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Integrative taxonomy documents two additional cryptic *Erithacus* species on the Canary Islands (Aves)

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Abstract

The European Robin *Erithacus rubecula* is currently treated as a single species with eight subspecies. A previous molecular study and new molecular, morphometric and bioacoustic data reported here strongly support the recognition of three species in this complex: *E. rubecula* (Europe, North Africa and Macaronesia except the central Canary Islands), *E. superbus* (Tenerife) and a recently described subspecies on Gran Canaria which we raise to species rank as *E. marionae*. The taxa on Tenerife and Gran Canaria have previously been lumped as a single taxon but differ from each other and from *E. rubecula* in territorial songs, *tic* calls, *seep* calls and wing length. All three species are characterised by moderate to high levels of interspecific mitochondrial DNA sequence divergence (mean 4.2–4.8%). Phylogenetic analysis indicates that *E. marionae* is sister to *E. superbus* + *E. rubecula*. Recognition of Gran Canaria and Tenerife Robins as separate species adds two single-island endemics to the Canary Islands avifauna.

KEYWORDS

cryptic speciation, endemism, Macaronesia, molecular systematics, phylogeography, species limits

1 | INTRODUCTION

The European Robin *Erithacus rubecula* (Linnaeus, 1758) is widely distributed in Europe east to western Siberia and northern Iran and south to North Africa and the Macaronesian Islands (Azores, Madeira, Canary Islands). Geographic variation in morphology in the European Robin is complex (Lack, 1951; Vaurie, 1959). In continental populations variation is primarily clinal, with clines of different characters running in different directions. Geographic variation among Canary Islands populations is discrete, involving several characters that vary

concordantly. Traditionally, geographic variation in the Robin is represented by the recognition of a polytypic species with eight subspecies (Vaurie, 1959; Ripley, 1964; Roselaar in Cramp, 1988; Collar, 2020; Gill et al., 2022).

In the Canary Islands (Figure 1), three recognised subspecies are found breeding. The populations in the western islands (La Palma, El Hierro and La Gomera) are very similar to European populations and are generally included in *E. r. rubecula*, although some authors consider these a separate subspecies '*E. r. microrhynchos*' Reichenow, 1906 (e.g. Hounsoume, 1993). *E. r. rubecula* also is a winter visitor to the eastern islands (Martín & Lorenzo, 2001). The

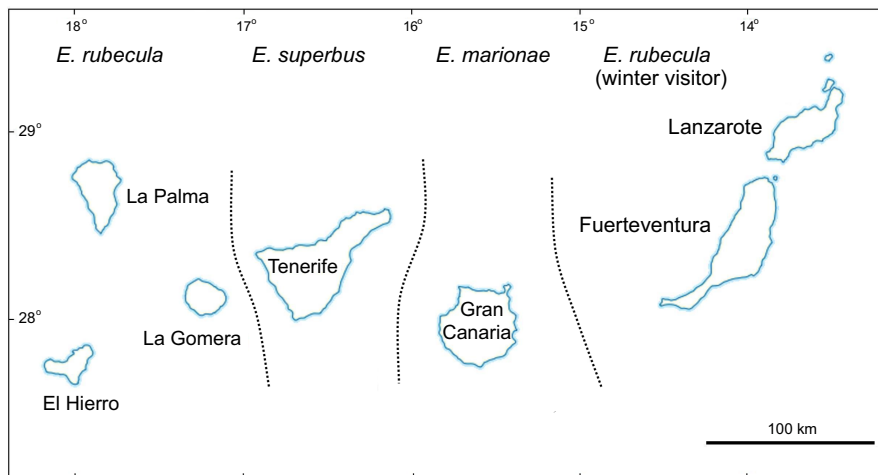


FIGURE 1 Map of the Canary Islands. Ranges of the three species of *Erithacus* are indicated (*E. rubecula* also occurs outside the Canary Islands)

taxon *superbus* Koenig, 1889 from Tenerife is considered to be distinct (e.g. Lack, 1946; Lack & Southern, 1949; Vaurie, 1959; Roselaar in Cramp, 1988). In morphology, *superbus* differs from other recognised subspecies by its richer red throat and breast, a pale eye-ring, less extensive red on the underparts, more olive-brown upperparts, a white belly, shorter wings and longer bill (Lack, 1946; Roselaar in Cramp, 1988; Bergmann & Schottler, 2001).

Tenerifean *superbus* also differs from European populations by their very distinctive songs, a fact that has long been recognised by visiting ornithologists familiar with European or west Canarian populations of *E. rubecula* (Bolle, 1854; Koenig, 1890; Lack & Southern, 1949). Since the late 1980s, several studies have compared songs and calls of Tenerifean *superbus* with European *rubecula* (Bildsøe & Dabelsteen, 1998; Larsen et al., 1997; Stock & Bergmann, 1988). Bergmann and Schottler (2001) have summarised the differences between Tenerifean *superbus* and European *rubecula* and suggested that species status is warranted for *E. superbus*.

Until very recently, the morphology and taxonomic status of the Gran Canaria population had not been studied in detail. A previous molecular study showed that the robin comprises three major clades, one restricted to Gran Canaria, another to Tenerife and a third including all other populations from the western Canary Islands (La Palma, El Hierro, La Gomera) and Europe (Dietzen et al., 2003). Gene trees of mitochondrial DNA sequences of Gran Canaria and Tenerife robins are reciprocally monophyletic with the exception of a single individual sampled on Tenerife with a haplotype typical of those from Gran Canaria (indicating occasional migration between the islands; Dietzen et al., 2003). Surprisingly, the Tenerife population was found to be more closely related to the west Canarian and European populations than to the population of Gran Canaria with which it had been previously included under the name *superbus*. These

results indicate that the taxon *superbus* is paraphyletic. Dietzen et al. (2003) also documented differences in wing length and wing shape between populations of Tenerife and Gran Canaria.

Dietzen et al. (2003) suggested that the robin complex represents a superspecies with three allopecies: *E. [rubecula] rubecula* containing all robin populations except those from the central Canary Islands, *E. [rubecula] superbus* from Tenerife, and a third taxon on Gran Canaria for which they introduced the name '*Erithacus [rubecula] marionae*'. The latter name does not fulfil the requirements of the International Code of Zoological Nomenclature (ICZN, 1999) and is therefore not available. A valid description was published subsequently (Dietzen et al., 2015).

In this study, we examine variation in the songs and calls of Gran Canaria, Tenerife and European robins, we provide new morphometric data from museum specimens and we expand the phylogenetic analysis of Dietzen et al. (Dietzen et al., 2003; Dietzen et al., 2015) by including new or previously unreported sequences from the Canary Islands, Madeira, Azores, Morocco, Corsica, mainland Europe and Georgia. These analyses, and additional morphometric data reported in Dietzen et al. (Dietzen et al., 2003; Dietzen et al., 2015), demonstrate that the European Robin consists of at least three major groups that are best treated as species.

2 | METHODS

2.1 | Molecular procedures and phylogenetic analyses

Six museum specimens were newly sampled from study skins collected in 1902–1912, including two *marionae* from Gran Canaria, two *superbus* from Tenerife, one

sardus from Corsica and one *caucasicus* from Georgia. New primers were designed (Table S1) to amplify and sequence short DNA fragments (160–200 bp, excluding primers). These primers were designed from Genbank sequences that were based on fresh tissue material. Voucher and GenBank accession numbers are provided in Table S2. Extraction, PCR amplification and sequencing followed procedures described by Irestedt et al. (2006). Newly generated DNA sequences are available on Genbank (accession numbers KJ200298 to KJ200303).

Cytochrome b (cyt b) sequences (1125 bp) of 92 *Erithacus* robins were included in the analysis. In addition to the six newly generated sequences, these included 61 sequences reported by Dietzen et al. (2003), one from Sangster et al. (2010), and 24 previously unreported cyt b sequences of *E. rubecula* from Germany ($N = 4$), Spain ($N = 3$), Morocco ($N = 8$), Madeira ($N = 4$), La Palma ($N = 1$) and the Azores ($N = 4$) which were obtained from GenBank (AY624077–AY624100). An additional member of Cossyphinae (*Stiphrornis sanghensis*, AF136731; Beresford & Cracraft, 1999), a member of Niltavinae (*Niltava sundara*, EF081354; Lei et al., 2007) and *Turdus philomelos* (AY495411; van der Meij et al., 2005) were used as outgroups.

Phylogenetic relationships among robins were estimated using MrBAYES version 3.2.2 (Ronquist et al., 2012). The best-fit model was estimated with MEGA5 (Tamura et al., 2011) using the Akaike Information Criterion. The selected model was GTR+G+I. Default priors in MrBAYES were used. We ran four Metropolis-coupled MCMC chains for 10 million generations and sampled the topology every 1000 generations. Convergence between the two MrBayes runs was assessed by comparing the posterior probability estimates for both analyses using the program AWTY (Nylander et al., 2008). The first 25% of the generations were discarded ('burn-in') and the posterior probability was then estimated for the remaining sampled generations.

To further evaluate statistical support for the topology, maximum likelihood (ML) bootstrapping was performed. ML analysis was conducted using RAxML v7.7.1 (Stamatakis et al., 2008). Clade support for the ML analysis was assessed by 1000 bootstrap replicates. Uncorrected p pairwise sequence divergences were calculated in MEGA7 (Kumar et al., 2016) with complete deletion of nucleotide positions with missing data. Sequence divergence values of five other Canarian endemic species and their sister species were newly calculated from GenBank sequences (Bensch et al., 2006; Dourado et al., 2014; Gonzalez et al., 2009; Helbig et al., 1996; Illera et al., 2008; Irestedt et al., 2011; Lifjeld et al., 2016; Suárez et al., 2009; van der Meij et al., 2005) with total deletion of missing

sites, resulting in strictly homologous sequence data, as recommended by Fregin et al. (2012).

2.2 | Vocalisations

Robins were recorded on Gran Canaria in May 2004 and April 2014, on Tenerife in May 2004, in the Netherlands in April 2004 and March–May 2005 and in Sweden in May 2009. Recordings were made using a Marantz PMD 222 or a Marantz PMD 670 recorder with a Sennheiser ME66 microphone. All recordings are deposited at the Macaulay Library, Cornell University, Ithaca, NY, USA. The data set was supplemented by recordings obtained from the Xeno-Canto database (<http://www.xeno-canto.org/>), the Tierstimmenarchiv (Berlin), the AVOCET database (<http://avocet.zoology.msu.edu/>), and commercial publications (Bergmann et al., 2008; Boesman, 2008; Bondesen & Hansen, n.d.; Chappuis, 2000; Hammick, 2003; Kettle & Ranft, 1992; Matheu, 2001; Moreno, 2000; Sample, 1996; Trilar, 2002). All song recordings were made in spring. Locations and recordists for all the recordings examined are listed in Table S3. All our recordings have been deposited at the British Library Sound Archive (collection title: European Robin WA 2022/002).

Variation in three vocalisations was studied: the song, the *tic* call and the *seep* call. In spring, only males sing whereas both sexes sing in fall and winter (Hoelzel, 1986; Lack, 1965). Songs are predominantly used for territorial advertisement (Chantrey & Workman, 1984; Hoelzel, 1986; Lack, 1965) and to a lesser extent for mate attraction (Lack, 1965). The *tic* call is used as an alarm call and in territorial conflicts (East, 1981; Lack, 1965). The *seep* call is used by females to beg food from their mates throughout the breeding season (Tobias & Seddon, 2002). All recordings in each class of vocalisations (song, *tic* call and *seep* call) were from different birds. A 'note' was defined as an unbroken trace on a spectrogram.

All measurements were made using CoolEdit 2000 (Johnston, 2000). For songs, the following measurements were recorded: (1) song duration; (2) number of phrases per song; (3) proportion of songs with a high frequency (>7 kHz) introductory note; (4) mean phrase duration (duration of all phrases in a song divided by the number of phrases); (5) song proportion (duration of all phrases in a song divided by the total song duration); (6) absolute phrase duration (duration of all phrases in a song); (7) duration of the first phrase; (8) total number of notes in a song; (9) proportion of unique notes in a song; (10) number of unique notes in a song; (11) proportion of frequency shifts (shifts >2 kHz) between phrases in a song (=number of freq shifts / [number of phrases minus one]); (12) number of notes in the first phrase; (13) proportion

of frequency shifts (>2 kHz) per song; (14) number of frequency shifts (>2 kHz) per song; (15) proportion of songs in which notes in the (last) phrase are repeated; (16) maximum frequency; (17) minimum frequency; (18) frequency range; (19) number of low-frequency notes in a song (LF, <4 kHz); (20) number of mid-frequency notes in a song (MF, 4–7 kHz); (21) number of high-frequency notes in a song (HF, >7 kHz); (22) proportion of low-frequency notes in a song (LF, <4 kHz); (23) proportion of mid-frequency notes in a song (MF, 4–7 kHz); and (24) proportion of high-frequency notes in a song (HF, >7 kHz). Some of these parameters have been used previously to differentiate between male and female *E. rubecula* (Hoelzel, 1986) and between *E. r. superbus* (Tenerife) and *E. rubecula* (Bergmann & Schottler, 2001; Larsen et al., 1997). Due to the large song repertoire of robins, and in order to give equal weight to individuals, means of 20–25 songs were computed for each recording. These means were used as sample points from which ranges, means and standard deviations were computed.

The number of unique songs in each recording was also determined, in steps of 5 songs. In the field it was noted whether recorded vocalisations were spontaneous or resulted from playback of previous recordings of the relevant population. For each character, it was assessed whether there is a significant difference between natural songs and songs after playback.

For *tic* and *seep*, calls the minimum and maximum frequency, and the frequency range were measured. In addition, for *seep* calls the frequency at the start and end of the call, and the change in frequency between start and end of the call were measured.

For taxonomic comparisons, recordings were grouped into three operational taxonomic units (Gran Canaria; Tenerife; and Europe, North Africa, Madeira and the western Canary Islands) based on the phylogroups defined by Dietzen et al. (2003).

2.3 | Morphology

Specimens of all recognised subspecies (Dickinson & Christidis, 2014), except *E. r. tataricus* from the Urals and SW Siberia were examined in The Natural History Museum, Tring (BMNH), Manchester Museum, University of Manchester (MMUM), Naturalis Biodiversity Centre, Leiden (NBC) (formerly Rijksmuseum voor Natuurlijke Historie; RMNH), Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK), Museum für Naturkunde, Berlin (ZMB) and the Swedish Museum of Natural History, Stockholm (NRM). Specimen localities are provided in Table S4.

Four standard morphometric variables (wing length, tail length, tarsus and bill to skull) were measured for 370 specimens. Measurements were taken as described in Cramp (1988). Sexes, as identified on the specimen labels, were treated separately in statistical analyses. Measurements were compared for three operational taxonomic units (Gran Canaria; Tenerife; and Europe, Middle East, North Africa, Azores and Madeira).

2.4 | Statistical analysis

One-way ANOVA with Bonferroni correction was used to determine whether song, call and morphometric parameters differed among groups. If the assumption of homogeneity of variances was violated, Tamhane correction was used. When assumptions of normal distribution were violated (as shown by the Komolgorov-Smirnov test), data were transformed (log, natural log or square root). If transformation was not possible, Mann–Whitney *U* test was used and significance determined using Holm's sequential Bonferroni test (Holm, 1979).

Principal component analysis (PCA) was used to explore song differentiation among the three groups. PCA reduces multiple variables to a limited number of uncorrelated variables. ANOVA and Tukey's post-hoc comparisons were used to test whether the three groups defined by molecular phylogeography differed from each other.

Canonical discriminant function analyses (DFA) were carried out on the acoustic variables of phrases to test whether the songs could be correctly assigned to the three phylogroups. DFA generates a set of criteria to assign songs to groups that are defined prior to the analysis. Prior to this, a tolerance test was conducted to assess the independence of each variable. Variables that fail the tolerance test, i.e. which are an almost linear combination of other variables, were excluded from subsequent analysis. Two DFAs were performed: (i) a 'descriptive' DFA, in which the observations used to develop the criteria are then subjected to these criteria; (ii) a 'predictive' DFA, which uses a jackknife procedure to obtain a more accurate test of the predictive performance of the DFA. In the jackknife procedure, the DFA is recalculated using the combination of variables of the initial DFA with one individual removed from the data set. The criteria are then used to classify the removed individual. This process was repeated eliminating each individual in turn from the data set.

PASW version 18.0 (SPSS Inc., 2009) was used to calculate all descriptive statistics and perform univariate and multivariate analyses.

3 | RESULTS

3.1 | Molecular phylogenetics

Across 964–1125 bp of cyt b for all taxa including out-group species, 241 bp were parsimony-informative. Within *Erithacus*, 86 bp were parsimony-informative. Phylogenetic reconstruction using Bayesian analysis identified three major clades within *Erithacus*, which were well-supported by Bayesian (PP 0.97–1.0) and ML analyses (bootstrap support 97–99%) (Figure 2). One clade includes all samples from Europe, Morocco and the Macaronesian islands (except Tenerife and Gran Canaria). This clade (*rubecula*-clade) includes previously unreported samples from Germany, Spain, Morocco, Madeira, La Palma and Azores. Robins from Tenerife formed a second clade (*superbus*-clade). A third clade included all samples from Gran Canaria, and a single bird on Tenerife (*marionae*-clade). The single sample from Georgia (*E. r. caucasicus*) represented a fourth major lineage which clustered with *E. superbus* but with poor support (PP 0.69, ML bootstrap support 67%). The latter two were sister to the *rubecula*-clade. This relationship was well supported by all analyses (PP 0.99, ML bootstrap support 94%).

Sequence divergence among the three clades was substantial (Table 1). The *marionae*-clade differed from the *rubecula*-clade by 4.2%, from the *superbus*-clade by 4.8% and from the single sample of *E. r. caucasicus* by 4.5%. Sequence divergence within the three major clades was low, with mean values ranging from 0.2% in the *marionae*-clade to 0.7% in the *superbus*-clade.

Sequence divergence in *Erithacus* was higher than observed in other Canarian endemic species and their closest relatives: *Columba bolli* – *C. trocaz* (2.5%), *Saxicola dacotiae* – *S. rubicola* (2.7%), *Phylloscopus canariensis* – *P. collybita* (3.5%), *Fringilla teydea* – *F. polatzeki* (2.0%) and *Fringilla canariensis* – *F. maderensis* (1.6%) (Table 1).

3.2 | Vocalisations

A total of 1413 songs of 60 individuals (29 *E. r. marionae* from Gran Canaria, 17 *E. r. superbus* from Tenerife, 14 *E. rubecula* from Europe) were used to test for differences among the three phylogeographically defined groups. In *E. r. marionae*, unprovoked songs and songs recorded after playback did not differ significantly in any of the 24 characters, and were combined in subsequent analyses. Too few songs from *E. r. superbus* and *E. rubecula* from Europe were available for meaningful comparisons between songs from both categories, and these were combined in subsequent analyses.

Song characteristics of *E. r. marionae*, *E. r. superbus* and *E. rubecula* from Europe are given in Table 2 and Figure S1. The song of *E. r. superbus* differs from those of European *E. rubecula* in (i) shorter song duration; (ii) fewer phrases per song; (iii) higher proportion of songs with a high-frequency introductory note; (iv) shorter phrase duration; (v) shorter absolute phrase duration; (vi) shorter duration of first phrase; (vii) fewer notes in song; (viii) fewer unique notes in song; (ix) fewer notes in first phrase; (xi) fewer frequency shifts; (xii) more repetition of notes in last phrase; (xiii) lower maximum frequency; (xiv) smaller frequency range; (xv) fewer low-, mid- and high-frequency notes; (xvi) higher proportion of LF notes; (xvii) lower proportion of mid-frequency notes; (xviii) higher proportion of high-frequency notes, and (xix) fewer unique songs (i.e. more repetitions of entire songs within a song sequence) (Figure 3, Table S5). The combined effect of these differences was easily heard in the field.

The song of *E. r. marionae* differs from those of European *E. rubecula* in (i) shorter song duration; (ii) fewer phrases per song; (iii) higher proportion of songs with a high frequency introductory note; (iv) shorter phrase duration; (v) shorter absolute phrase duration; (vi) shorter duration of first phrase; (vii) fewer notes in song; (viii) lower proportion of unique notes in song; (ix) fewer unique notes in song; (x) fewer notes in first phrase; (xi) higher proportion of frequency shifts; (xii) fewer frequency shifts; (xiii) more repetition of notes in last phrase; (xiv) higher minimum frequency; (xv) smaller frequency range; (xvi) fewer low-, mid- and high-frequency notes; (xvii) lower proportion of LF notes; (xviii) higher proportion of HF notes, and (xix) fewer unique songs (i.e. more repetitions of entire songs within a song sequence) (Figure 3, Table S5). Again, the combined effect of these differences was easily heard in the field.

Songs of *E. r. marionae* appear similar on sonagrams to those of *E. r. superbus* (Figure S1) but differed significantly in having (i) fewer low-frequency notes (<4 kHz) and more mid-frequency notes (4–7 kHz); (ii) higher minimum frequency; (iii) more (and higher proportion of) unique notes per song; (iv) less note repetition in the last phrase; and (v) higher proportion of unique songs (i.e. fewer repetitions of entire songs within a song sequence) (Figure 3, Table S5).

The songs of 60 individuals were used in the PCA. The results of the PCA on the 24 variables are summarised in Table S6. Four components with eigenvalues >1 were extracted from the dataset. The first principal component (PC1) accounted for 49.0% of the variance. PC2, PC3 and PC4 accounted for an additional 17.7%, 8.8% and 6.8% of the variance, respectively. PC1 was represented mostly by absolute phrase duration, number of unique notes in song, total number of notes in song,

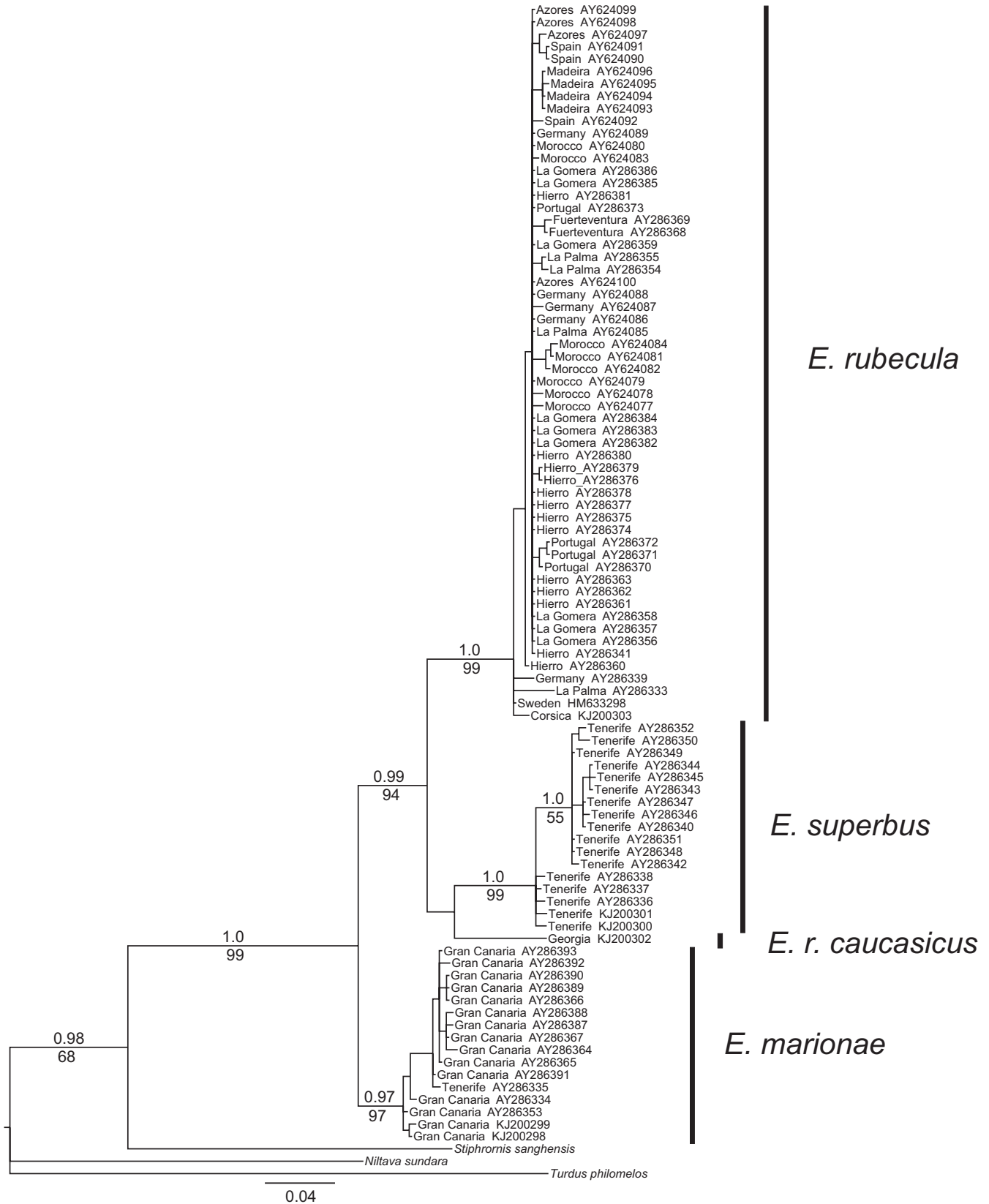


FIGURE 2 Majority-rule consensus tree obtained from Bayesian analysis of 1125 bp of cytochrome b sequences of 92 *Erithacus robins* and three outgroups. Numbers above and below branches indicate Bayesian posterior probabilities (pp) and bootstrap support from maximum likelihood analysis, respectively. Support values are only presented for nodes supported by $pp > .95$

TABLE 1 Levels of cytochrome *b* sequence divergence in robins (*Erithacus*) and four pairs of Canary Islands endemic species (marked with asterisk) and their sister-taxa

Species	Mean \pm SD	Range
Robins (interspecific)		
<i>Erithacus marionae</i> – <i>E. rubecula</i>	4.23 \pm 0.20	3.73–4.97
<i>Erithacus marionae</i> – <i>E. superbus</i>	4.57 \pm 0.16	4.22–5.09
<i>Erithacus marionae</i> – <i>E. (r.) caucasicus</i>	4.53 \pm 0.13	4.22–4.72
<i>Erithacus rubecula</i> – <i>E. superbus</i>	3.74 \pm 0.32	3.11–4.72
<i>Erithacus rubecula</i> – <i>E. (r.) caucasicus</i>	4.07 \pm 0.15	3.85–4.60
<i>Erithacus superbus</i> – <i>E. (r.) caucasicus</i>	4.21 \pm 0.20	3.85–4.47
Other Canary Islands endemics (interspecific)		
<i>Columba bollii</i> * – <i>C. trocaz</i>	2.47 \pm 0.17	2.24–2.73
<i>Phylloscopus canariensis</i> * – <i>P. collybita</i>	3.50 \pm 0.24	3.23–3.85
<i>Saxicola dacotiae</i> * – <i>S. rubicola</i>	2.68 \pm 0.22	2.36–3.11
<i>Fringilla teydea</i> * – <i>F. polatzeki</i> *	2.03 \pm 0.07	1.99–2.24
<i>Fringilla canariensis</i> * – <i>F. maderensis</i>	1.60 \pm 0.02	1.24–0.99
Robins (intraspecific)		
<i>Erithacus marionae</i>	0.23 \pm 0.17	0–0.62
<i>Erithacus rubecula</i>	0.29 \pm 0.25	0–1.24
<i>Erithacus superbus</i>	0.66 \pm 0.44	0–1.37

Note: All values are *p*-values calculated from strictly homologous sequence data of all taxa with complete deletion of missing sites.

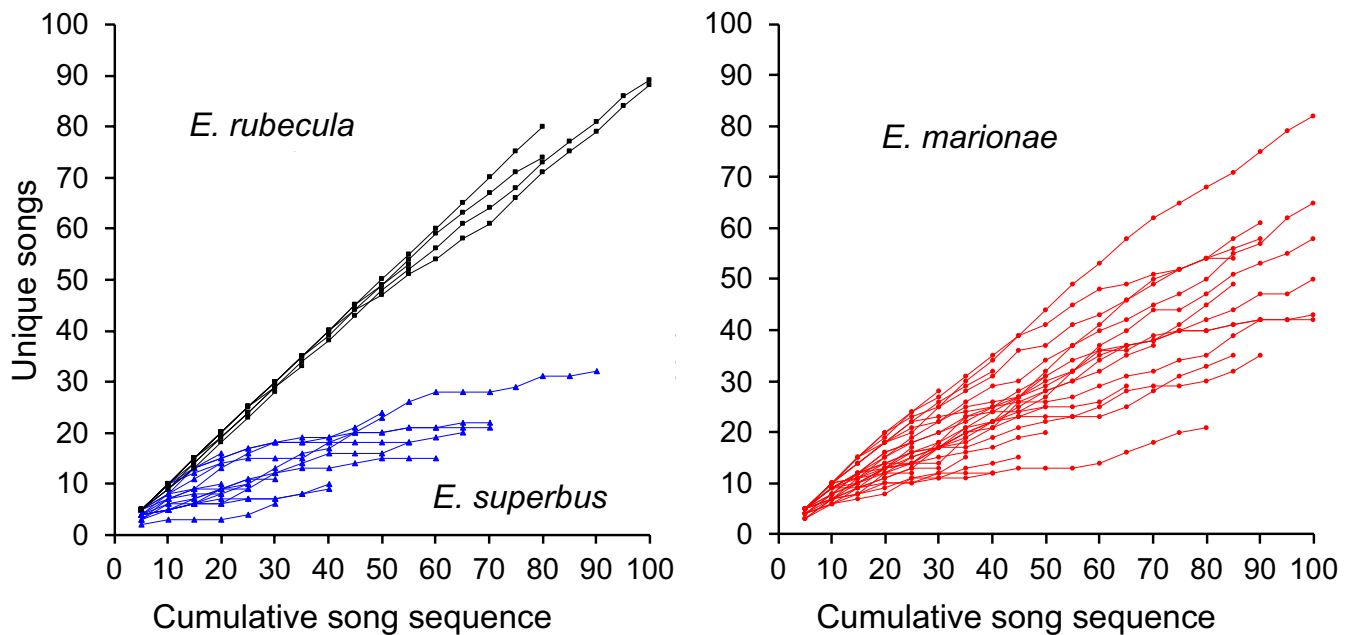


FIGURE 3 Number of unique song types in song sequences of three species of *Erithacus* robins

song duration, number of mid-frequency notes, number of low-frequency notes, number of notes in first phrase and mean phrase duration; PC2 was determined mostly by proportion of low-frequency notes, number of frequency shifts and proportion of mid-frequency notes; PC3 was determined mostly by frequency range, maximum frequency and minimum frequency; and PC4 mostly by proportion

of high-frequency notes, song proportion and number of phrases per song. The groups differed significantly for the first, second and fourth principal components (one-way ANOVA). Songs of *E. r. marionae* differed from those of *E. r. superbus* in PC2 ($p < .001$) and PC4 ($p < .05$), and from European *E. rubecula* in PC1 ($p < .001$). Songs of *E. r. superbus* differed from those of European *E. rubecula*

TABLE 2 Song characteristics of *Erethacus marionae*, *E. superbus* and *E. rubecula*

Variable	<i>Erethacus marionae</i> (N = 29)			<i>Erethacus superbus</i> (N = 17)			<i>Erethacus rubecula</i> (N = 14)			Significance		
	Mean ± SD	Range		Mean ± SD	Range		Mean ± SD	Range		<i>Marionae vs. superbus</i>	<i>Marionae vs. rubecula</i>	<i>Superbus vs. rubecula</i>
Song duration (s)	1.054 ± 0.170	0.774–1.453		1.066 ± 0.096	0.914–1.295		2.410 ± 0.334	1.932–3.179		n.s.	<i>p</i> < .001	<i>p</i> < .001
Number of phrases per song	2.869 ± 0.480	2.240–4.000		2.695 ± 0.737	1.840–5.120		3.736 ± 0.575	3.000–4.850		n.s.	<i>p</i> < .001	<i>p</i> < .001
Proportion of songs with high-frequency introductory note	0.892 ± 0.108	0.640–1.000		0.796 ± 0.160	0.400–1.000		0.414 ± 0.269	0.050–1.000		n.s.	<i>p</i> < .001	<i>p</i> < .001
Mean phrase duration (s)	0.342 ± 0.062	0.214–0.470		0.404 ± 0.116	0.180–0.601		0.649 ± 0.160	0.442–0.880		n.s.	<i>p</i> < .001	<i>p</i> < .001
Song proportion	0.815 ± 0.046	0.671–0.889		0.824 ± 0.064	0.733–0.939		0.868 ± 0.035	0.826–0.938		n.s.	<i>p</i> = .001	n.s.
Absolute phrase duration (s)	0.857 ± 0.159	0.594–1.193		0.879 ± 0.132	0.661–1.178		2.083 ± 0.268	1.641–2.597		n.s.	<i>p</i> < .001	<i>p</i> < .001
Duration of first phrase (s)	0.293 ± 0.079	0.144–0.448		0.320 ± 0.099	0.135–0.494		0.549 ± 0.176	0.097–0.828		n.s.	<i>p</i> < .001	<i>p</i> < .001
Total number of notes in song	7.111 ± 1.093	5.440–9.760		7.154 ± 1.829	4.440–11.200		18.764 ± 3.497	11.850–24.250		n.s.	<i>p</i> < .001	<i>p</i> < .001
Proportion of unique notes in song	0.684 ± 0.076	0.541–0.901		0.556 ± 0.094	0.371–0.698		0.896 ± 0.048	0.814–0.970		<i>p</i> < .001	<i>p</i> < .001	<i>p</i> < .001
Number of unique notes in song	4.422 ± 0.658	3.120–6.040		3.429 ± 0.511	2.520–4.450		16.604 ± 3.238	10.050–21.850		<i>p</i> < .001	<i>p</i> < .001	<i>p</i> = .001
Number of notes in first phrase	1.907 ± 0.735	1.040–4.280		1.982 ± 0.692	1.280–3.360		4.757 ± 1.650	1.050–6.700		n.s.	<i>p</i> < .001	<i>p</i> < .001
Proportion of frequency shifts	0.784 ± 0.099	0.550–0.940		0.744 ± 0.142	0.360–0.907		0.678 ± 0.104	0.521–0.890		n.s.	<i>p</i> < .05	n.s.
Number of frequency shifts	1.550 ± 0.418	0.840–2.600		1.370 ± 0.459	0.480–2.280		2.032 ± 0.589	1.350–3.200		n.s.	<i>p</i> < .01	<i>p</i> < .005
Note repetition in last phrase	0.583 ± 0.147	0.240–0.840		0.724 ± 0.145	0.500–1.000		0.196 ± 0.145	0.000–0.450		<i>p</i> < .01	<i>p</i> < .001	<i>p</i> < .001
Maximum frequency (Hz)	8437 ± 415	7597–9232		8234 ± 354	7411–8710		8647 ± 236	8338–9157		n.s.	n.s.	<i>p</i> < .01
Minimum frequency (Hz)	2864 ± 182	2552–3293		2672 ± 182	2321–3015		2627 ± 284	2079–3109		<i>p</i> < .05	<i>p</i> < .005	n.s.
Frequency range (Hz)	5573 ± 531	4305–6644		5562 ± 360	4595–6075		6020 ± 241	5450–6386		n.s.	<i>p</i> < .01	<i>p</i> < .05
Number of LF notes	2.554 ± 0.853	1.360–5.520		4.218 ± 1.577	2.440–7.580		8.695 ± 2.108	5.900–13.500		<i>p</i> < .001	<i>p</i> < .001	<i>p</i> < .001
Number of MF notes	2.548 ± 0.663	1.340–3.920		1.398 ± 0.583	0.100–2.238		6.904 ± 2.083	3.475–10.750		<i>p</i> < .001	<i>p</i> < .001	<i>p</i> < .001
Number of HF notes	2.009 ± 0.687	1.120–4.240		1.538 ± 0.300	0.880–1.880		3.166 ± 0.696	2.275–4.325		<i>p</i> < .05	<i>p</i> < .001	<i>p</i> < .001
Proportion of LF notes	0.377 ± 0.076	0.263–0.556		0.543 ± 0.085	0.404–0.692		0.466 ± 0.081	0.332–0.581		<i>p</i> < .001	<i>p</i> < .005	<i>p</i> < .05
Proportion of MF notes	0.331 ± 0.064	0.208–0.436		0.205 ± 0.085	0.019–0.357		0.351 ± 0.062	0.259–0.458		<i>p</i> < .001	n.s.	<i>p</i> < .001
Proportion of HF notes	0.293 ± 0.066	0.185–0.484		0.252 ± 0.059	0.127–0.331		0.183 ± 0.041	0.128–0.252		n.s.	<i>p</i> < .001	<i>p</i> < .01

Note: Significance levels are based on one-way ANOVA with Bonferroni correction.

in PC1 ($p < .001$) and PC2 ($p < .05$) (Tukey's post-hoc comparisons).

The initial DFA led to a 100% correct classification of the songs of each of the three groups. The variables most important in the discrimination were: absolute phrase duration, song duration, total number of notes in song, number of low frequency notes, number of mid frequency notes and mean phrase duration (Table S7). The first of the two discriminant functions accounted for 91.3% of the variation, and the second accounted for 8.7% of the variation (Table S7). A scatterplot of the first two roots is shown in Figure 4. The jackknife procedure also provided a high degree of predictive discrimination, with 55 of 60 (91.7%) individuals being correctly assigned to their taxon.

Characteristics of the *tic* calls are given in Table S8 and illustrated in Figure S2. The *tic* calls of both *E. r. marionae* and *E. r. superbus* had a significantly narrower frequency range than those of European *E. rubecula*. To the human ear, *tic* calls of *E. r. marionae* and *E. r. superbus* sound less sharp than those of European *E. rubecula*. The *tic* calls of *E. r. marionae* differed from *E. r. superbus* in significantly lower minimum and maximum frequency, and from European *E. rubecula* in significantly higher minimum frequency but lower maximum frequency (Mann-Whitney *U* test, Table S8). The *tic* calls of *E. r. superbus* differed from European *E. rubecula* in significantly higher minimum frequency (Mann-Whitney *U* test, Table S8). These differences remained significant after Holm's sequential Bonferroni test.

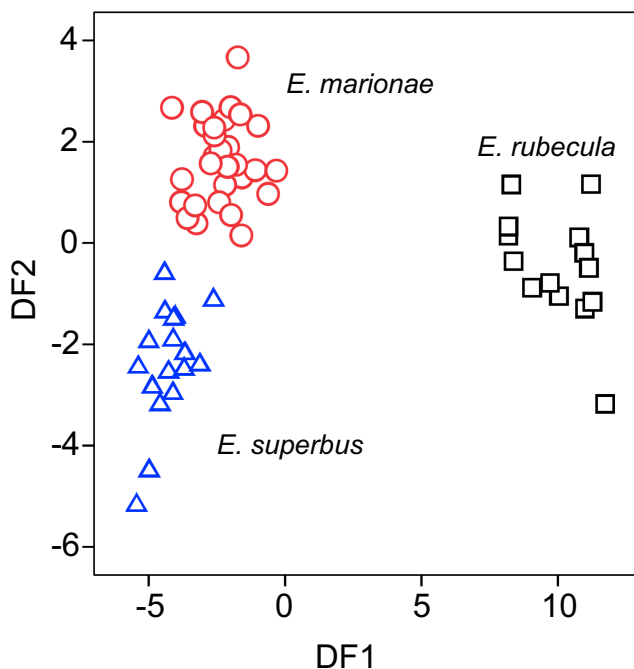


FIGURE 4 Discriminant function scatterplot of song variables. Depicted are the two roots of 24 song variables measured for *Erithacus marionae*, *E. superbus* and *E. rubecula* ($N = 60$)

The *seep* calls differed among the three groups (Table S9, Figure S3). In *E. r. marionae*, the *seep* call is a rising note. In *E. r. superbus*, the note first rises and then falls in pitch, whereas in *E. rubecula* from Europe the call is a falling note. Compared with European *E. rubecula*, *seep* calls of *E. r. marionae* and *E. r. superbus* had a significantly lower starting frequency, lower maximum frequency and a narrower frequency range (Mann-Whitney *U* test, Table S9). These differences remained significant after Holm's sequential Bonferroni test. The frequency change from start to end was positive in *E. r. marionae* but negative in *E. rubecula* from Europe. The *seep* call of *E. r. marionae* differed from that of *E. r. superbus* in greater frequency change from start to end (one-way ANOVA with Bonferroni correction, Table S9).

3.3 | Plumage

Both *E. r. superbus* and *E. r. marionae* (Figure S4) differ from *E. rubecula* from Europe and North Africa in (i) the presence of a pale eye ring, (ii) a darker and greyer band of ash-grey on forecrown and from side of crown down to side of breast, (iii) deeper rufous-chestnut face and chest, (iv) darker, greyish olive upperparts and (v) whiter belly and vent. These differences are also noticeable in live birds under field conditions (G.S., J.A.L. pers. obs.).

3.4 | Morphometrics

Measurements and results of statistical tests are given in Table S10. In both males and females, wing and bill length differed significantly among the three groups. Male and female *E. r. marionae* had shorter wings than both *E. r. superbus* and European robins of the corresponding sex. Similarly, male and female *E. r. superbus* robins had shorter wings than *E. rubecula* from Europe and North Africa. Bill length of male *E. r. marionae* did not differ from that of *E. r. superbus* robins but was significantly greater than that of *E. rubecula* from Europe and North Africa. Both male and female robins from *E. r. superbus* had longer bills than *E. rubecula* from Europe and North Africa of the corresponding sex.

4 | DISCUSSION

4.1 | Taxonomic status of Tenerife Robin

Erithacus superbus was originally described as a distinct species (Koenig, 1889). With the adoption of the polytypic species concept in the early 1900s, it was downgraded

to subspecific rank and included in *E. rubecula* (e.g. Bannerman, 1912; Polatzek, 1908). This treatment has been followed universally (Collar, 2020; Cramp, 1988; Gill et al., 2022; Lack, 1946; Ripley, 1964; Vaurie, 1959). More recently, Bergmann and Schottler (2001) proposed that *E. superbus* be reinstated as a full species, based on differences in plumage and songs, and the reduced response of *E. r. superbus* to songs of *E. rubecula* from Europe and North Africa. The differences in song duration and *tic* calls identified by Stock and Bergmann (1988) and Bergmann and Schottler (2001), and a difference in the proportion of low frequency notes in songs (Larsen et al., 1997), are corroborated by the present study. Our study has documented numerous other differences between the songs of *E. r. superbus* and *E. rubecula* from Europe and North Africa, and in the sonographic structure of female begging calls. In addition, differences between *E. r. superbus* and *E. rubecula* from Europe and North Africa have been documented in wing length and bill length (Dietzen et al., 2003; this study) and egg coloration (Koenig, 1890; Meade-Waldo, 1890; Bannerman, 1963; Schönwetter, 1960–1992). Furthermore, no haplotypes are shared between *E. r. superbus* and *E. rubecula* from Europe and North Africa (Dietzen et al., 2003, this study), and the two taxa are characterised by a high level of genetic divergence (Dietzen et al., 2003, this study).

The plumage, songs, *tic* calls and *seep* calls of *E. r. superbus* and *E. rubecula* from Europe and North Africa differ diagnosably and thus satisfy the diagnosability criterion of the Phylogenetic Species Concept (Cracraft, 1983). The criterion of reproductive isolation, the defining criterion of the Biological Species Concept, cannot be applied directly to taxa with allopatric breeding ranges (Mayr, 1969). However, three lines of evidence suggest that there are intrinsic barriers to interbreeding. First, Tenerife (*E. r. superbus*) and the west Canarian Islands La Palma, El Hierro and La Gomera (*E. r. rubecula*) are geographically close, the shortest distance being a narrow <30km stretch of water between La Gomera and Tenerife. Thus, on geographic grounds these populations may be expected to interbreed regularly, yet no shared haplotypes were found (Dietzen et al., 2003, this study), although this evaluation of gene flow is limited by the absence of nuclear markers and by the relatively low number of individuals sampled. In contrast, populations of *Phylloscopus canariensis*, *Anthus berthelotii*, *Serinus canaria* or the three *Sylvia* warblers breeding in the Canaries seem to interbreed regularly (Dietzen et al., 2006, 2008a; Illera et al., 2007, 2020). Second, *E. rubecula* from Europe and North Africa and *E. r. superbus* show differences in plumage and song characters. Such differences are commonly observed among closely related but reproductively isolated species in chats and flycatchers, including *Saxicola*, *Luscinia*, *Tarsiger*,

Phoenicurus and *Ficedula* (e.g. Cramp, 1988; Martens & Eck, 1995; Urquhart & Bowley, 2002). Furthermore, differences in plumage and song characters are known to be involved in species recognition and reproductive isolation in *Ficedula* (Alatalo et al., 1994; Qvarnström et al., 2006). Finally, a playback study has shown that *E. superbus* responds less often and less intensely to playback of songs of *E. rubecula* than to those of *E. superbus* (Stock & Bergmann, 1988), demonstrating that individuals of *E. superbus* are able to discriminate among songs of *E. rubecula* and *E. superbus*.

The combination of monophyly and evidence for intrinsic barriers to gene flow suggests that *E. superbus* and *E. rubecula* meet the criteria for species status proposed by Avise and Ball (1990) and Johnson et al. (1999). Application of the guidelines for assigning species rank proposed by Helbig et al. (2002) also suggests that *E. superbus* and *E. rubecula* should be treated as species: both taxa are diagnosable by plumage, song and calls, and the level of mtDNA divergence is similar to, or exceeds, that of other species pairs, including members of the closely related genera *Stiphrornis*, *Sheppardia* and *Cossypha* (Voelker et al., 2009), as well as five other endemic birds species on the Canary Islands (Table 1).

The well-supported monophyly of Tenerife and European robins in the cytochrome *b* gene tree (Figure 2) is concordant with differentiation in several other characters, which suggests that each taxon has a unique evolutionary history. We conclude that the robins on Tenerife represent a diagnosably distinct and potentially reproductively isolated lineage which merits treatment as a species (de Queiroz, 1999; Padial et al., 2010).

Erithacus rubecula and *E. superbus* satisfy all commonly applied species criteria, including diagnosability, reproductive isolation, monophyly of gene trees and combinations thereof (Avise & Ball, 1990; Helbig et al., 2002; Johnson et al., 1999). Thus, we agree with Bergmann and Schottler (2001) that *E. superbus* is best treated as a species. The name Tenerife Robin was proposed by Bergmann and Schottler (2001) and is appropriate. We propose the Spanish common name ‘Petirrojo de Tenerife’.

4.2 | Taxonomic status of gran Canaria Robin

The results of this study document that the taxon *mario-nae* represents a population distinct from both *E. superbus* and *E. rubecula*. This view is supported by several lines of evidence. Gran Canaria robins differ from *E. rubecula* in plumage (this study), morphometrics (Dietzen et al., 2003; this study), song (Tables 2 and S5, Figures 3, 4 and S1) and both *tic* (Figure S2) and *seep* calls (Figure S3) and from

E. superbus in song (Tables 2 and S5, Figures 3, 4 and S1), *tic* calls (Figure S2), *seep* calls (Figure S3) and wing length and shape (Dietzen et al., 2003, 2015). Although songs of Gran Canaria Robins are superficially similar to those of *E. superbus*, they could be correctly classified in 100% of the cases using multivariate analysis. In addition, if *E. rubecula* and *E. superbus* are accepted as species, the sister-group relationship of the Gran Canaria population to *E. rubecula* + *E. superbus* indicates that the Gran Canaria population should also be treated as a species. Furthermore, the high level of genetic divergence between the Gran Canaria clade and *E. superbus* (4.6%), *E. rubecula* (4.2%) and *E. r. caucasicus* (4.5%), indicates a long period of isolation. These levels of divergence are similar to or exceed those of other Canarian endemic species and their sister-taxa (Table 1). Valente et al. (2017) calculated the divergence of the Gran Canarian *E. r. marionae* from other *Erithacus* robins at 2.95 million years before present. Although sequence divergence should not be used in isolation to delimit species (Sangster, 2000), high levels of sequence divergence, in combination with a distinct phylogenetic position and differentiation in multiple characters, provide strong support for the hypothesis that the Gran Canaria Robin represents a unique lineage that should be recognised as a species under the general lineage concept of species (de Queiroz, 1999; Padial et al., 2010).

Dietzen et al. (2015) introduced the name *Erithacus rubecula marionae* for the Gran Canaria taxon. We conclude that this taxon is best treated as a species, which becomes *E. marionae*. Dietzen et al. (2015) proposed the English common name ‘Gran Canaria Robin’ and the Spanish common name ‘Petirrojo de Gran Canaria’.

4.3 | Taxonomic status of Caucasian Robin

Our phylogenetic analysis placed the single sample from Georgia (*E. r. caucasicus*) outside the *E. rubecula* clade, but its exact position was unresolved. The distinctiveness of this specimen is underscored by the high levels of sequence divergence from *E. rubecula* (4.1%) and *E. superbus* (4.2%) (Table 1). A previous study based on mitochondrial CO1 sequences also reported a high level of sequence divergence between a single bird from the Caucasus (Krasnodar, Russia) and six individuals from elsewhere in Russia (Kerr et al., 2009; see also Bilgin et al., 2016). Genetic distinctiveness of Caucasian populations was already documented for other Palearctic species, such as the Eurasian Nuthatch, *Sitta europaea* (Nazarizadeh et al., 2016; Päckert et al., 2020), the Coal Tit, *Periparus ater* (Tietze et al., 2011), the Dunnock, *Prunella modularis* (Drovetski et al., 2018) and the Eurasian Wren, *Troglodytes*

troglodytes (Albrecht et al., 2020). Morphologically, *E. r. caucasicus* differs from European *E. rubecula* by its rufous uppertail-coverts and basal half of the tail (Roselaar in Cramp, 1988). Unfortunately, sound recordings of the vocalisations of this taxon is limited to three recordings of the song of presumably the same individual in Azerbaijan (XC480540–42) and a recording of a call from Azerbaijan (XC480543). A proper evaluation of the taxonomic status of Caucasian robins should await detailed study of its phylogenetic position, vocalisations, morphology, geographic distribution and interactions with *E. rubecula* in any area of contact.

4.4 | Biogeography

Recognition of Tenerife and Gran Canaria Robins as separate species adds two single-island endemics to the Canary Islands avifauna. *Erithacus superbus* is one of four endemic bird taxa from Tenerife of which the evolutionary distinctiveness has been corroborated by a molecular phylogeographic study. The other three taxa are *Regulus regulus teneriffae*, *Fringilla canariensis canariensis* and *Cyanistes teneriffae teneriffae*. All three are also found on La Gomera.

Erithacus marionae is the second endemic taxon on Gran Canaria to be raised to species rank. Gran Canaria Blue Chaffinch *Fringilla polatzeki* is currently treated as a species based on differences from Tenerife Blue Chaffinch *F. teydea* in plumage, songs, calls, sperm morphology and mitochondrial and nuclear DNA sequences (Lifjeld et al., 2016; Pestano et al., 2000; Sangster et al., 2016). Two other endemic taxa are also phylogenetically distinct but have not been shown to differ diagnosably in song from their closest relatives. These are the Gran Canarian subspecies of African Blue Tit *Cyanistes teneriffae hedwigii* (Dietzen et al., 2008b; Illera et al., 2011; Kvist et al., 2005; Päckert et al., 2013) and Canary Islands Chaffinch *F. canariensis bakeri* (Illera et al., 2018; Recuerda et al., 2021; Suárez et al., 2009).

The pattern of phylogenetic relationships of robins suggests that the colonisation of the extant robins in the Canary Islands was not the result of one wave but two or three. This is similar to some other genera that contain endemic species of birds on the Canary Islands, such as *Fringilla* (Recuerda et al., 2021) and *Columba* (Gonzalez et al., 2009). The oldest event of colonisation was estimated to have occurred 2.95 (1.46–4.59) million years ago (Valente et al., 2017). The robins occurring on Tenerife colonised the island almost 1 million years after (2.17 [0.99–3.25] million years ago). Finally, the western robins colonised recently the remaining Canary Islands 0.75 (0.32–1.13) million years ago. (Valente et al., 2017).

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REFERENCES

- Alatalo, R. V., Gustafsson, L., & Lundberg, A. (1994). Male colouration and species recognition in sympatric flycatchers. *Proceedings of the Royal Society of London B*, 256, 113–118.
- Albrecht, F., Hering, J., Fuchs, E., Illera, J. C., Ihlow, F., Shannon, T. J., Collinson, J. M., Wink, M., Martens, J., & Päckert, M. (2020). Phylogeography of the Eurasian wren *Nannus troglodytes* (Aves: Passeriformes: Troglodytidae) reveals deep and complex diversification patterns of Ibero-Maghrebian and Cyrenaican populations. *PLoS One*, 15(3), e0230151.
- Avise, J. C., & Ball, R. M. (1990). Principles of genealogical concordance in species concepts and biological taxonomy. *Oxford Surveys in Evolutionary Biology*, 7, 45–67.
- Bannerman, D. A. (1912). The birds of gran Canaria. *Ibis*, 9(6), 557–627.
- Bannerman, D. A. (1963). *Birds of the Atlantic Islands. Volume 1. A history of the birds of the Canary Islands and the salvages*. Oliver & Boyd.
- Bensch, S., Irwin, D. E., Irwin, J. H., Kvist, L., & Åkesson, S. (2006). Conflicting patterns of mitochondrial and nuclear DNA diversity in *Phylloscopus* warblers. *Molecular Ecology*, 15, 161–171.
- Beresford, P., & Cracraft, J. (1999). Speciation in African Forest robins (*Stiphornis*): Species limits, phylogenetic relationships, and molecular biogeography. *American Museum Novitates*, 3270, 1–22.
- Bergmann, H.-H., Helb, H.-W., & Baumann, S. (2008). *Die Stimmen der Vögel Europas*. Aula Verlag.
- Bergmann, H.-H., & Schottler, B. H. (2001). Tenerife Robin – A species of its own? *Dutch Birding*, 23, 140–146.
- Bildsøe, M., & Dabelsteen, T. (1998). *Song differences between three subspecies (Erithacus r. rubecula, E. r. microrhyncha and E. r. superbus) of the robin: A statistical report*. Zoologisk Institut Copenhagen.
- Bilgin, R., Ebeoğlu, N., İnak, S., Kirpik, M. A., Horns, J. J., & Şekerçioğlu, Ç. H. (2016). DNA barcoding of birds at a migratory hotspot in eastern Turkey highlights continental phylogeographic relationships. *PLoS One*, 11(6), e0154454.
- Boesman, P. (2008). *Birds of Belgium and Holland*. Birdsounds.nl.
- Bolle, C. (1854). Bemerkungen über die Vögel der canarischen Inseln. *Journal für Ornithologie*, 2, 447–462.
- Bondesen, P., & Hansen, P. (n.d.). *Fuglesang 1*. Naturhistorisk Museum Århus.
- Chantrey, D. F., & Workman, L. (1984). Song and plumage effects of aggressive display by the European Robin *Erithacus rubecula*. *Ibis*, 126, 366–371.
- Chappuis, C. (2000). *African bird sounds. Birds of North, West and Central Africa*. Société d'Études Ornithologiques de France.
- Collar, N. (2020). *European Robin (Erithacus rubecula), version 1.0. In birds of the world* (del Hoyo J, Elliott A, Sargatal A, Christie DA & de Juana E (Eds)). Cornell Lab of Ornithology.
- Cracraft, J. (1983). Species concepts and speciation analysis. *Current Ornithology*, 3, 159–187.
- Cramp, S. (1988). *The birds of the Western palearctic. Volume 5*. Oxford Univ Press.
- de Queiroz, K. (1999). The general lineage concept of species and the defining properties of the species category. In R. A. Wilson (Ed.), *Species: New interdisciplinary essays* (pp. 49–89). MIT press.
- Dickinson, E. C., & Christidis, L. (Eds.). (2014). *The Howard and Moore complete checklist of the birds of the world. Fourth edition, vol 2: Passerines*. Aves Press.
- Dietzen, C., Garcia-del-Rey, E., Castro, G. D., & Wink, M. (2008a). Phylogenetic differentiation of *Sylvia* species (Aves: Passeriformes) of the Atlantic islands (Macaronesia) based on mitochondrial DNA sequence data and morphometrics. *Biological Journal of the Linnean Society*, 95, 157–174.
- Dietzen, C., Garcia-del-Rey, E., Castro, G. D., & Wink, M. (2008b). Phylogeography of the blue tit (*Parus teneriffae*-group) on the Canary Islands based on mitochondrial DNA and morphometrics. *Journal of Ornithology*, 149, 1–12.
- Dietzen, C., Michels, J. P., & Wink, M. (2015). Formal description of a new subspecies of the European Robin from gran Canaria Island, Spain (Aves: Muscicapidae: *Erithacus rubecula mari-onae* subsp. nov.). *Open Ornithology Journal*, 8, 39–42.
- Dietzen, C., Voigt, C., Wink, M., Gahr, M., & Leitner, S. (2006). Phylogeography of Island canary (*Serinus canaria*) populations. *Journal of Ornithology*, 147, 485–494.
- Dietzen, C., Witt, H.-H., & Wink, M. (2003). The phylogeographic differentiation of the robin *Erithacus rubecula*, Linnaeus 1758, on the Canary Islands revealed by mitochondrial DNA sequence data and morphometrics: Evidence for a new robin species on gran Canaria. *Avian Science*, 3, 115–131.

- Dourado, C. G., Duarte, M. A., Grosso, A. R., Bastos-Silveira, C., Marrero, P., Oliveira, P., Paulo, O. S., & Dias, D. (2014). Phylogenetic origin of the endemic pigeons from Madeira (*Columba trocaz*) and Azores Islands (*Columba palumbus azorica*). *Journal of Ornithology*, *155*, 71–82.
- Drovetski, S. V., Fadeev, I. V., Raković, M., Lopes, R. J., Boano, G., Pavia, M., Koblik, E. A., Lohman, Y. V., Red'kin, Y. A., Aghayan, S. A., Reis, S., Drovetskaya, S. S., & Voelker, G. (2018). A test of the European Pleistocene refugial paradigm, using a Western Palaearctic endemic bird species. *Proceedings of the Royal Society B*, *285*, 20181606.
- East, M. (1981). Alarm calling and parental investment in the Robin *Erithacus rubecula*. *Ibis*, *123*, 223–230.
- Fregin, S., Haase, M., Olsson, U., & Alström, P. (2012). Pitfalls in comparisons of genetic distances: A case study of the avian family Acrocephalidae. *Molecular Phylogenetics and Evolution*, *62*, 319–328.
- Gill, F., Donsker, D. & Rasmussen, P. (Eds) (2022). IOC World Bird List (v12.1). Retrieved from <https://doi.org/10.14344/IOC.ML.12.1>
- Gonzalez, J., Castro, G. D., Garcia-del-Rey, E., Berger, C., & Wink, M. (2009). Use of mitochondrial and nuclear genes to infer the origin of two endemic pigeons from the Canary Islands. *Journal of Ornithology*, *150*, 357–367.
- Hammick, J. (2003). *Bird song of a Dorset Wood & Heathland Garden*. Mandarin Productions.
- Helbig, A. J., Knox, A. G., Parkin, D. T., Sangster, G., & Collinson, M. (2002). Guidelines for assigning species rank. *Ibis*, *144*, 518–525.
- Helbig, A. J., Martens, J., Seibold, I., Henning, F., Schottler, B., & Wink, M. (1996). Phylogeny and species limits in the palearctic chiffchaff *Phylloscopus collybita* complex: Mitochondrial genetic differentiation and bioacoustic evidence. *Ibis*, *138*, 650–666.
- Hoelzel, A. R. (1986). Song characteristics and response to playback of male and female robins *Erithacus rubecula*. *Ibis*, *128*, 115–127.
- Holm, S. (1979). A simple sequential rejective multiple test procedure. *Scandinavian Journal of Statistics*, *6*, 65–70.
- Hounscome, M. V. (1993). Biometrics and origins of some Atlantic Island birds. *Boletim do Museu Municipal do Funchal, Supplement no. 2*, 107–129.
- ICZN. (1999). *International code of zoological nomenclature* (4th ed.). International Trust for Zoological Nomenclature.
- Illera, J. C., Emerson, B. C., & Richardson, D. S. (2007). Population history of Berthelot's pipit: Colonization, gene flow and morphological divergence in Macaronesia. *Molecular Ecology*, *16*, 4599–4612.
- Illera, J. C., Koivula, K., Broggi, J., Päckert, M., Martens, J., & Kvist, L. (2011). A multi-gene approach reveals a complex evolutionary history in the *Cyanistes* species group. *Molecular Ecology*, *20*, 4123–4139.
- Illera, J. C., Ramírez, Á., Rodríguez, L., Polypathellis, K., & Pérez-Tris, J. (2020). Maternal genetic structure reveals an incipient differentiation in the Canary Islands chiffchaff *Phylloscopus canariensis*. *Ardeola*, *67*, 401–414.
- Illera, J. C., Rando, J. C., Rodríguez-Exposito, E., Hernández, M., Claramunt, S., & Martín, A. (2018). Acoustic, genetic, and morphological analyses of the Canarian common chaffinch complex *Fringilla coelebs* ssp. reveals cryptic diversification. *Journal of Avian Biology*, *49*, e01885.
- Illera, J. C., Richardson, D. S., Helm, B., Atienza, J. C., & Emerson, B. C. (2008). Phylogenetic relationships, biogeography and speciation in the avian genus *Saxicola*. *Molecular Phylogenetics and Evolution*, *48*, 1145–1154.
- SPSS Inc. (2009). *PASW for windows. Version 18.0*. SPSS Inc.
- Irestedt, M., Gelang, M., Sangster, G., Olsson, U., Ericson, P. G. P., & Alström, P. (2011). Neumann's warbler *Hemitesia neumanni* (Sylvioidea): The sole African member of a Palaetropic Miocene avifauna. *Ibis*, *153*, 78–86.
- Irestedt, M., Ohlson, J. I., Zuccon, D., Källersjö, M., & Ericson, P. G. P. (2006). Nuclear DNA from old collections of avian study skins reveals the evolutionary history of the Old World suboscines (Aves, Passeriformes). *Zoologica Scripta*, *35*, 567–580.
- Johnson, N. K., Remsen, J. V., & Cicero, C. (1999). Resolution of the debate over species concepts in ornithology: A new comprehensive biologic species concept. *Proceedings of the International Ornithological Congress*, *22*, 1470–1482.
- Johnston, D. (2000). *CoolEdit 2000. Version 1.1*. Syntrellium software corporation.
- Kerr, K. C. R., Birks, S. M., Kalyakin, M. V., Red'kin, Y. A., Koblik, E. A., & Hebert, P. D. N. (2009). Filling the gap – CO1 barcode resolution in eastern palearctic birds. *Frontiers in Zoology*, *6*, 29.
- Kettle, R., & Ranft, R. (1992). *British bird sounds on CD*. British Library.
- Koenig, A. (1889). Vorläufige Notiz über zwei neue Vogelarten von den Canarischen Inseln. *Journal für Ornithologie*, *37*, 182–183.
- Koenig, A. (1890). Ergebnisse einer ornithologischen Reise nach Madeira und zu den Kanarischen Inseln. *Journal für Ornithologie*, *38*, 257–489.
- Kumar, S., Stecher, G., & Tamura, K. (2016). MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, *33*, 1870–1874.
- Kvist, L., Broggi, J., Illera, J. C., & Koivula, K. (2005). Colonisation and diversification of the blue tits (*Parus caeruleus teneriffae*-group) in the Canary Islands. *Molecular Phylogenetics and Evolution*, *34*, 501–511.
- Lack, D. (1946). The taxonomy of the Robin *Erithacus rubecula* (Linn.). *Bulletin of the British Ornithologists' Club*, *66*, 55–65.
- Lack, D. (1951). Geographical variation in *Erithacus rubecula*. *Ibis*, *93*, 629–630.
- Lack, D. (1965). *The life of the Robin* (4th ed.). Witherby.
- Lack, D., & Southern, H. N. (1949). Birds on Tenerife. *Ibis*, *91*, 607–626.
- Larsen, O. N., Dabelsteen, T., Pedersen, S. B., Bang-Møller, M., & Nogales, M. (1997). Competitive release of song in the Tenerifean Robin, *Erithacus rubecula superbus*. *Advances in Ethology*, *32*, 117.
- Lei, X., Lian, Z.-M., Lei, F.-M., Yin, Z.-H., & Zhao, H.-F. (2007). Phylogeny of some Muscicapinae species based on cyt b mitochondrial gene sequences. *Acta Zoologica Sinica*, *53*, 95–105.
- Lifjeld, J. T., Anmarkrud, J. A., Calabuig, P., Cooper, J. E., Johannessen, L. E., Johnsen, A., Kearns, A. M., Lachlan, R. F., Laskemoen, T., Marthinsen, G., Stensrud, E., & Garcia-del-Rey, E. (2016). Species-level divergences in multiple functional traits between the two endemic subspecies of blue chaffinches *Fringilla teydea* in Canary Islands. *BMC Zoology*, *1*(1), 4.
- Martens, J., & Eck, S. (1995). Towards an ornithology of the Himalayas: Systematics, ecology and vocalizations of Nepal birds. *Bonner Zoologische Monographien*, *38*, 1–445.

- Martin, A., & Lorenzo, J. A. (2001). *Aves del Archipiélago Canario*. Francisco Lemus Editor.
- Matheu, E. (2001). *Guía Práctica de Cantos Aves*. Alosa.
- Mayr, E. (1969). *Principles of systematic zoology*. McGraw-Hill.
- Meade-Waldo, E. G. (1890). Further notes on the birds of the Canary Islands. *Ibis*, 6(2), 429–438.
- Moreno, J. M. (2000). *Canto y Reclamos de las Aves de Canarias*. Turquesa Ediciones.
- Nazarizadeh, M., Kaboli, M., Rezaie, H. R., Harisini, J. I., & Pasquet, E. (2016). Phylogenetic relationships of Eurasian nuthatches (*Sitta europaea* Linnaeus, 1758) from the Alborz and Zagros Mountains, Iran. *Zoology in the Middle East*, 62, 217–226.
- Nylander, J. A. A., Wilgenbusch, J. C., Warren, D. L., & Swofford, D. L. (2008). AWTY (are we there yet?): A system for graphical exploration of MCMC convergence in Bayesian phylogenetics. *Bioinformatics*, 2008, 581–583.
- Päckert, M., Bader-Blukott, M., Künzelmann, B., Sun, Y. H., Hsu, Y. C., Kehlmaier, C., Albrecht, F., Illera, J. C., & Martens, J. (2020). A revised phylogeny of nuthatches (Aves, Passeriformes, *Sitta*) reveals insight in intra- and interspecific diversification patterns in the palearctic. *Vertebrate Zoology*, 70, 241–262.
- Päckert, M., Martens, J., Hering, J., Kvist, L., & Illera, J. C. (2013). Return flight to the Canary Islands—the key role of peripheral populations of Afrocanarian blue tits (Aves: *Cyanistes teneriffae*) in multi-gene reconstructions of colonization pathways. *Molecular Phylogenetics and Evolution*, 67, 458–467.
- Padial, J. M., Miralles, A., De la Riva, I., & Vences, M. (2010). The integrative future of taxonomy. *Frontiers in Zoology*, 7, 16.
- Pestano, J., Brown, R. P., Rodriguez, F., & Moreno, A. (2000). Mitochondrial DNA control region diversity in the endangered blue chaffinch, *Fringilla teydea*. *Molecular Ecology*, 9, 1421–1426.
- Polatzek, J. (1908). Die Vögel der Canaren. *Ornithologisches Jahrbuch*, 19, 161–197.
- Qvarnström, A., Haavie, J., Saether, S. A., Eriksson, D., & Part, T. (2006). Song similarity predicts hybridization in flycatchers. *Journal of Evolutionary Biology*, 19, 1202–1209.
- Recuerda, M., Illera, J. C., Blanco, G., Zardoya, R., & Milá, B. (2021). Sequential colonization of oceanic archipelagos led to species-level radiation in the common chaffinch complex (Aves: *Fringilla coelebs*). *Molecular Phylogenetics and Evolution*, 164, 107291.
- Ripley, S. D. (1964). Subfamily Turdinae. In H. G. Deignan, R. A. Paynter, & S. D. Ripley (Eds.), *Check-list of birds of the world* (Vol. 10, pp. 13–227). Museum of Comparative Zoology.
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A., & Huelsenbeck, J. P. (2012). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.
- Sample, G. (1996). *Collins field guide: Bird songs and calls of Britain and northern Europe*. Harper Collins.
- Sangster, G. (2000). Genetic distance as a test of species boundaries in the Citril finch *Serinus citrinella*: A critique and taxonomic reinterpretation. *Ibis*, 142, 487–490.
- Sangster, G., Alström, P., Forsmark, E., & Olsson, U. (2010). Multi-locus phylogenetic analysis of Old World chats and flycatchers reveals extensive paraphyly at family, subfamily and genus level (Aves: Muscipidae). *Molecular Phylogenetics and Evolution*, 57, 380–392.
- Sangster, G., Rodríguez-Godoy, F., Roselaar, C. S., Robb, M. A., & Luksenburg, J. A. (2016). Integrative taxonomy reveals Europe's rarest songbird species, the gran Canaria blue chaffinch *Fringilla polatzeki*. *Journal of Avian Biology*, 47, 159–166.
- Schönwetter, M. (1960–1992). *Handbuch der Oologie*. Akademie Verlag.
- Stamatakis, A., Hoover, P., & Rougemont, J. (2008). A rapid bootstrap algorithm for the RAxML web-servers. *Systematic Biology*, 57, 758–771.
- Stock, M., & Bergmann, H.-H. (1988). Der Gesang des Rotkehlchens (*Erythacus rubecula superbus*) von Teneriffa (Kanarische Inseln) – Struktur und Erkennen eines Inselndialektes. *Zoologisches Jahrbücher Physiologie*, 2, 197–212.
- Suárez, N. M., Betancor, E., Klassert, T. E., Almeida, T., Hernández, M., & Pestano, J. J. (2009). Phylogeography and genetic structure of the Canarian common chaffinch (*Fringilla coelebs*) inferred with mtDNA and microsatellite loci. *Molecular Phylogenetics and Evolution*, 53, 556–564.
- Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., & Kumar, S. (2011). MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution*, 28, 2731–2739.
- Tietze, D. T., Martens, J., Sun, Y. H., Liu Severinghaus, L., & Päckert, M. (2011). Song evolution in the coal tit. *Journal of Avian Biology*, 42, 214–230.
- Tobias, J., & Seddon, N. (2002). Female begging in European robins: Do neighbors eavesdrop for extrapair copulations? *Behavioral Ecology*, 13, 637–642.
- Trilar, T. (2002). *Forest birds of Slovenia*. Slovenian Museum of Natural History.
- Urquhart, E., & Bowley, A. (2002). *Stonechats. A Guide to the Genus Saxicola*. Christopher Helm.
- Valente, L., Illera, J. C., Havenstein, K., Pallien, T., Etienne, R. S., & Tiedemann, R. (2017). Equilibrium bird species diversity in Atlantic islands. *Current Biology*, 27, 1660–1666.
- van der Meij, M. A. A., de Bakker, M. A. G., & Bout, R. G. (2005). Phylogenetic relationships of finches and allies based on nuclear and mitochondrial DNA. *Molecular Phylogenetics and Evolution*, 34, 97–105.
- Vaurie, C. (1959). *The birds of the palearctic Fauna. Passeriformes*. Witherby.
- Voelker, G., Outlaw, R. K., & Bowie, R. C. K. (2009). Pliocene forest dynamics as a primary driver of African bird speciation. *Global Ecology and Biogeography*, 19, 111–121.

SUPPORTING INFORMATION

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