		
	Adj-R <sup>2</sup> = 0.0492			Adj-R <sup>2</sup> = 0.135			Adj-R <sup>2</sup> = 0.1942		
Parameter	C	T	P	C	T	P	C	T	P
IUCN category									
Intercept	<b>0.636 <math>\pm</math> 0.156</b>	<b>4.086</b>	<b>0.000</b>	<b>0.581 <math>\pm</math> 0.149</b>	<b>3.890</b>	<b>0.000</b>	-0.064 $\pm$ 0.128	-0.499	0.618
LC	-0.021 $\pm$ 0.028	-0.755	0.451	<b>0.079 <math>\pm</math> 0.027</b>	<b>2.886</b>	<b>0.004</b>	<b>0.172 <math>\pm</math> 0.023</b>	<b>7.354</b>	<b>0.000</b>
NT	-0.058 $\pm$ 0.044	-0.136	0.892	0.037 $\pm$ 0.042	0.890	0.374	<b>0.088 <math>\pm</math> 0.036</b>	<b>2.461</b>	<b>0.014</b>
VU	-0.058 $\pm$ 0.045	-1.277	0.202	0.018 $\pm$ 0.044	0.417	0.677	<b>0.137 <math>\pm</math> 0.037</b>	<b>3.670</b>	<b>0.000</b>
EN	-0.080 $\pm$ 0.042	-1.886	0.060	0.000 $\pm$ 0.041	-0.005	0.996	<b>0.137 <math>\pm</math> 0.035</b>	<b>3.929</b>	<b>0.000</b>
CR	-	-	-	-	-	-	-	-	-
EW	<b>-0.185 <math>\pm</math> 0.089</b>	<b>-2.064</b>	<b>0.039</b>	<b>-0.194 <math>\pm</math> 0.086</b>	<b>-2.256</b>	<b>0.025</b>	-0.009 $\pm$ 0.074	-0.128	0.899
Migratory habit									
Migratory	-	-	-	-	-	-	-	-	-
Non-migratory	-0.005 $\pm$ 0.019	-0.269	0.787	<b>0.042 <math>\pm</math> 0.019</b>	<b>2.222</b>	<b>0.027</b>	<b>0.058 <math>\pm</math> 0.016</b>	<b>3.639</b>	<b>0.000</b>
Forest dependence									
High	-	-	-	-	-	-	-	-	-
Medium	-0.001 $\pm$ 0.037	-0.006	0.994	-0.031 $\pm$ 0.035	-0.890	0.374	<b>-0.084 <math>\pm</math> 0.030</b>	<b>-2.792</b>	<b>0.006</b>
Low	-0.005 $\pm$ 0.035	-0.163	0.870	-0.015 $\pm$ 0.034	-0.456	0.649	-0.021 $\pm$ 0.029	-0.744	0.458
Not occurring in forests	0.034 $\pm$ 0.038	0.902	0.368	0.024 $\pm$ 0.037	0.652	0.515	-0.045 $\pm$ 0.031	-1.426	0.155
Habitat type									
Terrestrial	<b>-0.059 <math>\pm</math> 0.023</b>	<b>-2.572</b>	<b>0.011</b>	<b>-0.079 <math>\pm</math> 0.022</b>	<b>-3.561</b>	<b>0.000</b>	<b>-0.041 <math>\pm</math> 0.019</b>	<b>-2.149</b>	<b>0.032</b>
Not restricted to the terrestrial environment	-	-	-	-	-	-	-	-	-

the genetic diversity of populations based on variations at microsatellite loci (Rajkumar et al., 2008; Zanetti et al., 2011; Babar et al., 2012). The large number of studies in *Gallus gallus* with its wide distribution obviates the obvious influence of its economic interest on the studies. Likewise, since *Passer domesticus* is widely distributed with generally large population sizes, it has been used as a model to predict cases of treatment bias given that individuals in a population differ in their susceptibility to capture (Simons et al., 2015).

#### Genetic diversity of bird populations

The lack of significant differences between *Aquila chrysaetos* populations can be explained by the migratory nature of this species in Europe. It is categorized as LC in the European Red List with the expectation of increasing the size of local populations (European Red List, 2015). Native to mainland Europe and the Mediterranean, it currently occurs in the UK with a resident and most likely introduced population (Harrop et al., 2013). This would explain the limited differences



in the population-level patterns of diversity. Neither did we find significant differences between the mean genetic diversity values of *Bubo bubo*; populations that are declining in many parts of its range in Europe (Tucker and Heath, 1994) despite being categorized as LC in the European Red List. In general, studies evaluating the genetic diversity of European raptors are being encouraged as a strategy for the conservation of these birds (e.g., Martínez-Cruz, 2011).

Czech populations of *Tetrao urogallus* showed larger values of  $H_o$  and  $H_e$  than the Spanish populations. The distribution of this species extends across most of Europe, but its distribution in the Iberian Peninsula is restricted to northern Spain. Unlike other populations living in pure- or mixed-conifer forests, the local *Tetrao urogallus cantabricus* only inhabits purely deciduous forests, and this specificity has put the population at risk (Storch et al., 2006). A study examining the genetic differentiation between this and other European populations showed that the birds from Cantabria form a clade with low genetic variability that differs from all other populations (Rodríguez-Muñoz et al., 2007).

We also found differences between the average  $H_o$  and  $H_e$  values obtained for a Spanish population and an Austrian population of *Cyanistes caeruleus*, with the largest heterozygosity found in the Spanish population. This species is widely distributed throughout Europe and is native to both of the surveyed countries, but studies by Kvist et al. (1999, 2004), who analysed mitochondrial DNA sequences, proposed that regions in Europe were recolonized by this species from two different Pleistocene refugia after the last ice age through a colonization route from the Balkans to central and northern Europe as well as a route from the Iberian peninsula to the north and east. The differences we found between the mean genetic diversity values for the species in Spain and Austria can be explained by the possible isolation of the populations in Pleistocene refugia, which would allow different degrees of change in the populations. For *Nipponia nippon*, we found similar mean genetic diversity values between a Japanese and a Chinese population. The historical distribution of this species included the Russian Far East, China, and Japan, but it is now extinct throughout most of its range (IUCN category EN). Drastic reductions in populations of *Nipponia nippon* were caused by deforestation of nesting habitat, over-hunting and loss of wetlands as well as use of agrochemicals in rice fields, especially during the 1950s, which reduced the abundance and diversity of its preys (Li et al., 2009; Changqing, 2010). Overall, the observed genetic diversity was low in both populations, and the inbreeding coefficients were positive and high, reflecting the degree of risk to the populations of this species.

#### Genetic diversity, ecological attributes and conservation status

As expected, the non-independence of sister clades in ecological attributes and conservation status (i.e., related species tend to have more similar ecological attributes than expected and therefore also conser-

vation status) add a significant effect to the patterns of genetic diversity observed for birds. When the phylogenetic signal was taken into account, the pGLS confirmed that conservation status is reflected in the levels of genetic diversity sampled in birds; the lower the heterozygosity values the higher the risk of extinction. Consistently, the lowest averages of  $H_o$  and  $H_e$  were observed in birds of the EW category. Birds classified as threatened, possibly occurring with small and fragmented populations, tended to have lower heterozygosity. The risk of extinction is reportedly higher for small populations (e.g., Mace et al., 2008; Frankham, 2015) because they are more susceptible to genetic drift with accumulation of deleterious recessive alleles due to inbreeding (Hedrick and Garcia-Dorado, 2016), and loss of locally adapted traits (Frankham, 1995).

Non-migratory species showed the lowest levels of  $H_o$  and  $H_e$ , confirming our hypothesis. The dispersal ability through flight routes contributes significantly to the increase of gene flow in migratory species (Losos et al., 2013) and consequently decreases the population structure in this group of birds. Paradis et al. (1998) reported that migratory bird species disperse more than resident birds. Dispersal is a fundamental component of metapopulations, gene flow, and genetic structure (Neigel and Avise, 1993), and is dependent on phylogeny (Paradis et al., 1998). However, our results lead us to question whether the greater diversity observed in migratory species is not simply a sampling bias, since the dispersion of these species facilitates their sampling. Gilroy et al. (2016), however, observed that populations of migratory birds showed higher intra-population variability (migratory diversity) and considered that they tended to decline less because they are more resistant to environmental changes.

When we analysed the isolated effect of each variable, we found the lowest significant mean values of  $H_e$  occurred in bird species that naturally occur in forests and are therefore highly dependent on forest ecosystems. This result evidences the importance of forests as places of shelter and breeding for birds (e.g., LaManna and Martin, 2016; Selwood et al., 2017; Giubbina et al., 2018), so that species that have no access to food or reproductive resources in these environments may experience negative effects. These results are important at a time when many of the major forest ecosystems worldwide—especially in the neotropics—are experiencing severe disturbances (Hansen et al., 2013) which directly affect bird species (e.g., Pereira et al., 2014). Ram et al. (2017) showed that forest birds have more positive tendencies than non-forest birds in face of climatic changes, suggesting that these species are positively affected by factors other than climate. Alternatively, loss of diversity in non-forest birds can perhaps be explained by high exposure to predation and hunting in such environments. Features such as landscape composition influence predation patterns at finer scales (e.g., Thompson et al., 2002; Stephens et al., 2003; Chiavacci et al., 2018). For example, the abundance of some common nest predators (e.g., *Procyon lotor*) tends to be higher in more intensive agricultural landscapes (Chalfoun et al., 2002).

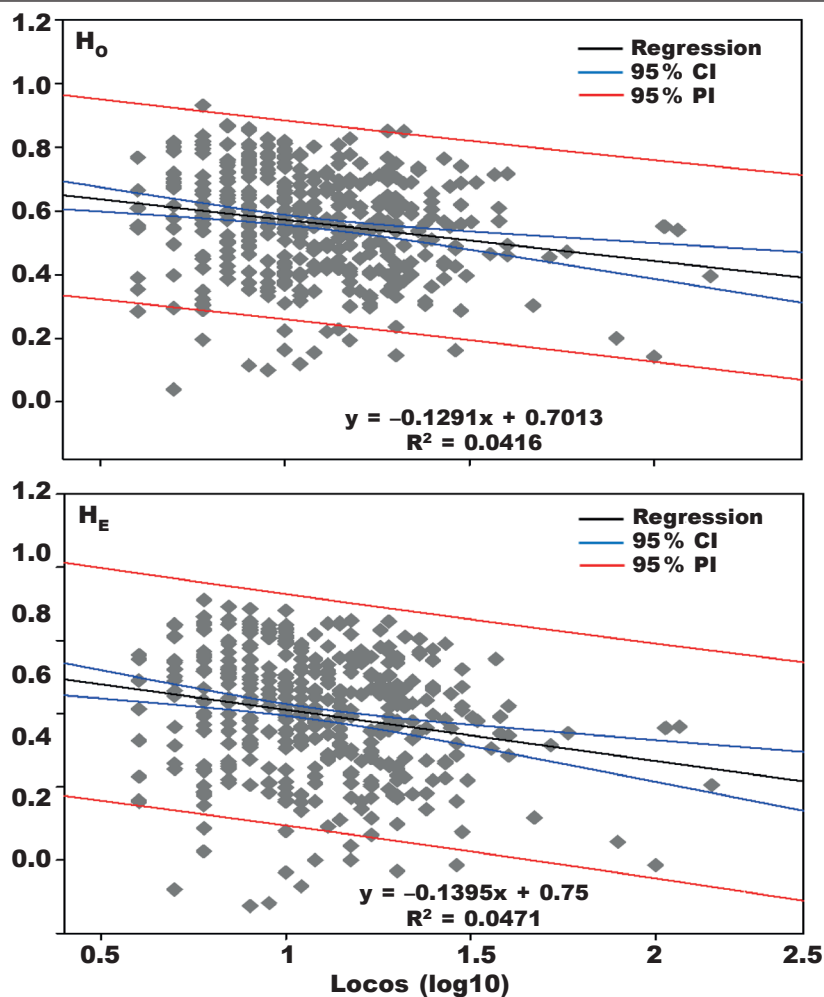


Fig. 3. Correlation between the genetic diversity estimates ( $H_o$  and  $H_e$ ) and the number of loci evaluated in the articles: CI, confidence interval; PI, prediction interval.

*Fig. 3. Correlación entre las estimaciones de la diversidad genética ( $H_o$  y  $H_e$ ) y el número de loci evaluados en los artículos: CI, intervalo de confianza; PI, intervalo de predicción.*

The categories and criteria developed by the IUCN have been important in designing conservation plans and strategies (Miller et al., 2007), but current efforts have been focused on species and on the global conservation plan. However, conservation actions should be implemented at the population level as extinction rates are estimated to be three to eight times higher than extinction rates of species (Hughes et al., 1997), and it is at this level that substantial losses of genetic diversity occur (Garner et al., 2005). Many bird populations have been identified as threatened (e.g., Alves et al., 2010; Van De Pol et al., 2010; Fernandes-Ferreira et al., 2012; Dunham and Grand, 2017; Yong et al., 2018), which implies the risk to further decrease the heterozygosity values reported for species outside of the LC category and expose their populations to risk of local extinction (Garcia and Marini, 2006). However, since both population size and

geographical range are two of the key criteria used by the IUCN to assign threat status, and as both are directly linked to heterozygosity, several studies assessing conservation priorities have excluded species with small populations and/or populations with narrow geographical ranges (Fisher et al., 2003; Jones et al., 2003). Therefore, it is important to include genetic diversity of populations when determining global conservation actions.

The lowest mean  $H_o$  and  $H_e$  values were observed in Otidiformes, Accipitriformes, Gaviiformes and Ciconiiformes, which supports the hypothesis that the solitary behaviour of species of Otidiformes (previously included in Gruiformes but currently considered a proper order) and aspects of their reproductive behaviour, including monogamy and nesting at ground level, might be affecting their genetic diversity as species with complex social systems are more vulnerable to

the effects of low population densities (Brito, 2009). For example, breeding pairs show low reproductive success unless a minimum number of helpers are present to aid in nest defence against predators and food provisioning for chicks (Brito et al., 2004). Conversely, the genetic patterns of Accipitriformes (traditionally included in the order Falconiformes but currently elevated to a proper order; Hackett et al., 2008) have been strongly affected by interspecific hybridization and anthropogenic disturbances (e.g., Poulakakis et al., 2008; Nam and Lee, 2009; Väli et al., 2010). Falconiformes species are mostly birds of prey with naturally low abundances, so given the lack of mating partners these species tend to hybridize, promoting population declines that put them under threat (Randler, 2006). Additionally, species with a high degree of habitat specialization and small clutch sizes are strongly associated with small population sizes, limited geographical ranges and, thus, higher extinction risk (Krüger and Radford, 2008). Ferrer and Negro (2004) have demonstrated that large predators, such as eagles and lynxes, highly specialised in certain prey species, and with small populations, are permanently threatened with extinction. Furthermore, birds in the orders Gaviiformes and Ciconiiformes have been affected by changes in land use and degradation of freshwater systems because of their high dependence on aquatic habitats (Arzel et al., 2015), vulnerability to pathogens (Silva et al., 2010), and exposure to pollutants derived from aquatic contamination (Fontenelle, 2006). There are strong examples in the literature suggesting that populations of many Ciconiiformes have undergone genetic bottlenecks as evidenced by the loss of genetic diversity and an increase in deleterious mutations (Li et al., 2014) due to inbreeding, climate change, habitat loss, hunting and environmental pollution, especially by agrochemicals (e.g., Zhang et al., 2004; Miño et al., 2009).

Significant correlations were observed between the number of loci used and the estimates of  $H_O$  and  $H_E$ . Although the relationships were negative, they nevertheless suggest that low microsatellite locus sample sizes may bias diversity estimates. Small numbers of loci can be used only when evaluating a large number of individuals and when the mean heterozygosity of the population is high (Nei, 1978). Thus, given the number of individuals sampled, the studies we evaluated apparently failed to follow the basic requirements for the estimation of genetic diversity (i.e., they used small numbers of loci despite the mean heterozygosity values being high). However, the number of alleles per locus seems to be a good indicator of accuracy when assessing genetic distances with microsatellite markers. Kalinowski (2002) showed that good results can be achieved using few loci with several alleles or many loci with few alleles.

In recent centuries bird species have been deteriorating in status and becoming extinct at a rate that may be 2–3 orders of magnitude higher than in pre-human times (Brooke et al., 2008). Relating genetic diversity estimates with IUCN Red List categories represents an attempt to understand the circumstances under which a bird species becomes

extinct, since it is possible to link these figures to high rates of inbreeding or reduced effective population size and gene flow. Brooke et al. (2008) showed that conservation actions have benefited species on the verge of extinction, but are less directed or have less effect on moderately endangered species. We are aware that the IUCN has specific guidelines to address genetic issues in reintroductions and translocations of species (IUCN/SSC, 2013), but as the status of birds has worsened worldwide with populations declining faster than ever, especially those of the Pacific marine species (BirdLife, 2013), studies on genetic diversity of bird populations should be promoted to identify populations at risk.

## Conclusion

Studies including bird genetic diversity data obtained using microsatellite markers increased significantly between 2013 and 2014, reflecting the popularization of this technique during this period. However, most of these studies were conducted on Passeriformes and/or taxa belonging to the least concern (LC) IUCN category, suggesting that sampling effort is an obstacle to the application of molecular techniques to study less abundant and/or threatened species.

Our findings show that ecological attributes of bird species such as migratory habit, forest dependence and habitat type have a significant effect on genetic diversity parameters.

More importantly, we corroborate our hypothesis that bird species classified under the most threatened IUCN categories (i.e. EW) have lower values of genetic diversity especially for  $H_O$  and  $H_E$ , whereas species classified under LC have higher values. This indicates that populations with high genetic diversity have a larger effective population size and therefore a lower extinction risk.

From the perspective of conservation genetics, we believe that genetic diversity data should be incorporated and support current criteria for the IUCN Red List to generate a more complex and realistic picture of the conservation status of avian species.

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### Supplementary material

Table 1s. Species found in published papers, with the respective IUCN categories and taxonomic classification regarding order and family.

Tabla 1s. Especies encontradas en artículos publicados, con las respectivas categorías de la UICN y la clasificación taxonómica con respecto al orden y la familia.

Species	IUCN	Order	Family
<i>Acanthisitta chloris</i>	LC	Passeriformes	Acanthisittidae
<i>Accipiter gentilis</i>	LC	Falconiformes	Accipitridae
<i>Aceros leucocephalus</i>	NT	Coraciiformes	Bucerotidae
<i>Aceros waldeni</i>	CR	Coraciiformes	Bucerotidae
<i>Acrocephalus arundinaceus</i>	LC	Passeriformes	Sylviidae
<i>Acrocephalus familiaris</i>	CR	Passeriformes	Sylviidae
<i>Acrocephalus paludicola</i>	VU	Passeriformes	Sylviidae
<i>Acrocephalus schoenobaenus</i>	LC	Passeriformes	Sylviidae
<i>Acrocephalus scirpaceus</i>	LC	Passeriformes	Sylviidae
<i>Acrocephalus sechellensis</i>	VU	Passeriformes	Sylviidae
<i>Aegithalos caudatus</i>	LC	Passeriformes	Aegithalidae
<i>Aegithalos concinnus</i>	LC	Passeriformes	Aegithalidae
<i>Aegithalos glaucogularis</i>	LC	Passeriformes	Aegithalidae
<i>Aerodramus fuciphagus</i>	LC	Apodiformes	Apodidae
<i>Aethia cristatella</i>	LC	Charadriiformes	Alcidae
<i>Aethia psittacula</i>	LC	Charadriiformes	Alcidae
<i>Aethia pusilla</i>	LC	Charadriiformes	Alcidae
<i>Aethia pygmaea</i>	LC	Charadriiformes	Alcidae
<i>Agelaius phoeniceus</i>	LC	Passeriformes	Icteridae
<i>Agelaius xanthomus</i>	EN	Passeriformes	Icteridae
<i>Alectoris rufa</i>	LC	Galliformes	Phasianidae
<i>Alecturus risora</i>	VU	Passeriformes	Tyrannidae
<i>Alectura lathamii</i>	LC	Galliformes	Megapodiidae
<i>Alle alle</i>	LC	Charadriiformes	Alcidae
<i>Alophoixus pallidus</i>	LC	Passeriformes	Pycnonotidae
<i>Amazona aestiva</i>	LC	Psittaciformes	Psittacidae
<i>Amazona leucocephala</i>	NT	Psittaciformes	Psittacidae
<i>Amazona vittata</i>	CR	Psittaciformes	Psittacidae
<i>Ammodramus caudacutus</i>	VU	Passeriformes	Emberizidae
<i>Anas laysanensis</i>	CR	Anseriformes	Anatidae
<i>Anas platyrhynchos</i>	LC	Anseriformes	Anatidae
<i>Anas superciliosa</i>	LC	Anseriformes	Anatidae
<i>Anodorhynchus hyacinthinus</i>	EN	Psittaciformes	Psittacidae
<i>Anodorhynchus leari</i>	EN	Psittaciformes	Psittacidae
<i>Anthobaphes violacea</i>	LC	Passeriformes	Nectariniidae
<i>Anthornis melanura</i>	LC	Passeriformes	Meliphagidae
<i>Aphrastura spinicauda</i>	LC	Passeriformes	Furnariidae

Table 1s. (Cont.).

Species	IUCN	Order	Family
<i>Aquila audax</i>	LC	Accipitriformes	Accipitridae
<i>Aquila chrysaetos</i>	LC	Falconiformes	Accipitridae
<i>Aquila fasciatus</i>	LC	Falconiformes	Accipitridae
<i>Ara ararauna</i>	LC	Psittaciformes	Psittacidae
<i>Ara chloropterus</i>	LC	Psittaciformes	Psittacidae
<i>Ara macao</i>	LC	Psittaciformes	Psittacidae
<i>Arborophila rufipectus</i>	EN	Galliformes	Phasianidae
<i>Ardea herodias</i>	LC	Ciconiiformes	Ardeidae
<i>Arrmon torquatus</i>	LC	Passeriformes	Emberizidae
<i>Athene cunicularia</i>	LC	Strigiformes	Strigidae
<i>Atlapetes latinuchus</i>	LC	Passeriformes	Emberizidae
<i>Atlapetes pallidiceps</i>	EN	Passeriformes	Emberizidae
<i>Atrichornis clamosus</i>	EN	Passeriformes	Atrichornithidae
<i>Balearica regulorum</i>	EN	Gruiformes	Gruidae
<i>Bartramia longicauda</i>	LC	Charadriiformes	Scolopacidae
<i>Biziura lobata</i>	LC	Anseriformes	Anatidae
<i>Branta bernicla</i>	LC	Anseriformes	Anatidae
<i>Branta canadensis</i>	LC	Anseriformes	Anatidae
<i>Buarremon torquatus</i>	LC	Passeriformes	Emberizidae
<i>Bubo blakistoni</i>	EN	Strigiformes	Strigidae
<i>Bubo bubo</i>	LC	Strigiformes	Strigidae
<i>Bucanetes githagineus</i>	LC	Passeriformes	Fringillidae
<i>Bucephala islandica</i>	LC	Anseriformes	Anatidae
<i>Bucorvus leadbeateri</i>	VU	Coraciiformes	Bucorvidae
<i>Burhinus oedicephalus</i>	LC	Charadriiformes	Burhinidae
<i>Buteo buteo</i>	LC	Falconiformes	Accipitridae
<i>Buteo ridgwayi</i>	CR	Falconiformes	Accipitridae
<i>Calidris alba</i>	LC	Charadriiformes	Scolopacidae
<i>Calidris ptilocnemis</i>	LC	Charadriiformes	Scolopacidae
<i>Calidris temminckii</i>	LC	Charadriiformes	Scolopacidae
<i>Callipepla squamata</i>	LC	Galliformes	Odontophoridae
<i>Calyptorhynchus banksii</i>	LC	Psittaciformes	Psittacidae
<i>Calyptorhynchus baudinii</i>	EN	Psittaciformes	Psittacidae
<i>Calyptorhynchus latirostris</i>	EN	Psittaciformes	Psittacidae
<i>Campylopterus curvipennis</i>	LC	Caprimulgiformes	Trochilidae
<i>Campylorhynchus brunneicapillus</i>	LC	Passeriformes	Troglodytidae
<i>Carpodacus mexicanus</i>	LC	Passeriformes	Fringillidae
<i>Catharus ustulatus</i>	LC	Passeriformes	Turdidae
<i>Centrocercus urophasianus</i>	NT	Galliformes	Phasianidae
<i>Cerorhinca monocerata</i>	LC	Charadriiformes	Alcidae

Table 1s. (Cont.).

Species	IUCN	Order	Family
<i>Chalcites basalıs</i>	LC	Cuculiformes	Cuculidae
<i>Chalcites lucidus</i>	LC	Cuculiformes	Cuculidae
<i>Chalcites minutillus</i>	LC	Cuculiformes	Cuculidae
<i>Chamaea fasciata</i>	LC	Passeriformes	Timaliidae
<i>Charadrius marginatus</i>	LC	Charadriiformes	Charadriidae
<i>Charadrius pecuarius</i>	LC	Charadriiformes	Charadriidae
<i>Charadrius thoracicus</i>	VU	Charadriiformes	Charadriidae
<i>Chersophilus duponti</i>	NT	Passeriformes	Alaudidae
<i>Chiroxiphia caudata</i>	LC	Passeriformes	Pipridae
<i>Chlamydotis macqueenii</i>	VU	Otidiformes	Otididae
<i>Chlidonias hybrida</i>	LC	Charadriiformes	Laridae
<i>Chondestes grammacus</i>	LC	Passeriformes	Emberizidae
<i>Ciconia ciconia</i>	LC	Ciconiiformes	Ciconiidae
<i>Cinclus cinclus</i>	LC	Passeriformes	Cinclidae
<i>Cinnyris stuhlmanni</i>	LC	Passeriformes	Nectariniidae
<i>Circus pygargus</i>	LC	Accipitriformes	Accipitridae
<i>Colaptes auratus</i>	LC	Piciformes	Picidae
<i>Colinus virginianus</i>	NT	Galliformes	Odontophoridae
<i>Columba janthina nitens</i>	NT	Columbiformes	Columbidae
<i>Columba livia</i>	LC	Columbiformes	Columbidae
<i>Coracias garrulus</i>	NT	Coraciiformes	Coraciidae
<i>Coracina newtoni</i>	CR	Passeriformes	Campephagidae
<i>Corapipo altera</i>	LC	Passeriformes	Pipridae
<i>Corvus brachyrhynchos</i>	LC	Passeriformes	Corvidae
<i>Corvus corone</i>	LC	Passeriformes	Corvidae
<i>Corvus moneduloides</i>	LC	Passeriformes	Corvidae
<i>Coturnix japonica</i>	NT	Galliformes	Phasianidae
<i>Crax globulosa</i>	EN	Galliformes	Cracidae
<i>Crossoptilon auritum</i>	LC	Galliformes	Phasianidae
<i>Culicivora caudacuta</i>	VU	Passeriformes	Tyrannidae
<i>Cyanistes caeruleus</i>	LC	Passeriformes	Paridae
<i>Cyanocitta stelleri</i>	LC	Passeriformes	Corvidae
<i>Cyanopsitta spixii</i>	CR	Psittaciformes	Psittacidae
<i>Cygnus atratus</i>	LC	Anseriformes	Anatidae
<i>Cygnus buccinator</i>	LC	Anseriformes	Anatidae
<i>Cyphorhinus phaeocephalus</i>	LC	Passeriformes	Troglodytidae
<i>Dasyornis brachypterus</i>	EN	Passeriformes	Dasyornithidae
<i>Dendrocincla turdina</i>	LC	Passeriformes	Dendrocolaptidae
<i>Dendroica chrysoparia</i>	EN	Passeriformes	Parulidae
<i>Dinornis robustus</i>	EX	Dinornithiformes	Dinornithidae

Table 1s. (Cont.).

Species	IUCN	Order	Family
<i>Diomedea exulans</i>	VU	Procellariiformes	Diomedidae
<i>Dromaius novaehollandiae</i>	LC	Struthioniformes	Dromaiidae
<i>Drymodes brunneopygia</i>	LC	Passeriformes	Sylviidae
<i>Eclectus roratus</i>	LC	Psittaciformes	Psittacidae
<i>Egretta eulophotes</i>	VU	Pelecaniformes	Ardeidae
<i>Egretta rufescens</i>	NT	Ciconiiformes	Ardeidae
<i>Elaenia ruficeps</i>	LC	Passeriformes	Tyrannidae
<i>Emberiza cia</i>	LC	Passeriformes	Emberizidae
<i>Emberiza citrinella</i>	LC	Passeriformes	Emberizidae
<i>Emberiza schoeniclus</i>	LC	Passeriformes	Emberizidae
<i>Emeus crassus</i>	EX	Struthioniformes	Dinornithidae
<i>Empidonax traillii</i>	LC	Passeriformes	Tyrannidae
<i>Epthianura albifrons</i>	LC	Passeriformes	Meliphagidae
<i>Eudocimus ruber</i>	LC	Ciconiiformes	Threskiornithidae
<i>Eudyptes chrysolophus</i>	VU	Sphenisciformes	Spheniscidae
<i>Eudyptula minor</i>	LC	Sphenisciformes	Spheniscidae
<i>Eulidia yarrellii</i>	EN	Apodiformes	Trochilidae
<i>Euryapteryx curtus</i>	EX	Dinornithiformes	Emeidae
<i>Falco deiroleucus</i>	NT	Falconiformes	Falconidae
<i>Falco naumanni</i>	LC	Falconiformes	Falconidae
<i>Falco peregrinus</i>	LC	Falconiformes	Falconidae
<i>Falco sparverius</i>	LC	Falconiformes	Falconidae
<i>Falco tinnunculus</i>	LC	Falconiformes	Falconidae
<i>Ficedula hypoleuca</i>	LC	Passeriformes	Muscicapidae
<i>Ficedula parva</i>	LC	Passeriformes	Muscicapidae
<i>Francolinus francolinus</i>	LC	Galliformes	Phasianidae
<i>Fringilla teydea</i>	NT	Passeriformes	Fringillidae
<i>Fulica alai</i>	VU	Gruiformes	Rallidae
<i>Galerida cristata</i>	LC	Passeriformes	Alaudidae
<i>Galerida theklae</i>	LC	Passeriformes	Alaudidae
<i>Gallinula chloropus</i>	LC	Gruiformes	Rallidae
<i>Gallinula galeata sandvicensis</i>	LC	Gruiformes	Rallidae
<i>Gallus gallus</i>	LC	Galliformes	Phasianidae
<i>Garrulax elliotii</i>	LC	Passeriformes	Timaliidae
<i>Gavia immer</i>	LC	Gaviiformes	Gaviidae
<i>Geospiza magnirostris</i>	LC	Passeriformes	Emberizidae
<i>Geothlypis beldingi</i>	EN	Passeriformes	Parulidae
<i>Grus carunculatus</i>	VU	Gruiformes	Gruidae
<i>Grus japonensis</i>	EN	Gruiformes	Gruidae
<i>Grus leucogeranus</i>	CR	Gruiformes	Gruidae



Table 1s. (Cont.).

Species	IUCN	Order	Family
<i>Grus paradisea</i>	VU	Gruiformes	Gruidae
<i>Guira guira</i>	LC	Cuculiformes	Cuculidae
<i>Gyps bengalensis</i>	CR	Accipitriformes	Accipitridae
<i>Gyps indicus</i>	CR	Accipitriformes	Accipitridae
<i>Gyps tenuirostris</i>	CR	Accipitriformes	Accipitridae
<i>Haliaeetus albicilla</i>	LC	Falconiformes	Accipitridae
<i>Haliaeetus vociferoides</i>	CR	Falconiformes	Accipitridae
<i>Harpia harpyja</i>	NT	Accipitriformes	Accipitridae
<i>Henicorhina leucophrys</i>	LC	Coraciiformes	Bucerotidae
<i>Heteralocha acutirostris</i>	EX	Passeriformes	Callaeatidae
<i>Himantopus leucocephalus</i>	LC	Charadriiformes	Recurvirostridae
<i>Himantopus novaezelandiae</i>	CR	Charadriiformes	Recurvirostridae
<i>Hippolais icterina</i>	LC	Passeriformes	Sylviidae
<i>Hippolais polyglotta</i>	LC	Passeriformes	Sylviidae
<i>Hirundo rustica</i>	LC	Passeriformes	Hirundinidae
<i>Lagonosticta sanguinodorsalis</i>	LC	Passeriformes	Estrildidae
<i>Lagopus muta pyrenaica</i>	LC	Galliformes	Phasianidae
<i>Laniarius atrococcineus</i>	LC	Passeriformes	Malaconotidae
<i>Larus marinus</i>	LC	Charadriiformes	Laridae
<i>Larus saundersi</i>	VU	Charadriiformes	Laridae
<i>Larus smithsonianus</i>	LC	Charadriiformes	Laridae
<i>Leptoptilos crumenifer</i>	LC	Ciconiiformes	Ciconiidae
<i>Limnithlypis swainsonii</i>	LC	Passeriformes	Parulidae
<i>Liocichla steerii</i>	LC	Passeriformes	Timaliidae
<i>Lonchura cantans</i>	LC	Passeriformes	Estrildidae
<i>Malurus coronatus</i>	LC	Passeriformes	Maluridae
<i>Meleagris gallopavo</i>	LC	Galliformes	Phasianidae
<i>Melospiza melodia</i>	LC	Passeriformes	Emberizidae
<i>Merops ornatus</i>	LC	Coraciiformes	Meropidae
<i>Mimus parvulus</i>	LC	Passeriformes	Mimidae
<i>Modulatrix stictigula</i>	LC	Passeriformes	Muscicapidae
<i>Mohoua ochrocephala</i>	EN	Passeriformes	Acanthizidae
<i>Morphnus guianensis</i>	NT	Accipitriformes	Accipitridae
<i>Mycteria americana</i>	LC	Ciconiiformes	Ciconiidae
<i>Neothraupis fasciata</i>	NT	Passeriformes	Thraupidae
<i>Nestor notabilis</i>	VU	Psittaciformes	Strigopidae
<i>Ninox connivens</i>	LC	Strigiformes	Strigidae
<i>Ninox novaeseelandiae</i>	LC	Strigiformes	Strigidae
<i>Ninox strenua</i>	LC	Strigiformes	Strigidae
<i>Nipponia nippon</i>	EN	Ciconiiformes	Threskiornithidae

Table 1s. (Cont.).

Species	IUCN	Order	Family
<i>Nisaetus nipalensis</i>	LC	Falconiformes	Accipitridae
<i>Notiomystis cincta</i>	VU	Passeriformes	Meliphagidae
<i>Nucifraga columbiana</i>	LC	Passeriformes	Corvidae
<i>Numida meleagris</i>	LC	Galliformes	Numididae
<i>Nycticorax nycticorax</i>	LC	Ciconiiformes	Ardeidae
<i>Oceanodroma leucorhoa</i>	LC	Procellariiformes	Hydrobatidae
<i>Orthonyx temminckii</i>	LC	Passeriformes	Orthonychidae
<i>Otis tarda</i>	VU	Gruiformes	Otididae
<i>Oxyura jamaicensis</i>	LC	Anseriformes	Anatidae
<i>Oxyura leucocephala</i>	EN	Anseriformes	Anatidae
<i>Pachycephala pectoralis</i>	LC	Passeriformes	Pachycephalidae
<i>Pachyornis elephantopus</i>	EX	Struthioniformes	Dinornithidae
<i>Paradoxornis heudei</i>	NT	Passeriformes	Timaliidae
<i>Pandion haliaetus</i>	LC	Accipitriformes	Pandionidae
<i>Paradoxornis heudei</i>	NT	Passeriformes	Timaliidae
<i>Parus caeruleus</i>	LC	Passeriformes	Paridae
<i>Parus major</i>	LC	Passeriformes	Paridae
<i>Passer domesticus</i>	LC	Passeriformes	Passeridae
<i>Passer montanus</i>	LC	Passeriformes	Passeridae
<i>Pauxi mitu</i>	EW	Galliformes	Cracidae
<i>Pauxi tuberosa</i>	LC	Galliformes	Cracidae
<i>Pelecanus onocrotalus</i>	LC	Pelecaniformes	Pelecanidae
<i>Penelopides affinis</i>	LC	Coraciiformes	Bucerotidae
<i>Penelopides manillae</i>	LC	Coraciiformes	Bucerotidae
<i>Penelopides panini</i>	EN	Coraciiformes	Bucerotidae
<i>Perisoreus infaustus</i>	LC	Passeriformes	Corvidae
<i>Petrochelidon fulva</i>	LC	Passeriformes	Hirundinidae
<i>Petroica australis</i>	LC	Passeriformes	Petroicidae
<i>Petroica goodenovii</i>	LC	Passeriformes	Petroicidae
<i>Peucaea aestivali</i>	NT	Passeriformes	Emberizidae
<i>Phalacrocorax aristotelis</i>	LC	Suliformes	Phalacrocoracidae
<i>Phalacrocorax atriceps</i>	LC	Suliformes	Phalacrocoracidae
<i>Phalacrocorax fuscescen</i>	LC	Pelecaniformes	Phalacrocoracidae
<i>Philesturnus carunculatus</i>	NT	Passeriformes	Callaeatidae
<i>Philesturnus rufusater</i>	NT	Passeriformes	Callaeatidae
<i>Philomachus pugnax</i>	LC	Charadriiformes	Scolopacidae
<i>Phoebastria albatrus</i>	VU	Procellariiformes	Diomedidae
<i>Phoebastria immutabilis</i>	NT	Procellariiformes	Diomedidae
<i>Phoebastria nigripes</i>	NT	Procellariiformes	Diomedidae
<i>Phoeniconaias minor</i>	NT	Phoenicopteriformes	Phoenicopetridae

Table 1s. (Cont.).

Species	IUCN	Order	Family
<i>Phyllastrephus flavostriatus</i>	LC	Passeriformes	Pycnonotidae
<i>Phylloscopus ijimae</i>	VU	Passeriformes	Sylviidae
<i>Picoides tridactylus</i>	LC	Piciformes	Picidae
<i>Pipilo crissalis</i>	LC	Passeriformes	Emberizidae
<i>Platalea ajaja</i>	LC	Ciconiiformes	Threskiornithidae
<i>Plegadis chihi</i>	LC	Ciconiiformes	Threskiornithidae
<i>Pluvialis dominica</i>	LC	Charadriiformes	Charadriidae
<i>Podargus strigoides</i>	LC	Caprimulgiformes	Podargidae
<i>Podiceps grisegena</i>	LC	Podicipediformes	Podicipedidae
<i>Poecile hudsonicus</i>	LC	Passeriformes	Paridae
<i>Poephila cincta</i>	LC	Passeriformes	Estrildidae
<i>Poicephalus robustus</i>	LC	Psittaciformes	Psittacidae
<i>Pomarea dimidiata</i>	VU	Passeriformes	Monarchidae
<i>Pomatostomus temporalis</i>	LC	Passeriformes	Pomatortomidae
<i>Procnias tricarunculata</i>	VU	Passeriformes	Cotingidae
<i>Prunella modularis</i>	LC	Passeriformes	Prunellidae
<i>Pseudonestor xanthophrys</i>	CR	Passeriformes	Fringillidae
<i>Psittacula eques</i>	EN	Psittaciformes	Psittacidae
<i>Puffinus carneipes</i>	LC	Procellariiformes	Procellariidae
<i>Pycnonotus sinensis</i>	LC	Passeriformes	Pycnonotidae
<i>Pygoscelis antarctica</i>	LC	Sphenisciformes	Spheniscidae
<i>Pyrrhonorax pyrrhonorax</i>	LC	Passeriformes	Corvidae
<i>Rallus elegans</i>	NT	Gruiformes	Rallidae
<i>Ramphocelus bresilius</i>	LC	Passeriformes	Thraupidae
<i>Rhynchotus rufescens</i>	LC	Tinamiformes	Tinamidae
<i>Saxicola torquatus</i>	LC	Passeriformes	Muscicapidae
<i>Serinus rufobrunneus</i>	LC	Passeriformes	Fringillidae
<i>Setophaga striata</i>	LC	Passeriformes	Parulidae
<i>Spizella wortheni</i>	EN	Passeriformes	Emberizidae
<i>Stipiturus malachurus</i>	LC	Passeriformes	Maluridae
<i>Struthio camelus</i>	LC	Struthioniformes	Struthionidae
<i>Sturnus unicolor</i>	LC	Passeriformes	Sturnidae
<i>Sylvia conspicillata</i>	LC	Passeriformes	Sylviidae
<i>Tachycineta albilinea</i>	LC	Passeriformes	Hirundinidae
<i>Tachycineta bicolor</i>	LC	Passeriformes	Hirundinidae
<i>Tachycineta leucorrhoa</i>	LC	Passeriformes	Hirundinidae
<i>Taeniopygia guttata</i>	LC	Passeriformes	Estrildidae
<i>Tarsiger cyanurus</i>	LC	Passeriformes	Muscicapidae
<i>Telespiza cantans</i>	VU	Passeriformes	Fringillidae
<i>Terpsiphone mutata</i>	LC	Passeriformes	Monarchidae

Table 1s. (Cont.).

Species	IUCN	Order	Family
<i>Terpsiphone corvina</i>	CR	Passeriformes	Monarchidae
<i>Tetrao tetrax</i>	LC	Galliformes	Phasianidae
<i>Tetrao urogallus</i>	LC	Galliformes	Phasianidae
<i>Thamnophilus cryptoleucus</i>	NT	Passeriformes	Thamnophilidae
<i>Thaumastura cora</i>	LC	Apodiformes	Trochilidae
<i>Turdus merula</i>	LC	Passeriformes	Turdidae
<i>Tyto alba</i>	LC	Strigiformes	Tytonidae
<i>Upupa epops</i>	LC	Coraciiformes	Upupidae
<i>Uria aalge</i>	LC	Charadriiformes	Alcidae
<i>Uria lomvia</i>	LC	Charadriiformes	Alcidae
<i>Urosphena squameiceps</i>	LC	Passeriformes	Sylviidae
<i>Xenicus gilviventris</i>	VU	Passeriformes	Acanthisittidae
<i>Zenaida aurita</i>	LC	Columbiformes	Columbidae
<i>Zosterops abyssinicus</i>	LC	Passeriformes	Zosteropidae
<i>Zosterops borbonicus</i>	LC	Passeriformes	Zosteropidae
<i>Zosterops lateralis</i>	LC	Passeriformes	Zosteropidae
<i>Zosterops poliogastrus</i>	LC	Passeriformes	Zosteropidae
<i>Zosterops senegalensis</i>	LC	Passeriformes	Zosteropidae
<i>Zosterops vaghani</i>	LC	Passeriformes	Zosteropidae
<i>Zosterops virens</i>	LC	Passeriformes	Zosteropidae