Molecular Phylogenetics and Evolution 164 (2021) 107291

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Sequential colonization of oceanic archipelagos led to a species-level radiation in the common chaffinch complex (Aves: *Fringilla coelebs*)

María Recuerda [a,*], Juan Carlos Illera [b], Guillermo Blanco [a], Rafael Zardoya [a], Borja Milá [a]

[a] National Museum of Natural Sciences, Spanish National Research Council (CSIC), Madrid 28006, Spain
[b] Biodiversity Research Unit (UO-CSIC-PA), Oviedo University, 33600 Mieres, Asturias, Spain

ARTICLE INFO

Keywords:
Islands
Phylogenomics
Phylogeography
Speciation
Species delimitation
Systematics

ABSTRACT

Oceanic archipelagos are excellent systems for studying speciation, yet inference of evolutionary process requires that the colonization history of island organisms be known with accuracy. Here, we used phylogenomics and patterns of genetic diversity to infer the sequence and timing of colonization of Macaronesia by mainland common chaffinches (*Fringilla coelebs*), and assessed whether colonization of the different archipelagos has resulted in a species-level radiation. To reconstruct the evolutionary history of the complex we generated a molecular phylogeny based on genome-wide SNP loci obtained from genotyping-by-sequencing, we ran ancestral range biogeographic analyses, and assessed fine-scale genetic structure between and within archipelagos using admixture analysis. To test for a species-level radiation, we applied a probabilistic tree-based species delimitation method (mPTP) and an integrative taxonomy approach including phenotypic differences. Results revealed a circuitous colonization pathway in Macaronesia, from the mainland to the Azores, followed by Madeira, and finally the Canary Islands. The Azores showed surprisingly high genetic diversity, similar to that found on the mainland, and the other archipelagos showed the expected sequential loss of genetic diversity. Species delimitation methods supported the existence of several species within the complex. We conclude that the common chaffinch underwent a rapid radiation across Macaronesia that was driven by the sequential colonization of the different archipelagos, resulting in phenotypically and genetically distinct, independent evolutionary lineages. We recommend a taxonomic revision of the complex that takes into account its genetic and phenotypic diversity.

1. Introduction

Oceanic archipelagos are excellent model systems to study evolution and have been crucial in advancing our understanding of species diversification and ecosystem assembly processes (Emerson, 2002; Losos and Ricklefs, 2009; Warren et al., 2015; Patiño et al., 2017; Whittaker et al., 2017)(Leroy et al., 2021). According to island biogeography theory, the number of species that can colonize and thrive on an oceanic island is a dynamic process primarily determined by the size of the island and its distance from the mainland (MacArthur and Wilson, 1967; Valente et al., 2017, 2020). Upon arrival, the original colonizers would start diverging from their mainland ancestors through neutral and/or selective processes (Warren et al., 2015). In many cases, the colonization of an archipelago is accompanied by an acceleration of net diversification rates (e.g. Delmore et al., 2020). This leads to species radiations in which phenotypic diversification could be driven either by adaptation to vacant ecological niches and available resources in the different islands (Schluter, 2000; Grant and Grant, 2008; Blanco et al., 2014), or by genetic drift and sexual selection in geographic isolation (Rundell and Price, 2009), although both types of processes can be at work within a single radiation (Gillespie et al., 2020).

Although evolutionary history is often simplified in oceanic archipelagos relative to continents, island colonization can be a complex process that can include multiple colonization and extinction events, back colonizations, as well as the maintenance of gene flow within and between archipelagos, and even with the continent (Illera et al., 2012; Morinha et al., 2020). When inferring the colonization history of oceanic archipelagos, it has been usually assumed that the original settlers originated from the closest mainland area (Grant, 1979; Thornton, 2007), subsequently following a chronological sequence of colonization consistent with a "stepping-stone model" (Funk and Wagner, 1995; Juan et al., 2000; Beheregaray et al., 2004; VanderWerf et al., 2010). However, this basic model is one of many possible ones (Sanmartín et al., 2008), and molecular phylogenetic analyses using exhaustive regional

* Corresponding author at: Museo Nacional de Ciencias Naturales, Calle José Gutiérrez Abascal 2, Madrid 28006, Spain.
E-mail address: mariarecuerdacarrasco@gmail.com (M. Recuerda).

https://doi.org/10.1016/j.ympev.2021.107291
Received 13 January 2021; Received in revised form 28 July 2021; Accepted 5 August 2021
Available online 9 August 2021

sampling are increasingly reporting counterintuitive colonization routes, suggesting that long distance migration events could be disrupted by a diverse range of factors (Emerson et al., 1999; Nathan, 2006; Felicísimo et al., 2008; Sequeira et al., 2008; Illera et al., 2012; Stervander et al., 2015; Morinha et al., 2020). Hence, in order to understand the evolutionary divergence of island biota, it is essential to set a robust phylogenetic framework to identify the closest living mainland relative, the phylogenetic relationships among insular species and populations, the timing and sequence of colonization (i. e., the order in which different islands were occupied), and the history of gene flow among insular populations within and between archipelagos (Whittaker and Fernández-Palacios, 2007; Losos and Ricklefs, 2009; Warren et al., 2015).

The common chaffinch (*Fringilla coelebs*) complex represents a sound system to study speciation processes on oceanic islands, as its broad geographic range includes Eurasia, Northern Africa, and the Atlantic Ocean archipelagos of Macaronesia, including Azores, Madeira and the Canary Islands, but not the Selvagens and Cabo Verde (Shirihai and Svensson, 2018). Common chaffinches on the mainland and the archipelagos differ genetically and in color pattern, morphology, and vocalizations (Grant, 1979; Lynch and Baker, 1994; Illera et al., 2018; Samarasin-dissanayake, 2010; Lachlan et al., 2013). Insular common chaffinches have characteristic dark blue-gray dorsal plumage, a larger body mass, shorter wings, as well as longer tarsi and bills compared to continental specimens (Grant, 1979). In addition, there are notable genetic and phenotypic differences among populations between and within the different archipelagos (see below). Although all common chaffinches are currently classified as a single species with several subspecific taxa, it has been suggested that mainland populations and the different archipelago radiations could be part of a multi-species complex (Illera et al., 2016).

Early proposals for the origin of Macaronesian chaffinches assumed the independent colonization of each archipelago from its nearest mainland, with phenotypic similarities among insular populations resulting from evolutionary convergence (Grant, 1979). In contrast, more recent studies based on mitochondrial DNA sequence data favored a single wave of colonization starting from Europe to Azores, Madeira, and finally the Canary Islands (Marshall and Baker, 1999), though limited genetic sampling and weak phylogenetic signal provided only tentative support for this hypothesis. Here, we tested these alternative hypotheses on the timing and colonization route of the common chaffinch radiation by building a robust phylogeny based on thousands of genome-wide loci. Genome-wide datasets based on SNP (single nucleotide polymorphism) loci have proven useful in resolving phylogenetic relationships at various evolutionary timescales, from deep nodes (Sackton et al., 2019) to very recent radiations (Stervander et al., 2015; Friis et al., 2016; Kozak et al., 2018; Meier et al., 2018). Based on a well-resolved phylogeny, we used biogeographical inference to estimate ancestral ranges using a dispersal-cladogenesis-extinction model that takes founder-event speciation into account and is thus particularly suited for oceanic island systems (de Queiroz, 2005; Gillespie et al., 2012; Matzke, 2013). Finally, in order to determine whether the colonization of oceanic archipelagos has resulted in a species-level radiation, we took an integrative taxonomy approach to determine the number of species in the complex according to different methods of species delimitation. This exercise has clear evolutionary and taxonomic implications, but also potentially major conservation impact for the taxa involved, most of which have restricted ranges and small population sizes (Whittaker et al., 2005).

2. Materials and methods

2.1. Study system and sample collection

The common chaffinch is currently considered to be a polytypic species composed of about 16 subspecies (Clement, 2020) which can be divided into three main geographic groups: a Eurasian group that includes the nominate form (*coelebs*) and related subspecies; a North African group that includes forms *africana*, *spodiogenys* and *harterti* (Svensson, 2015); and a Macaronesian group that includes *moreletti* from the Azores, *maderensis* from Madeira, and four subspecies on the Canary Islands, *canariensis* on Tenerife and La Gomera, *palmae* on La Palma, *ombriosa* on El Hierro, and the recently described *bakeri* on Gran Canaria (Martín and Lorenzo, 2001; Suárez et al., 2009; Illera et al., 2018).

For the present study we obtained blood samples from wild populations in Europe (Segovia, Spain), North West Africa (Ceuta, Spain), the Azores, Madeira and the Canary Islands, so that subspecies included were *coelebs*, *africana*, *moreletti*, *maderensis*, *canariensis*, *palmae*, *ombriosa* and *bakeri* (Fig. 1, Table S1). Birds were captured in the field using mist nets, and each individual was marked with a uniquely numbered Portuguese or Spanish aluminium band to avoid resampling. Birds were captured during the breeding season. Blood samples were obtained by venipuncture of the brachial vein and stored in absolute ethanol at −20 °C in the laboratory until DNA extraction.

2.2. SNP genotyping and analysis

High quality genomic DNA was extracted using a QIAGEN Blood and Tissue kit (Qiagen, Valencia, CA) following the manufacturer's protocol. SNP discovery was done using a genotyping-by-sequencing approach (Elshire et al., 2011) with restriction enzyme *PstI*, and sequencing was carried out on an Illumina Hiseq X Ten platform. Forward raw reads were trimmed to remove low quality ends using TrimGalore! V, 0.4.4 (http://www.bioinformatics. babraham.ac.uk/projects/trim_galore). We aligned the reads against the first version of the high-quality common chaffinch reference genome (GCA_015532645.1, Recuerda et al., 2021) using BWA 0.7.16 (Li and Durbin, 2009), using the "–mem" algorithm and default parameters. The reference genome was mapped against the zebra finch (*Taeniopygia guttata*) genome v87 available in Ensembl (Yates et al., 2016). We used the Chromosembler tool available in Satsuma (Grabherr et al., 2010) obtaining a final assembly 906.9 Mb in length and an N50 of 69.09 Mb. Variant calling was performed with GATK 3.6 HaplotypeCaller and GenotypeGVCFs tools (McKenna et al., 2010), calling all samples together with a minimum base and mapping quality score of 30. The variant dataset obtained was filtered using VCFtools version 0.1.15 (Danecek et al., 2011) keeping biallelic sites with a depth ranging between 4 and 60, a phred quality score over 30, and a minor allele frequency over 0.018. Indels were also removed along with sites with over 75% missing data and showing significant deviation from Hardy-Weinberg equilibrium (p-value $< 10^{-4}$). To recover the chromosomal coordinates of the scaffolds obtained with HiRiseTM, we mapped and oriented them against the zebra finch (*Taeniopygia guttata*) genome v87 available in ensembl (Yates et al., 2016). We used the Chromosembler tool available in Satsuma (Grabherr et al., 2010) resulting in a final genome assembly 955.9 Mb length and a N50 of 71.46 Mb.

In order to separate neutral loci from loci under divergent selection we used BayeScan v2.1 (Foll and Gaggiotti, 2008) to detect outlier loci in an F_{ST} distribution. We ran the program on a dataset of 159,534 loci with the default sample size of 5,000, a thinning interval of 200, a total of 20 pilot runs of 10,000 iterations each, and a burn-in of 100,000. We checked for convergence and set the false discovery rate (FDR) parameter at 0.1, obtaining 157,366 neutral SNPs and 2168 outliers. We filtered the neutral dataset for linkage disequilibrium (LD) using the snpgdsLDpruning function from the {SNPRELATE} package (Zheng et al., 2012) in R version 3.4.3 (R Core Team, 2017), resulting in a final dataset of 100,166 neutral SNPs.

2.3. Genetic diversity

Our final SNP dataset was composed of 81 individuals of the common chaffinch divided into two mainland and seven insular populations

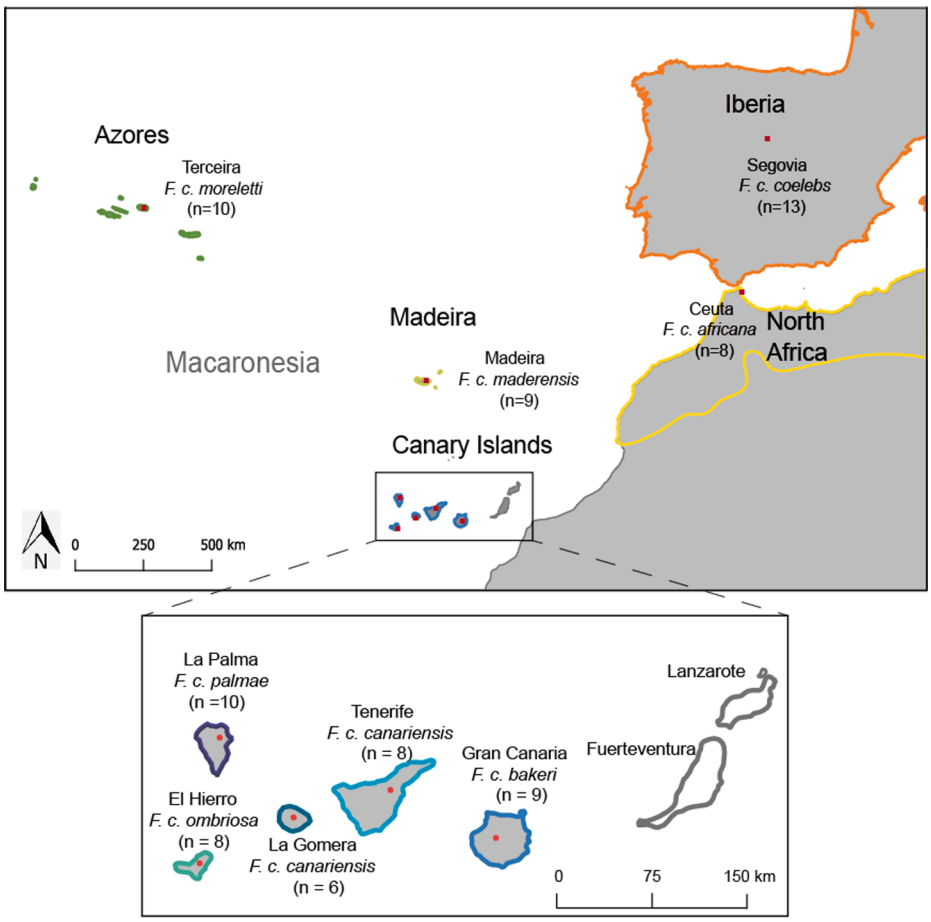

Fig. 1. Distribution map of the common chaffinch in the study area. Note the species is absent in the eastern Canary islands of Fuerteventura and Lanzarote. Red dots correspond to sampling sites and sample sizes are indicated in parentheses. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Descriptive genetic statistics of the common chaffinch populations obtained with 159,534 SNPs: Locality, sample size (n), nucleotide diversity (π), observed heterozygosity (H_o) and expected heterozygosity (H_e). All F_{IS} values were significant (one sample *t*-test, $p < 0.0001$).

Region/Locality	n	π	H_o	H_e
Mainland	21	0.193	0.160	0.187
Africa (Ceuta)	8	0.177	0.160	0.165
Europe (Segovia)	13	0.188	0.159	0.177
Macaronesia	60	0.075	0.049	0.074
Azores (Terceira)	10	0.140	0.116	0.130
Madeira	9	0.051	0.047	0.048
Canary Islands	41	0.045	0.034	0.045
Gran Canaria	9	0.035	0.033	0.033
Tenerife	8	0.032	0.030	0.030
La Gomera	6	0.041	0.039	0.038
La Palma	10	0.031	0.031	0.029
El Hierro	8	0.042	0.039	0.039

(Table 1). Using the complete SNP dataset (159,534 loci), we calculated for each population: nucleotide diversity (π), the expected and observed heterozygosities (H_e and H_o) and pairwise F_{ST} among populations. All statistics were calculated using STACKS v 1.47 (Catchen et al., 2013). A one-sample *t*-test was used to determine whether the mean F_{IS} score in each population was statistically different from zero using R version 3.4.3 (R Core Team, 2017).

For comparative purposes, we also estimated genetic diversity and demographic parameters using coding regions from the mitochondrial genome (900 bp of the *atp8* and *atp6* genes, and 835 bp of the *nad2* gene), both individually and as a concatenated dataset (1,735 bp). The mitochondrial genes were amplified using primers L5215 (5′-TATCGGGCCCATACCCCGAAAAT-3′) (Hackett, 1996) and H6313 (5′-CTCTTATTTAAGGCTTTGAAGGC-3′) (Sorenson et al., 1999) for *nad2* and L8929 (5′-GGACAATGCTCAGAAATCTCGCGG-3′) (Eberhard and Bermingham, 2005) and H9855 (5′-ACGTAGGCTTGGATTATKGC-TACWGC-3′) (Sorenson et al., 1999) for *atp8* and *atp6*. PCR products were purified with an ethanol precipitation and sequenced by Sanger sequencing. Sequences were aligned using Sequencher 4.1.1 (Genecodes Inc., Ann Arbor, MI, USA) and the accuracy of variable sites was checked visually on the chromatograms. We calculated haplotype (*h*) and nucleotide (π) diversity indices per population, pairwise genetic distances and performed Fu's neutrality test (designed to detect changes in population growth; Fu, 1997) using Arlequin v. 3.5 (Excoffier and Lischer, 2010).

2.4. Phylogenetic analysis and estimation of divergence times.

To infer the evolutionary history of common chaffinches in the Macaronesian region we reconstructed a phylogenetic tree based on the neutral SNP dataset (100,166 loci), including a Tenerife blue chaffinch (*Fringilla teydea*) as outgroup. We built a maximum-likelihood (ML) tree using RAxML v8.1.16 (Stamatakis, 2014), using a GTR + GAMMA substitution model with the Lewis ascertainment bias correction as recommended. We implemented the rapid bootstrap algorithm (Stamatakis et al., 2008) and evaluated node support with 1000 replicates.

To estimate the timing of island colonization, we used three mitochondrial genes (*nad2*, *atp8* and *atp6*, Table S1) to reconstruct a

chronogram with Bayesian inference in BEAST v 1.8.4 (Drummond et al., 2012), using the CIPRES Science Gateway (Miller et al., 2010) and excluding the outgroup to avoid long-branch effects (Drummond and Bouckaert, 2015). We concatenated all genes (1,735 bp) and selected the best-fitting substitution model with Partitionfinder 2.1.1 (Lanfear et al., 2016), using the Akaike Information Criterion (AIC). The model selected for all markers and all codon positions was GTR + I. Based on results from preliminary runs, we implemented a strict molecular clock with a lognormal distribution of the mutation rate, setting mean values of 0.029 and 0.019 substitutions/site/My for *nad2* and *atp8&6* genes, respectively (Lerner et al., 2011). The haplotype networks for *nad2* and *atp8&6* genes were generated using Hapview (Salzburger et al., 2011) with maximum likelihood trees constructed using Geneious 10.2.2 (https://www.geneious.com) with default parameters.

We also estimated divergence times from a Bayesian phylogenetic tree using SNAPP, a template within BEAST version 2.5.1 (Bouckaert et al., 2018) using the CIPRES Science Gateway (Miller et al., 2010,). SNAPP infers the species tree from biallelic SNPs integrating over all possible gene trees by the implementation of the multispecies coalescent model. We used the neutral SNP dataset restricted to two individuals per population and allowing 5% of missing data, which resulted in 15,836 SNP loci. We used the script "snapp_prp.rb" (Stange et al., 2018) to generate the XML input file keeping the original settings, except that the MCMC chain was set to 2,000,000 generations. We used the RAxML tree as starting tree and set four constraints: (1) The monophyly of North Africa; (2) the monophyly of Europe; (3) the monophyly of the clade including all the insular populations; and (4) given the lack of common chaffinch fossil records in Macaronesia, we used a secondary calibration point based on our dating of the common chaffinch colonization of Macaronesia with mtDNA. We set a lognormal distribution for the divergence time of the insular clade with mean at 0.83 Ma (offset = 0, standard deviation = 0.1). A previous study based on a standard cyt-*b* calibration of 0.01 subs/site/lineage/ma obtained a similar date of 0.82 ma (Illera et al., 2018).

For both Bayesian analyses we checked for convergence using Tracer v 1.6 (Rambaut et al., 2014), ensuring that the estimated sample sizes (ESS) were over 200. Node ages and credible intervals (95% highest posterior density, HPD) were estimated, the best tree was generated using TREEANNOTATOR v1.8.4. (Drummond et al., 2012) and was displayed using FigTree v.1.4.3 (Rambaut, 2017).

2.5. Ancestral range estimation

Ancestral range estimation for the common chaffinch across Macaronesia was performed with the SNAPP phylogeny using the BioGeoBEARS package in R (Matzke, 2013). Among the dispersal-extinction-cladogenesis (DEC) models, we selected the DEC + J model. The "j" parameter allows for "founder-event speciation", which assumes that upon colonization of a remote locality, the founding population becomes instantly genetically distinct from the ancestral population (Matzke, 2014), a model that is appropriate for oceanic island systems, in which speciation takes place relatively quickly following colonization (De Queiroz, 2005; Cowie and Holland, 2006; Gillespie et al., 2012). Even though the DEC + J model may have a tendency to underestimate anagenetic events of dispersal and local extinction, which are probabilistic with respect to time, while inflating cladogenetic events of range expansion which are not time related (Ree and Sanmartín, 2018), we selected this model as the most biologically appropriate for our island scenario, where each taxon occupies a unique area that was likely sequentially colonized. We did not compare different models because according to Ree and Sanmartín (2018), their likelihoods are not statistically comparable, so that biological considerations are recommended for model selection instead. We set nine locations corresponding to the two continental areas (Europe and North Africa), which are also separated by sea, and the seven insular populations (Terceira in the Azores, Madeira, Gran Canaria, Tenerife, La Gomera, La Palma and El Hierro).

2.6. Genetic structure

To assess patterns of genetic structure and admixture between and within archipelagos, we used the program Structure (Pritchard et al., 2000) with the neutral SNP dataset, excluding the outgroup and filtered for missing data (5%), which resulted in a total of 16,416 loci. We used PGDSPIDER (Lischer and Excoffier, 2012) to convert the vcf file to the Structure format, ran preliminary analyses to infer the lambda value, and then ran analyses five times per K value, each one including 100,000 iterations and a burn-in of 50,000 iterations. The first analysis included individuals from all localities, with K values ranging from 2 to 9. To improve resolution in specific areas, we also ran separate region-specific analyses of the two mainland populations (K = 2–5), and the Canary Islands (K = 2–5). The structure plots were generated using CLUMPAK (Kopelman et al., 2015). The optimal K value was determined by the natural logarithm of the probability of the data [ln(Pr(X|K)] as described in the Structure manual. In order to check the robustness of results, we performed the same three analyses of population structure with Admixture v1.3.0 (Alexander et al., 2009) using the complete dataset of neutral SNPs (100,166 loci) with 200 bootstrap replicates.

To estimate fine-scale population structure and quantify the ancestry sources of each common chaffinch population, we used fineRADstructure (Malinsky et al., 2018), which uses information on haplotype linkage and common ancestry among individuals to produce a summary of nearest-neighbor haplotype relationships in the dataset in the form of a co-ancestry matrix. We converted the vcf file of neutral SNPs into fineRADstructure format using radiator (Gosselin, 2019) and we ran the pipeline using default parameters with 100,000 MCMC generations, sampling every 1,000 steps, and a burn-in of 100,000 steps. The tree was constructed with the fineSTRUCTURE algorithm (Lawson et al., 2012) with 10,000 iterations. The results obtained were plotted in R by adapting the scripts provided in http://cichlid.gurdon.cam.ac.uk/fineRADstructure.html.

2.7. Species delimitation

To estimate the number of species in the common chaffinch radiation, we applied the multi-rate Poisson Tree Processes (mPTP) method for species delimitation (Kapli et al., 2017). The mPTP method is based on a rooted phylogenetic tree obtained by probabilistic methods, and it attempts to differentiate speciation from coalescence processes, allowing different intraspecific coalescent rates and a constant speciation rate, assuming that branching events within species are more frequent than between species. For input, we used the RAxML tree based on neutral SNPs, and we ran 10 independent MCMC chains of 10^8 steps, logged every one million generations, with a burn-in of two million steps. We used the "-multi" option to allow variance in coalescent rates among species, and the minimum branch length used was 0.001831, as calculated with the tool "minbr_auto". Average node support values (AVS) were generated for each clade by the MCMC method, with values close to one indicating a robust ML delimitation. We set a conservative threshold for support values over 75 to consider clusters as different candidate species (Kapli et al., 2017). We ensured chain convergence using the Average Standard Deviation of Support Values (ASDDSV), which quantifies the similarity among independent MCMC runs.

In addition to the mPTP analysis we applied an integrative taxonomic approach to species delimitation (Padial et al., 2010). In addition to the genetic data, we took into account differences in plumage coloration (Fig. 7) as well as previously published morphological data (Grant, 1979) and bioacoustic data (Lachlan et al., 2013). Finally, we applied a scoring system for avian species delimitation proposed by Tobias et al. (2010) which is based on phenotypic and geographic data, and has been adopted by some major avian taxonomic systems (del Hoyo et al., 2020; Handbook of the Birds of the World and BirdLife International, 2019).

The method scores and combines the strongest differences in five types of avian traits: morphology, acoustics, plumage, ecology, behavior, and geographical relationships, and assigns species status if the total score reaches or exceeds an arbitrary threshold value (See supplementary Methods, File S1). This points-based scoring system has received some criticism due to the subjectivity involved in the scoring itself, and because the quantitative criteria are based on fairly arbitrary magnitudes of difference that are broadly applied across taxa (Winker, 2010b). However, the method has demonstrated to be useful when used for taxonomical purposes (Winker, 2021) and its performance has been found to be high when tested against recently accepted splits (Tobias et al., 2021).

3. Results

3.1. SNP genotyping

We obtained 27,052,300 reads from GBS, which resulted in 15,506,115 reads after trimming. The mapping using BWA resulted in 207,339,592 primary aligned reads mapped to the common chaffinch reference genome. The variant calling with GATK generated 1,988,317 variants and after filtering with VCFTOOLS we obtained 159,534 variants with an average depth per site of 16.5.

3.2. Genetic diversity and differentiation

Genetic diversity indices were lower on islands than on the mainland (Table 1). Nucleotide diversity and heterozygosity were highest in mainland populations, followed by Azores and Madeira, with the Canary Islands showing the lowest values (Table 1). Pairwise F_{ST} values among populations ranged from 0.07 to 0.16, with an average of 0.13 (Table 2). The lowest differentiation was found among the common chaffinches of Europe and North Africa, the latter being more differentiated from all insular populations than the former. The Azores population showed the lowest differentiation from mainland populations, and both Azores and Madeira showed similar values of differentiation with respect to the Canary Islands. Within the Canary Islands, F_{ST} values were generally consistent with geographic proximity among islands, with values ranging from 0.09 between Tenerife and La Gomera, and 0.14 between Gran Canaria and the other islands. Genetic distances calculated with the mtDNA dataset showed a similar pattern to that found for SNP markers (Tables 4, S3).

3.3. Phylogenetic analysis, colonization route and divergence times

The ML phylogenetic tree based on 100,166 neutral SNPs was highly resolved, with maximal node support for clades separating the different archipelagos and the different islands within the Canary archipelago (Fig. 2). The phylogenetic tree based on mitochondrial markers showed a similar topology to the genome-wide phylogeny, except for two relationships, which were not highly supported: (1) the two mainland populations (Europe and North Africa) formed a single clade (Fig. 3a); (2) the population of Gran Canaria was sister to a clade including two sister subclades: (a) the westernmost islands of La Palma and El Hierro, and (b) the geographically close islands of Tenerife and La Gomera. Individuals within the Tenerife-La Gomera clade showed an incomplete sorting of haplotypes despite a higher proportion of private haplotypes per island (Fig. 3a). Haplotype networks revealed that the *nad2* gene showed higher diversity than the *atp8&6* genes except in Madeira and La Palma, and showed better sorting of haplotypes between the two mainland populations and the Tenerife/La Gomera clade, yet neither marker showed complete lineage sorting relative to the genome-wide phylogeny (Fig. 3b,c, Tables 3 and S2), which provided higher phylogenetic resolution than the mtDNA data.

Dating estimates indicated that insular populations diverged from the mainland around 0.83 million years ago (HPD: 0.38–1.48 Ma), Madeira diverged from the Canary Islands about 0.70 Ma ago (HPD: 0.34–1.28), and the Canary Islands differentiated from each other within the last half million years (Fig. 3a).

The SNAPP phylogenetic tree recovered the same topology as the mitochondrial phylogenetic tree but separated the insular populations of Tenerife and La Gomera (Fig. 4). The ancestral range estimation confirmed that colonization of the Atlantic Islands started in Azores, then Madeira, and finally the Canary Islands (Fig. 4). However, the mainland starting point was not clear, with both Europe and North Africa showing similar probabilities. Within the Canary Islands, the analysis suggested that the first island to be colonized was Gran Canaria, but the ancestral range of the remaining islands was not resolved.

3.4. Genetic structure and admixture analysis

The Structure analysis based on the genome-wide SNP dataset revealed marked genetic structure across the region that was consistent with the ML phylogeny. The optimal number of genetic clusters was K = 6, with clusters corresponding to North Africa, Europe, Azores, Madeira, Gran Canaria and the remaining Canary Islands, respectively (Fig. 5a). An analysis restricted to the mainland individuals confirmed the separation of both populations as the best clustering (Fig. 5b, Fig. S2, Fig. S3), and a separate analysis of the Canarian archipelago yielded five clusters with high posterior probability of assignment of all individuals to each of the five islands at K = 5 (Fig. 5c). In the latter analysis, K = 2 separated Gran Canaria from the rest, K = 3 additionally separated the western islands (La Palma and El Hierro) and the central islands (Tenerife and La Gomera), and K = 4 and K = 5 separated these two pairs of islands from each other, although La Gomera showed a small proportion of admixture with Tenerife. The Admixture results were generally consistent with the Structure analysis, with the same optimal number of clusters but some differences in the sequence of population separation (Fig. S2, Table S4). In both analyses, the Azores shared some variance with the mainland at K = 2, and Gran Canaria shared some variance with Madeira, being the first island to separate from the rest within the Canary archipelago.

The FineRADstructure analysis showed consistent results with previous analyses and divided individuals into the same nine populations

Table 2
Fixation index (F_{ST}) values among populations of the common chaffinch obtained with 159,534 SNPs. EUR (Iberian Peninsula), AFR (North Africa), AZO (Azores), MAD (Madeira), GCA (Gran Canaria), TEN (Tenerife); GOM (La Gomera), HIE (El Hierro) and PAL (La Palma).

	EUR	AZO	MAD	GC	TEN	GOM	PAL	HIE
AFR	0.069	0.127	0.152	0.148	0.150	0.133	0.152	0.143
EUR		0.094	0.113	0.109	0.111	0.097	0.113	0.105
AZO			0.155	0.157	0.159	0.143	0.161	0.151
MAD				0.159	0.163	0.147	0.158	0.150
GCA					0.135	0.127	0.140	0.136
TEN						0.089	0.134	0.126
GOM							0.118	0.113
PAL								0.096

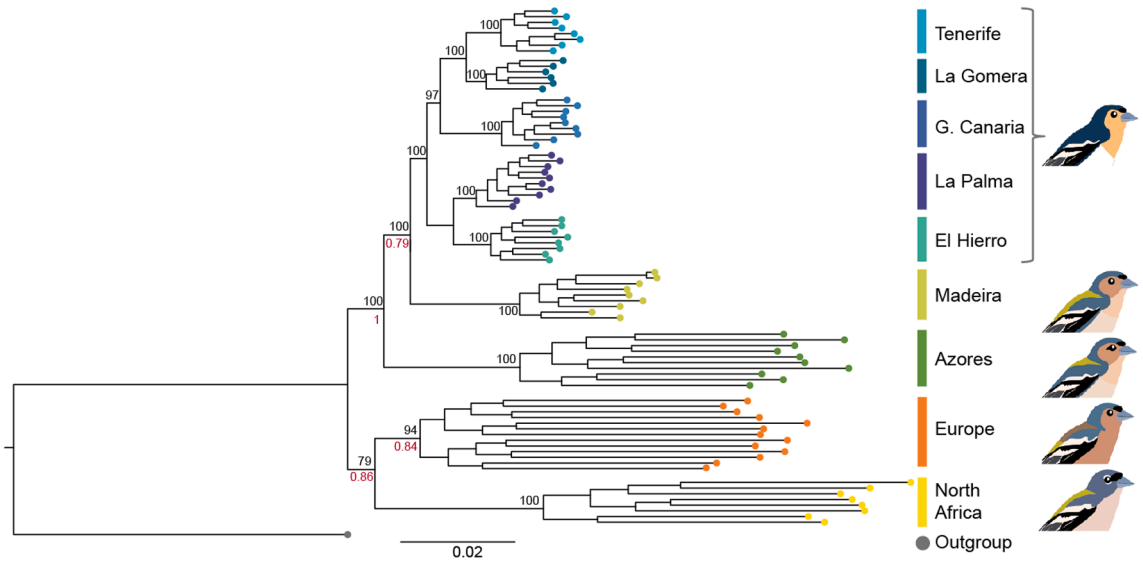

Fig. 2. Maximum likelihood phylogenetic tree based on 100,166 genome-wide neutral SNP loci performed using RAxML with 1000 rapid bootstraps and using the blue chaffinch (*Fringilla teydea)* as the outgroup. Figures in black are node support values. Figures in red correspond to Average support values (AVS) from the mPTP species delimitation method. Sketches on the right depict the main phenotypic differences between forms, with chaffinches from the Canary Islands represented by subspecies *palmae*. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

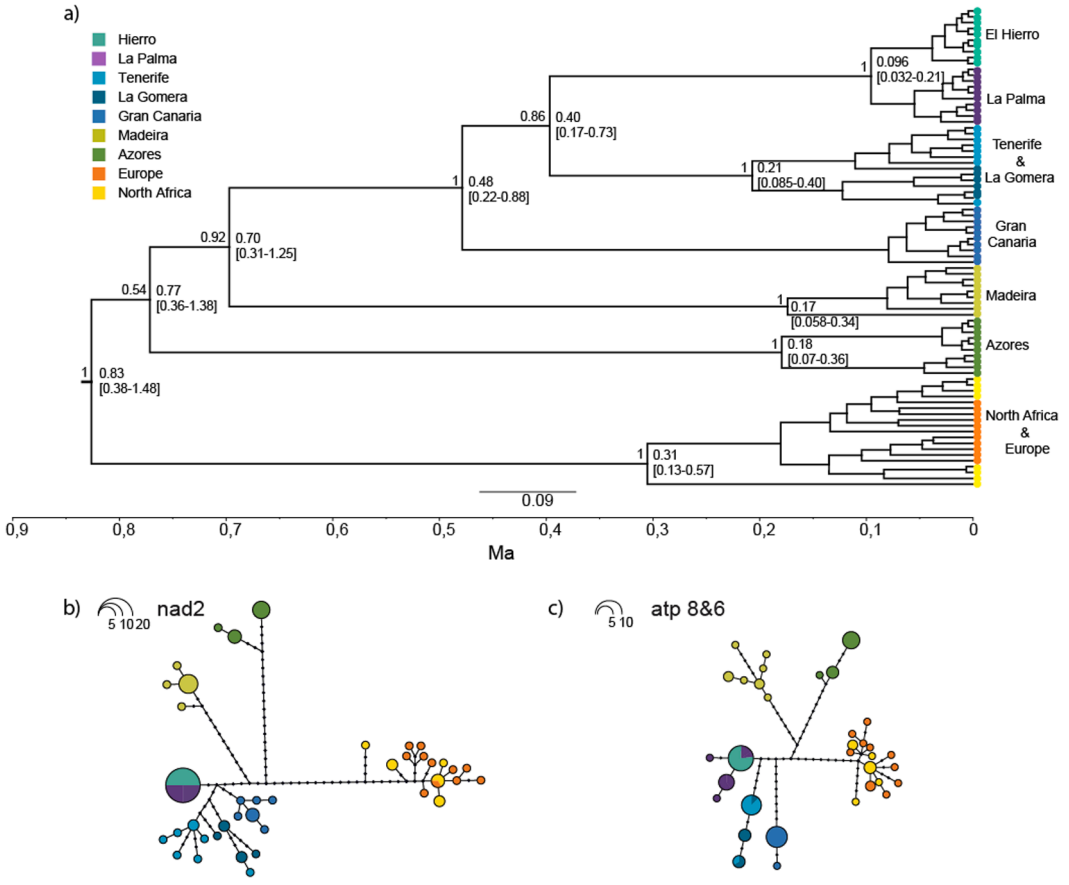

Fig. 3. (a) Ultrametric Bayesian tree based on three mitochondrial genes (*atp8*, *atp6* and *nad2*,) obtained with BEAST. Values on the left of each node represent posterior probability of node support. Values on the right of each node represent node age in million years, with confidence intervals (95% HPD) in brackets. (b) Haplotype networks based on *nad2* and (c) *atp8&6* genes. Circles correspond to haplotypes, and their size is proportional to the frequency of each haplotype in the population. Black dots along branches correspond to unsampled or extinct haplotypes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3
Genetic diversity and population expansion indices of common chaffinch populations. MtDNA genes used include *atp8* and *atp6* genes (900 bp), *nad2* (835 bp) concatenated (1,735 bp). Included are DNA marker, geographic region, sample size (n), number of haplotypes (No. haps), haplotype diversity (h), nucleotide diversity (π), Fu's neutrality test (F_S). Statistical significance of F_S values is indicated by asterisks (* $p = 0.05$, ** $p = 0.01$ and ***, $p = 0.001$). EUR (Iberian Peninsula), AFR (North Africa), AZO (Azores), MAD (Madeira), GCA (Gran Canaria), TEN (Tenerife); GOM (La Gomera), HIE (El Hierro) and PAL (La Palma).

DNA marker	Region	n	No. haps.	$h \pm$ SD	$\pi \pm$ SD	F_S
atp8&6 + nad2						
	AFR	8	6	0.93 ± 0.084	0.0043 ± 0.0405	0.33
	EUR	11	11	1.00 ± 0.039	0.0045 ± 0.0394	−5.10 **
	AZO	9	4	0.69 ± 0.15	0.0036 ± 0.0430	3.27
	MAD	9	7	0.94 ± 0.07	0.0024 ± 0.0261	−1.67
	GCA	8	6	0.90 ± 0.11	0.0009 ± 0.1912	−3.44 ***
	TEN	8	7	0.96 ± 0.08	0.0024 ± 0.0293	−2.32
	GOM	6	4	0.87 ± 0.13	0.0039 ± 0.0408	1.78
	PAL	10	4	0.89 ± 0.08	0.0005 ± 0.0145	−1.02
	HIE	10	1	0.00 ± 0.00	0.0000 ± 0.0000	0.00

(Fig. 6). The plot also showed clear regional structure among populations with two main clusters, one formed by the continental individuals along with Azores, and the other including the remaining insular populations. Coancestry relationships among populations revealed that the Azores shares more ancestry with Europe than with North Africa. Within the insular cluster, two pairs within the Canary Islands show high coancestry (Tenerife and La Gomera, and La Palma and El Hierro, respectively).

3.5. Species delimitation

The 10 independent MCMC runs of mPTP suggested species-level designation for the five main clades in the ML phylogeny, corresponding to Europe, North Africa, Azores, Madeira and the Canary Islands, with support values ranging from 0.79 to 1 (Fig. 2, values in red). In addition, mPTP suggested one additional clade within Europe, with a support value of 0.84.

We integrated the molecular data from the mPTP analysis with phenotypic data and all five clades identified by mPTP showed congruent differentiation in phenotypic traits, mainly in terms of plumage color but also morphology and bioacoustics. When scoring differences in plumage coloration (Fig. 7) and morphology (Table S6) among pairs of subspecies using the five most prominent traits (Tobias et al., 2010), all comparisons reached the minimum threshold for species designation (Table S5).

4. Discussion

4.1. Colonization history in the common chaffinch radiation

Our results from molecular phylogenies, ancestral range estimation, and coancestry analyses, provide strong and consistent support for a colonization of Macaronesia by the common chaffinch that took place from the mainland, via the Azores and Madeira to the Canary Islands, and resulted in a rapid species-level radiation. This circuitous colonization route seems counterintuitive from a biogeographic perspective, given the large distance separating the Azores from the mainland (*ca.* 1300 km) compared to the other archipelagos, and suggests that factors other than mere geographic distance were at play in the common chaffinch radiation. Although the topologies of the phylogenetic trees do not allow determining whether the original colonizers of the Azores came from Europe or North Africa, the coancestry analysis with fineRADstructure, along with the genetic distances based on both datasets, suggests that a European origin is more likely. The estimation of the colonization time of these Atlantic islands by the common chaffinch obtained with BEAST coincides with previous estimates of about one million years before present (Illera et al., 2018), which is relatively recent compared to the age of most of the islands (Illera et al., 2012). The estimated colonization time falls within the last 3 million years, a period found to include most colonization events by Macaronesian bird taxa (Valente et al., 2017). This period coincides with the establishment of most Macaronesian laurel forests in the Plio-Pleistocene (2.6 Ma), and with the movement of the trade wind zone over the islands during the Pleistocene (2.6–0.01 Ma), which provided sufficient precipitation and moisture (Kondraskov et al., 2015). The phylogenomic tree obtained with ~ 100,000 neutral SNPs provided enough resolution to reveal independently evolving, monophyletic lineages of the common chaffinch on each archipelago. Results also suggest shared ancestry of all the Macaronesian islands, followed by divergence with restricted gene flow among islands. This single-wave colonization history is supported by shared phenotypic characters among insular populations. Macaronesian chaffinches show plumage patterns with blue-gray dorsal coloration and reduced green and red patches (Grant, 1980); longer tarsi and shorter wings than their mainland counterparts (Grant, 1979; Dennison and Baker, 1991), as documented for other passerines (Wright et al., 2016); and decreasing song complexity after each colonization event (Lynch and Baker, 1994; Lachlan et al., 2013). Overall, this pattern of shared traits among all insular populations is more consistent with common ancestry than convergence following independent colonizations from the nearest mainland (Marshall and Baker, 1999). Given the phylogenetic relationships among all insular populations, common ancestry is more parsimonious than the alternative hypothesis of repeated, independent evolution of these traits on each island under common selective pressures.

Table 4
Genetic distances between the different lineages of the common chaffinch using the *atp8* and *atp6* genes (900 bp) and *nad2* (835 bp) concatenated (1,735 bp). Above the diagonal: average number of pairwise differences between populations. Below the diagonal: corrected average pairwise differences. Along the diagonal (in italics): average number of pairwise differences within populations. EUR (Iberian Peninsula), AFR (North Africa), AZO (Azores), MAD (Madeira), GCA (Gran Canaria), TEN (Tenerife); GOM (La Gomera), HIE (El Hierro) and PAL (La Palma).

	AFR	EUR	AZO	MAD	GCA	TEN	GOM	PAL	HIE
atp8&6 + nad2									
AFR	*7.46*	8.38	59.75	52.13	48.13	48.31	48.88	36.92	36.13
EUR	0.76	*7.76*	61.86	53.33	49.36	50.53	50.88	39.24	38.55
AZO	52.91	54.87	*6.22*	50.78	50.22	46.46	47.85	40.92	40.22
MAD	46.31	47.37	45.58	*4.17*	39.00	37.35	38.80	31.91	31.11
GCA	43.64	44.73	46.36	36.17	*1.50*	26.38	28.00	18.80	18.00
TEN	42.37	44.43	41.13	33.05	23.41	*4.43*	8.92	15.18	14.38
GOM	41.74	43.60	41.34	33.31	23.85	3.30	*6.80*	16.80	16.00
PAL	32.72	34.89	37.34	29.36	17.58	12.49	12.93	*0.93*	0.80
HIE	32.39	34.66	37.11	29.03	17.25	12.16	12.60	0.33	*0.00*

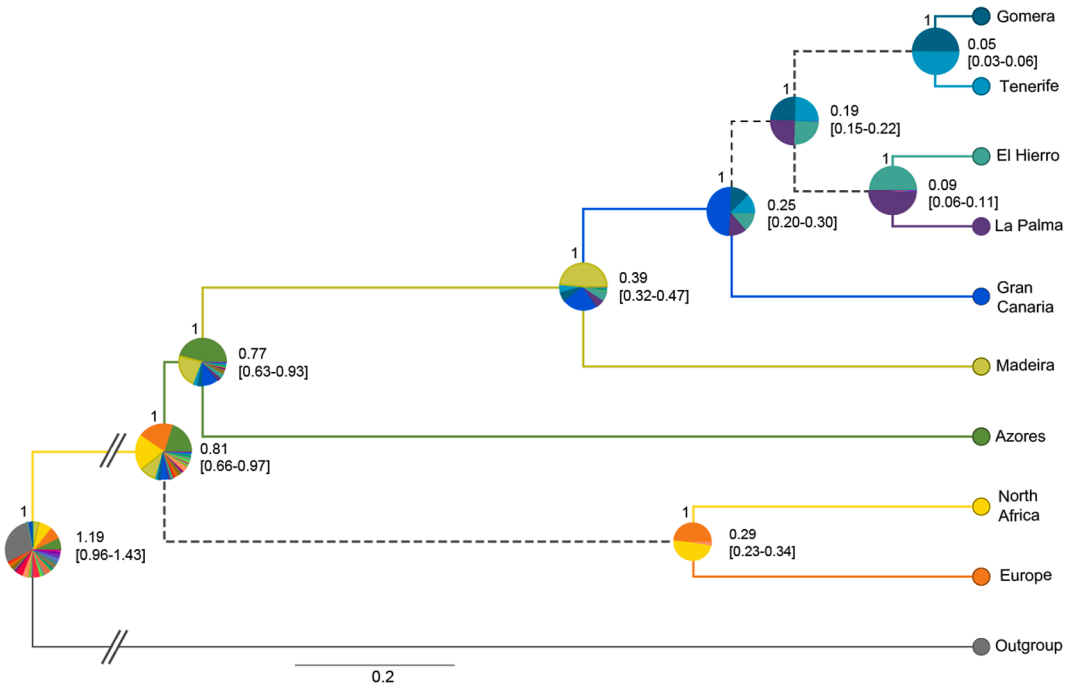

Fig. 4. Ancestral range estimation of common chaffinch populations. Inference based on a dispersal-extinction-cladogenesis model with founder event (DEC + J), with the Bayesian phylogeny based on 15,836 neutral SNPs. Pie diagrams at each node represent the inferred geographical ranges for each ancestral taxon, with the probability of each area indicated by its respective color. Branch color represents the most likely state for each branch. Dashed branches indicate that multiple states were tied. Figures above pies represent posterior probabilities of node support, and figures to the right of each node correspond to age in Ma, with confidence intervals (95% HPD) in brackets. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

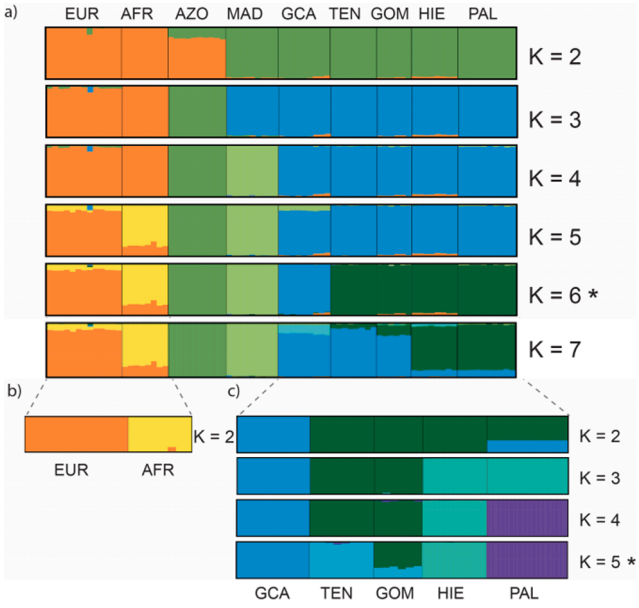

Fig. 5. STRUCTURE analysis plots for (a) all chaffinch populations with K ranging from 2 to 7 (plots for K = 8 and 9 are not shown as they do not differ from K = 7), (b) mainland populations only for K = 2, and (c) Canary Islands populations only with K ranging from 2 to 5. EUR (Iberia), AFR (North Africa), AZO (Azores), MAD (Madeira), GCA (Gran Canaria), TEN (Tenerife); GOM (La Gomera), HIE (El Hierro) and PAL (La Palma). Asterisks (*) mark the optimal K value for each analysis.

Unlike the Azores, where gene flow appears to have prevented the differentiation of common chaffinch populations among islands (Baker et al., 1990; Rodrigues et al., 2014), those in the Canary Islands have diverged markedly from each other, giving rise to a range of phenotypes currently grouped into four different subspecific taxa (Illera et al., 2018). Partly because of this recent inter-island differentiation, inferring the specific order in which the Canary Islands were colonized is challenging (Marshall and Baker, 1999). The absence of the common chaffinch in the eastern-most islands of Lanzarote and Fuerteventura may be due to the current lack of suitable habitat, which is known to have varied widely over time due to the frequent extinction-recolonization events of their flora (García-Verdugo et al., 2019), but whether or not the common chaffinch was present there in the past cannot be determined from available data. For the islands where the common chaffinch is present, we obtained conflicting results and found evidence consistent with both an east-to-west and a west-to-east pattern of colonization. On one hand, our results support the eastward colonization because La Palma is closest to Madeira in the haplotype networks and shows lower genetic distance with Madeira than Gran Canaria. This route may have been favoured by the wind patterns that blow south-eastwards from the Azores in winter (Grant, 1980), as previously proposed (e.g., Grant, 1980; Marshall and Baker, 1999; Suárez et al., 2009; Lachlan et al., 2013). On the other hand, the mitochondrial DNA tree, the ancestral range estimation and the population structure analysis are more consistent with a westward colonization starting from Gran Canaria. More research will be needed to disentangle the specific common chaffinch colonization within the Canary Islands, an archipelago with a diverse range of avian colonization histories given its proximity to neighboring archipelagos and mainland (Illera et al., 2012; Morinha et al., 2020).

The progressive reduction of genetic diversity from the Azores to the Canary Islands is also consistent with the colonization route, and expected when islands are sequentially colonized from other islands by small groups of individuals from source populations of progressively smaller effective population size (Clegg et al., 2002). Genetic diversity in the Azores was similar to that found on mainland populations and an order of magnitude higher than that found on other archipelagos. This suggests that a relatively large group of original colonizers (or multiple colonization events in a short period of time), arrived to Azores, avoiding a major founder event (James et al., 2016), but also that

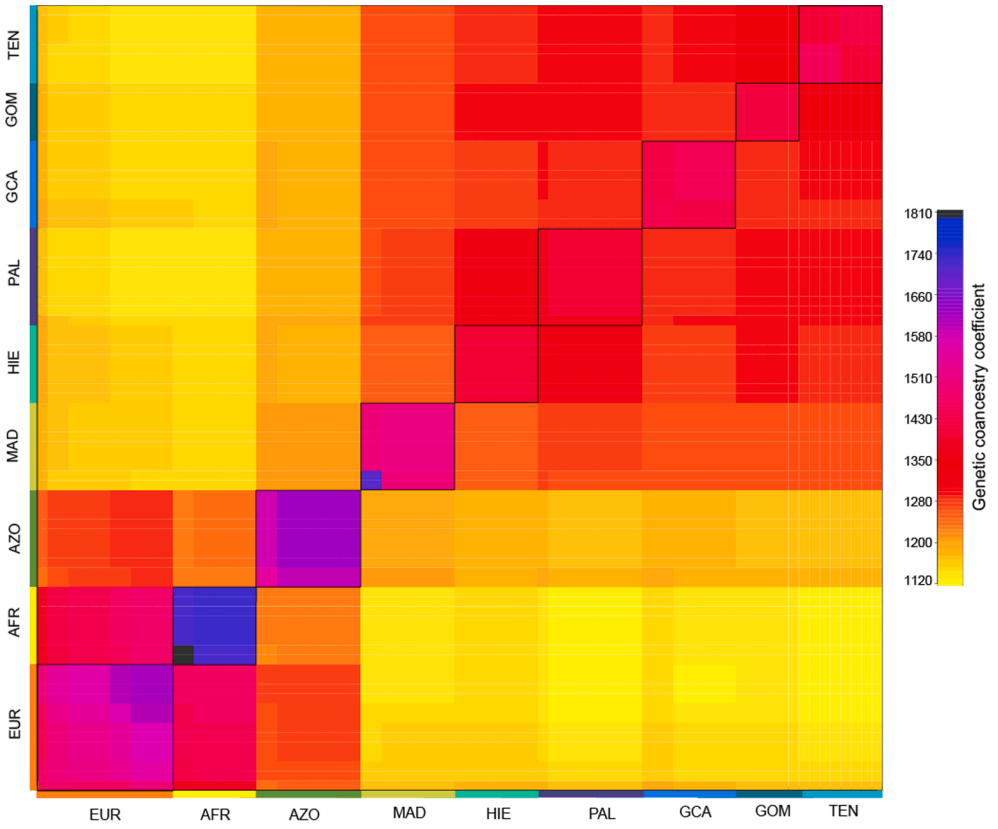

Fig. 6. Matrix of pairwise genetic co-ancestry values among chaffinch populations. Averaged co-ancestry coefficients per population are color-coded from low (yellow) to high (black). Individuals clustering into populations are shown along the diagonal (squares framed in black). EUR (Iberia), AFR (North Africa), AZO (Azores), MAD (Madeira), GCA (Gran Canaria), TEN (Tenerife); GOM (La Gomera), HIE (El Hierro) and PAL (La Palma). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

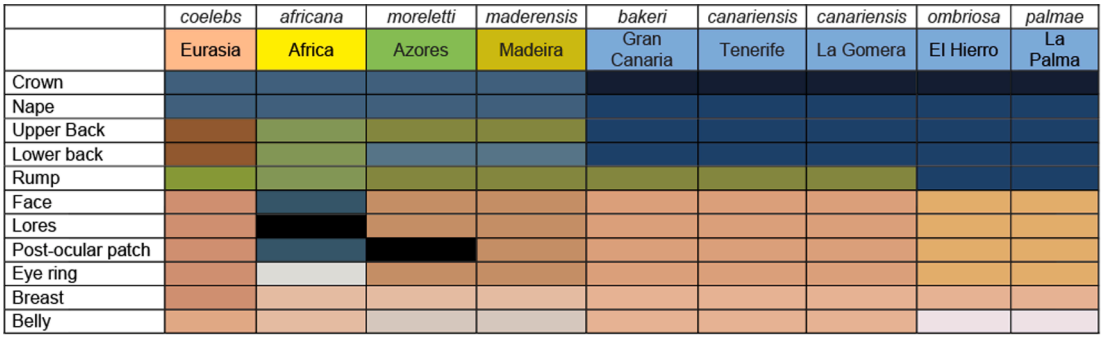

Fig. 7. Summary of the main phenotypic differences among males of the different chaffinch taxa. Colors depicted for the different body parts are approximate estimates of real colors obtained from photographs (see Methods). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

effective population size was maintained relatively large over time. Indeed, in addition to the magnitude of potential founder events, the surface area of suitable common chaffinch habitat in the different islands and the presence of gene flow among them are also likely to have influenced present levels of genetic diversity. Except for La Palma, where common chaffinches have stable breeding populations in dry pine forests, Macaronesian common chaffinches are largely restricted to *monteverde* humid habitats, from cloud forest to moist heaths, and the geographic area of these habitat types varies widely among islands (Martín and Lorenzo, 2001). While most of the Azores are humid enough to sustain common chaffinch populations, suitable habitat decreases markedly with latitude, becoming less abundant in Madeira, and restricted to small "islands within islands" in the Canaries, where humid habitats are more restricted than in the other archipelagos (Fernández-Palacios, 2009). In turn, gene flow among the Azores, which has prevented genetic differentiation among islands (Rodrigues et al., 2014), has favored the maintenance of high population sizes and genetic diversity, in contrast to the Canary Islands, where populations have become isolated from each other due to highly restricted gene flow.

The chaffinch taxa produced in the Macaronesian archipelagos differ from each other mostly in plumage coloration, and to a much lesser degree in morphological characters. This is similar to what has been observed in non-adaptive avian radiations, such as those in South American capuchino seedeaters (Campagna et al., 2012), North American juncos (Friis and Milá, 2020), or European wagtails (Ödeen and Björklund, 2003), where taxa differ in color traits with a simple genetic basis (Campagna et al., 2017; Abolins-Abols et al., 2018), yet are relatively uniform in morphology. This suggests that drift and sexual selection have been the main drivers of the phenotypic diversification, with morphological adaptation to local ecological conditions playing a relatively minor role (Rundell and Price, 2009), likely due to the ecological similarity between Macaronesia and its mainland. This is in contrast to well-studied adaptive radiations such as that of the Darwin's finches in the Galapagos Islands (Grant and Grant, 2008; Lamichhaney

et al., 2015), or the honeycreepers in Hawaii (Lerner et al., 2011). Within a similar time frame to that of the chaffinch diversification, these two radiations gave rise to markedly diverse beak morphologies as populations of the original colonizers adapted through strong directional selection to the food resources available in the different islands. In the case of the honeycreepers, which belong to the same family Fringillidae as chaffinches, morphological divergence was accompanied by a stunning diversification in color patterns and other ornamental traits (Freed et al., 1987), suggesting the combined action of natural and sexual selection (Gillespie et al., 2020). Even though the common chaffinches have not diversified bill morphology to that extent, natural selection has likely played a role in modifying their morphology, especially the size and shape of their beaks (Grant, 1979).

4.2. Systematics and taxonomy of the chaffinch radiation

Our species delimitation analyses suggest that the common chaffinch radiation has resulted in several species-level taxa. The genome-wide analysis of genetic variation revealed the existence of several distinct evolutionary lineages evolving independently from each other, and species delimitation analyses provided support for the existence of at least five different species within the complex. The mPTP method provided support for the five nodes corresponding to North Africa, Europe, Azores, Madeira and Canary Islands, respectively. The additional supported clade within Europe could be due to high genetic diversity of the European population, and does not seem to be associated with phenotypic differences or geographical limits. The Structure and Admixture analyses for the continental clades showed that for $K > 2$, some individuals of the Iberian population show some divergence, but do not correspond to the clades in the phylogenomic tree (Fig. S3). Marked phenotypic divergence among major lineages was confirmed by Tobias' et al. (2010) delimitation method, which was also consistent with the five-species hypothesis. Even though, plumage coloration and morphological differences among *F. c. moreletti* and *F. c. maderensis* were less prominent than between other members of the complex, they are known to differ in other characters relevant to reproductive isolation like territorial male song (Lachlan et al., 2013), that were not included in our analysis.

We concur with previous studies on this system (Marshall and Baker, 1999; Suárez et al., 2009; Rodrigues et al., 2014; Illera et al., 2016; Perktaş et al., 2017; Clement, 2018), on the need for a taxonomic revision of this group, and based on their and our results, we propose that the common chaffinch be divided into five different species, corresponding to Eurasia (*Fringilla coelebs*), North Africa (*Fringilla spodiogenys/africana*), Azores (*Fringilla moreletti*), Madeira (*Fringilla maderensis*) and the Canary Islands (*Fringilla canariensis*). *F. coelebs* would include all subspecies closely related and phenotypically similar to *F. c. coelebs* found across continental Eurasia. Although populations on the different Canary Islands are genetically distinct, their phenotypic differentiation is relatively minor, and we propose to maintain their current subspecific status within *F. canariensis*. Such a subspecific classification would be as follows: *F. canariensis canariensis* on Tenerife and La Gomera, *F. canariensis palmae* on La Palma, *F. canariensis ombriosa* on El Hierro, and *F. canariensis bakeri* on Gran Canaria.

North African subspecies *spodiogenys* and *harterti* were not included in this study, yet they are phenotypically similar to *africana* (Svensson, 2015; Perktaş et al., 2017). The early molecular study by Marshall and Baker (1999) reported *spodiogenys* as a divergent lineage that was basal to the *Fringilla coelebs* complex in a mtDNA phylogeny, yet more recent molecular analyses using nuclear DNA markers indicate that the two North African subspecies are indeed closely related sister taxa (Samarasin-Dissanayake, 2010). This result is consistent with both phenotype and geography, and suggests that mtDNA may not be suitable to recover the evolutionary history of these taxa. Based on this evidence, and since *spodiogenys* Bonaparte 1841 was described before *africana* Levaillant 1850 and *harterti* Svensson 2015, we recommend recognizing species *Fringilla spodiogenys* with three subspecies (*F. spodiogenys spodiogenys*, *F. spodiogenys africana*, and *F. spodiogenys harterti*).

Recognizing the new proposed species should be consistent with most species concepts that take into account evidence for independent evolving lineages and phenotypic differentiation (De Queiroz, 2007; Sangster, 2013; Gill, 2014). The taxonomic upgrade from subspecies to species is likely to have important conservation implications, as species tend to receive more conservation attention than subspecies (Winker, 2010a, 2010b; Sangster et al., 2016). Specifically, species status would guarantee that the conservation status of each chaffinch taxon is evaluated by the International Union for Conservation of Nature (IUCN), taking into account their distribution area and population size independently, making the difference especially for the more restricted insular populations (Martín, 2009). Hence, conservation biogeography (Whittaker et al., 2005), which includes the distribution of taxa in the conservation criteria by applying biogeographical analysis is important for the improvement of biodiversity conservation. This may in turn help preserve the genetic diversity of the species complex, which is crucial for the resilience to environmental change in the current scenario of climate change, especially given the reduced genetic variability found across the region.

4.3. Conclusions

The colonization of Macaronesia by the common chaffinch has resulted in an evolutionary radiation as populations differentiated phenotypically and genetically in the different archipelagos, and even between islands within the Canary archipelago. The molecular phylogeny was instrumental in revealing a circuitous colonization route from the mainland to the faraway Azores, and then south to Madeira and the Canary Islands. Relatively minor differences in morphology between insular and mainland chaffinches compared to differences in coloration, suggest that drift due to founder events, along with sexual selection acting on plumage coloration and song, are likely the major factors driving the common chaffinch radiation in Macaronesia. The sequential colonization of three Atlantic archipelagos and Northern Africa has led to the formation of at least four new species-level taxa in the genus *Fringilla*, and our results should help further our understanding of the evolutionary processes involved.

CRediT authorship contribution statement

María Recuerda: Conceptualization, Investigation, Data curation, Formal analysis, Visualization, Writing – original draft. **Juan Carlos Illera:** Investigation, Resources, Writing – review & editing, Funding acquisition. **Guillermo Blanco:** Conceptualization, Investigation, Resources, Writing – review & editing, Funding acquisition. **Rafael Zardoya:** Conceptualization, Writing – review & editing. **Borja Milá:** Conceptualization, Investigation, Resources, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Mitochondrial markers sequences are deposited at Gen Bank, the accession numbers are (MW460715- MW460796) for *atp8&6* and (MW460797-MW460875) for *nad2* (see Table S1 for details). SNP raw data is deposited at NCBI under the SRA data project PRJNA692563 with accession numbers (SAMN17349018 - SAMN17349101), see Table S1 for details) and the vcf datasets are deposited in *Figshare* (https://doi.org/10.6084/m9.figshare.13562582). The *Fringilla*

coelebs reference genome is deposited at NCBI (Accession number: JADKPM000000000.1).

Acknowledgement

We are grateful to Félix Medina and the Cabildo of La Palma for logistical support during our work on La Palma. Garajonay National Park provided logistical support and permits for sampling within this protected area. The Cabildos of Tenerife and Gran Canaria provided the permits for working within the network of protected areas. Regional governments of the Canaries, Azores and Madeira issued the necessary research and sampling permits for collecting blood samples. Óscar Frías provided excellent help with fieldwork in Iberia, Canaries and Ceuta. Thanks to Pepe Navarrete for greatly facilitating field work and logistics while sampling in Ceuta. Andrea S. Messeguer provided useful advice on the biogeographical analysis. The research was funded by Spain's Ministry of Science grants CGL2015-66381P, PGC-2018-098897-B-I00, and PGC2018-097575-B-I00. MR was supported by a doctoral fellowship from the Spanish Ministry of Education, Culture, and Sport (FPU16/05724), and JCI was funded by a GRUPIN research grant from the Regional Government of Asturias (Ref.: IDI/2018/000151).

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2021.107291.

References

Abolins-Abols, M., Kornobis, E., Ribeca, P., Wakamatsu, K., Peterson, M.P., Ketterson, E., Milá, B., 2018. A role for differential gene regulation in the rapid diversification of melanic plumage coloration in the dark-eyed junco (*Junco hyemalis*). Mol. Ecol. 27, 4501–4515. https://doi.org/10.1111/mec.14878.

Alexander, D.H., Novembre, J., Lange, K., 2009. Fast model-based estimation of ancestry in unrelated individuals. Genome Res. 19 (9), 1655–1664. https://doi.org/10.1101/gr.094052.109.

Baker, A.J., Dennison, M.D., Lynch, A., Le Grand, G., 1990. Genetic divergence in peripherally isolated populations of chaffinches in the Atlantic islands. Evolution 44 (4), 981–999. https://doi.org/10.1111/evo.1990.44.issue-410.1111/j.1558-5646.1990.tb03819.x.

Beheregaray, L.B., Gibbs, J.P., Havill, N., Fritts, T.H., Powell, J.R., Caccone, A., 2004. Giant tortoises are not so slow: rapid diversification and biogeographic consensus in the Galápagos. Proc. Natl. Acad. Sci. 101, 6514–6519. https://doi.org/10.1073/pnas.0400393101.

Blanco, G., Laiolo, P., Fargallo, J.A., 2014. Linking environmental stress, feeding-shifts and the 'island syndrome': a nutritional challenge hypothesis. Popul. Ecol. 56 (1), 203–216. https://doi.org/10.1007/s10144-013-0404-3.

Bouckaert, R., Vaughan, T.G., Barido-Sottani, J., Duchêne, S., Fourment, M., Gavryushkina, A., Heled, J., Jones, G., Kühnert, D., De Maio, N., Matschiner, M., Mendes, F.K., Müller, N.F., Ogilvie, H.A., du Plessis, L., Popinga, A., Rambaut, A., Rasmussen, D., Siveroni, I., Suchard, M.A., Wu, C.-H., Xie, D., Zhang, C., Stadler, T., Drummond, A.J., Pertea, M., 2018. BEAST 2.5: an advanced software platform for Bayesian evolutionary analysis. PLoS Comput. Biol. 15 (4), e1006650. https://doi.org/10.1371/journal.pcbi.1006650.

Campagna, L., Repenning, M., Silveira, L.F., Fontana, C.S., Tubaro, P.L., Lovette, I.J., 2017. Repeated divergent selection on pigmentation genes in a rapid finch radiation. Scientific Adv. 3 (5), e1602404. https://doi.org/10.1126/sciadv.1602404.

Campagna, L., Benites, P., Lougheed, S.C., Lijtmaer, D.A., Di Giacomo, A.S., Eaton, M.D., Tubaro, P.L., 2012. Rapid phenotypic evolution during incipient speciation in a continental avian radiation. Proc. R. Soc. B: Biol. Sci. 279 (1734), 1847–1856. https://doi.org/10.1098/rspb.2011.2170.

Catchen, J., Hohenlohe, P.A., Bassham, S., Amores, A., Cresko, W.A., 2013. Stacks: an analysis tool set for population genomics. Mol. Ecol. 22 (11), 3124–3140. https://doi.org/10.1111/mec.12354.

Clegg, S.M., Degnan, S.M., Kikkawa, J., Moritz, C., Estoup, A., Owens, I.P.F., 2002. Genetic consequences of sequential founder events by an island-colonizing bird. Proc. Natl. Acad. Sci. 99 (12), 8127–8132. https://doi.org/10.1073/pnas.102583399.

Clement, P., 2018. Common Chaffinch (Fringilla coelebs). In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A., de Juana, E. (Eds.), Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona.

Clement, P., 2020. Common Chaffinch (Fringilla coelebs), version 1.0. In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A., de Juana (Eds.), Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA. DOI: 10.2173/bow.comcha.01.

Cowie, R.H., Holland, B.S., 2006. Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. J. Biogeogr. 33 (2), 193–198. https://doi.org/10.1111/jbi.2006.33.issue-210.1111/j.1365-2699.2005.01383.x.

Delmore, K.E., Illera, J.C., Pérez-Tris, J., Segelbacher, G., Lugo Ramos, J.S., Durieux, G., Ishigohoka, J., Liedvogel, M., 2020. The evolutionary history and genomics of European blackcap migration. Elife 9, e54462. https://doi.org/10.7554/eLife.54462.

Danecek, P., Auton, A., Abecasis, G., Albers, C.A., Banks, E., DePristo, M.A., Handsaker, R.E., Lunter, G., Marth, G.T., Sherry, S.T., McVean, G., Durbin, R., 2011. The variant call format and VCFtools. Bioinformatics 27 (15), 2156–2158. https://doi.org/10.1093/bioinformatics/btr330.

Queiroz, A., 2005. The resurrection of oceanic dispersal in historical biogeography. Trends Ecol. Evol. 20 (2), 68–73. https://doi.org/10.1016/j.tree.2004.11.006.

De Queiroz, K., 2007. Species concepts and species delimitation. Syst. Biol. 56, 879–886. https://doi.org/10.1080/10635150701701083.

del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A., Kirwan, G. (Eds.), 2020. Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona (retrieved from http://www.hbw.com/ on 01 Abril 2020).

Dennison, Michael D., Baker, Allan J., 1991. Morphometric variability in continental and Atlantic island populations of chaffinches (Fringilla coelebs). Evolution 45 (1), 29–39. https://doi.org/10.1111/evo.1991.45.issue-110.1111/j.1558-5646.1991.tb05263.x.

Drummond, A.J., Bouckaert, R.R., 2015. Bayesian evolutionary analysis with BEAST. Cambridge University Press.

Drummond, A.J., Suchard, M.A., Xie, D., Rambaut, A., 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Mol. Biol. Evol. 29, 1969–1973. https://doi.org/10.1093/molbev/mss075.

Eberhard, Jessica R., Bermingham, Eldredge, 2005. Phylogeny and comparative biogeography of *Pionopsitta* parrots and Pteroglossus toucans. Mol. Phylogenet. Evol. 36 (2), 288–304. https://doi.org/10.1016/j.ympev.2005.01.022.

Elshire, Robert J., Glaubitz, Jeffrey C., Sun, Qi, Poland, Jesse A., Kawamoto, Ken, Buckler, Edward S., Mitchell, Sharon E., Orban, Laszlo, 2011. A robust, simple genotyping-by-sequen- cing (GBS) approach for high diversity species. PLoS ONE 6 (5), e19379. https://doi.org/10.1371/journal.pone.0019379.

Emerson, Brent C., Oromí, Pedro, Hewitt, Godfrey M., 1999. MtDNA phylogeography and recent intra-island diversification among Canary Island Calathus beetles. Mol. Phylogenet. Evol. 13 (1), 149–158. https://doi.org/10.1006/mpev.1999.0644.

Emerson, B.C., 2002. Evolution on oceanic islands: molecular phylogenetic approaches to understanding pattern and process. Mol. Ecol. 11, 951–966.

Excoffier, Laurent, Lischer, Heidi E., 2010. Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Mol. Ecol. Resour. 10 (3), 564–567. https://doi.org/10.1111/men.2010.10.issue-310.1111/j.1755-0998.2010.02847.x.

Foll, M., Gaggiotti, O., 2008. A genome-scan method to identify selected loci appropriate for both dominant and codominant markers: a Bayesian perspective. Genetics 180, 977–993. https://doi.org/10.1534/genetics.108.092221.

Freed, Leonard A., Conant, Sheila, Fleischer, Robert C., 1987. Evolutionary ecology and radiation of Hawaiian passerine birds. Trends Ecol. Evol. 2 (7), 196–203. https://doi.org/10.1016/0169-5347(87)90020-6.

Friis, G., Milá, B., 2020. Change in sexual signaling traits outruns morphological divergence in a recent avian radiation across an ecological gradient. J. Evol. Biol. 33, 1276–1293. https://doi.org/10.1111/jeb.13671.

Friis, Guillermo, Aleixandre, Pau, Rodríguez-Estrella, Ricardo, Navarro-Sigüenza, Adolfo G., Milá, Borja, 2016. Rapid postglacial diversification and long-term stasis within the songbird genus *Junco*: phylogeographic and phylogenomic evidence. Mol. Ecol. 25 (24), 6175–6195. https://doi.org/10.1111/mec.2016.25.issue-2410.1111/mec.13911.

Fu, Y.X., 1997. Statistical tests of neutrality of mutations.

Felicísimo, Ángel M., Muñoz, Jesús, González-Solis, Jacob, Figuerola, Jordi, 2008. Ocean surface winds drive dynamics of transoceanic aerial movements. PLoS ONE 3 (8), e2928. https://doi.org/10.1371/journal.pone.0002928.

Fernández-Palacios, J.M., 2009. 9360 Laurisilvas macaronésicas (Laurus, Ocotea). In: VVAA (Ed.), against population growth, hitchhiking and background selection. Genetics, 147, pp. 915–925.

Funk, V.A., Wagner, W.L., 1995. Biogeographic patterns in the Hawaiian Islands. In: Wagner, W.L., Funk, V.L. (Eds.), Hawaiian biogeography: evolution on a hot spot archipelago. Smithsonian Institution Press, Washington, DC, pp. 379–419.

Grabherr, M.G., Russell, P., Meyer, M., Mauceli, E., Alfoldi, J., Di Palma, F., Lindblad-Toh, K., 2010. Genome-wide synteny through highly sensitive sequence alignment: Satsuma. Bioinformatics 26 (9), 1145–1151. https://doi.org/10.1093/bioinformatics/btq102.

García-Verdugo, Carlos, Caujapé-Castells, Juli, Illera, Juan Carlos, Mairal, Mario, Patiño, Jairo, Reyes-Betancort, Alfredo, Scholz, Stephan, 2019. Pleistocene extinctions as drivers of biogeographical patterns on the easternmost Canary Islands. J. Biogeogr. 46 (5), 845–859. https://doi.org/10.1111/jbi.2019.46.issue-510.1111/jbi.13563.

Gill, Frank B., 2014. Species taxonomy of birds: which null hypothesis? The Auk: Ornithological Adv. 131 (2), 150–161. https://doi.org/10.1642/AUK-13-206.1.

Grant, P.R., 1979. Evolution of the chaffinch, *Fringilla coelebs*, on the Atlantic Islands. Biol. J. Linn. Soc. 11, 301–332. https://doi.org/10.1111/j.1095-8312.1979.tb00042.x.

Grant, P.R., 1980. Colonization of Atlantic islands by chaffinches (*Fringilla* spp.). Bonner Zoologische Beiträge 31, 311.

Grant, P.R., Grant, B. Rosemary, 2008. How and why species multiply: the radiation of Darwin's finches. Princeton University Press.

Gillespie, Rosemary G., Baldwin, Bruce G., Waters, Jonathan M., Fraser, Ceridwen I., Nikula, Raisa, Roderick, George K., 2012. Long-distance dispersal: a framework for hypothesis testing. Trends Ecol. Evol. 27 (1), 47–56. https://doi.org/10.1016/j.tree.2011.08.009.

Gillespie, R.G., Bennett, G.M., De Meester, L., Feder, J.L., Fleischer, R.C., Harmon, L.J., Hendry, a. P., Knope, M.L., Mallet, J., Martin, C., Parent, C.E., Patton, A.H., Pfennig, K.S., Rubinoff, D., Schluter, D., Seehausen, O., Shaw, K.L., Stacy, E., Stervander, M., Stroud, J.T., Wagner, C. & Wogan, G.O.U., 2020. Comparing adaptive radiations across space, time, and taxa. J. Heredity, 111, 1–20. https://doi.org/10.1093/jhered/esz064.

Gosselin, T., 2019. radiator: RADseq Data Exploration, Manipulation and Visualization using R. DOI: 10.5281/zenodo.1475182, https://thierrygosselin.github.io/radiator/.

Hackett, Shannon J., 1996. Molecular phylogenetics and biogeography of tanagers in the genusRamphocelus (Aves). Mol. Phylogenet. Evol. 5 (2), 368–382. https://doi.org/10.1006/mpev.1996.0032.

Handbook of the Birds of the World and BirdLife International, 2019. Handbook of the Birds of the World and BirdLife International digital checklist of the birds of the world. Version 4. Available at: http://datazone.birdlife.org/userfiles/file/Species/Taxonomy/HBW-BirdLife_Checklist_v4_Dec19.zip.

Illera, J.C., Rando, J.C., Richardson, D.S., Emerson, B.C., 2012. Age, origins and extinctions of the avifauna of Macaronesia: a synthesis of phylogenetic and fossil information. Quat. Sci. Rev. 50, 14–22. https://doi.org/10.1016/j.quascirev.2012.07.013.

Illera, J.C., Spurgin, L.G., Rodriguez-Exposito, E., Nogales, M., Rando, J.C., 2016. What are we learning about speciation and extinction from the Canary Islands? Ardeola 63, 15–34. https://doi.org/10.13157/arla.63.1.2016.rp1.

Illera, Juan Carlos, Rando, Juan Carlos, Rodriguez-Exposito, Eduardo, Hernández, Mariano, Claramunt, Santiago, Martín, Aurelio, 2018. Acoustic, genetic, and morphological analyses of the Canarian common chaffinch complex *Fringilla coelebs* ssp. reveals cryptic diversification. J. Avian Biol. 49 (12) https://doi.org/10.1111/jav.2018.v49.i1210.1111/jav.01885.

James, J.E., Lanfear, R., Eyre-Walker, A., 2016. Molecular evolutionary consequences of island colonization. Genome Biology Evolution, 8, 1876–1888. DOI: 10.1093/gbe/evw120.

Juan, Carlos, Emerson, Brent C., Oromí, Pedro, Hewitt, Godfrey M., 2000. Colonization and diversification: towards a phylogeographic synthesis for the Canary Islands. Trends Ecol. Evol. 15 (3), 104–109. https://doi.org/10.1016/S0169-5347(99)01776-0.

Kapli, P., Lutteropp, S., Zhang, J., Kobert, K., Pavlidis, P., Stamatakis, A., Flouri, T., 2017. Multi-rate Poisson tree processes for single-locus species delimitation under maximum likelihood and Markov chain Monte Carlo. Bioinformatics 33, 1630–1638. https://doi.org/10.1093/bioinformatics/btx025.

Kondraskov, Paulina, Schütz, Nicole, Schüßler, Christina, de Sequeira, Miguel Menezes, Guerra, Arnoldo Santos, Caujapé-Castells, Juli, Jaén-Molina, Ruth, Marrero-Rodríguez, Águedo, Koch, Marcus A., Linder, Peter, Kovar-Eder, Johanna, Thiv, Mike, Buerki, Sven, 2015. Biogeography of Mediterranean hotspot biodiversity: re-evaluating the'Tertiary relict'hypothesis of Macaronesian laurel forests. PLoS ONE 10 (7), e0132091. https://doi.org/10.1371/journal.pone.0132091.

Kopelman, N.M., Mayzel, J., Jakobsson, M., Rosenberg, N.A., Mayrose, I., 2015. Clumpak: a program for identifying clustering modes and packaging population structure inferences across K. Mol. Ecol. Resour. 15, 1179–1191. https://doi.org/10.1111/1755-0998.12387.

Kozak, K.M., McMillan, O., Joron, M., Jiggins, C.D., 2018. Genome-wide admixture is common across the *Heliconius* radiation. BioRxiv 414201. https://doi.org/10.1101/414201.

Lamichhaney, Sangeet, Berglund, Jonas, Almén, Markus Sällman, Maqbool, Khurram, Grabherr, Manfred, Martinez-Barrio, Alvaro, Promerová, Marta, Rubin, Carl-Johan, Wang, Chao, Zamani, Neda, Grant, B. Rosemary, Grant, Peter R., Webster, Matthew T., Andersson, Leif, 2015. Evolution of Darwin's finches and their beaks revealed by genome sequencing. Nature 518 (7539), 371–375. https://doi.org/10.1038/nature14181.

Lachlan, RobertF., Verzijden, MachteldN., Bernard, CarolineS., Jonker, PeterPaul, Koese, Bram, Jaarsma, Shirley, Spoor, Willemijn, Slater, PeterJ.B., ten Cate, Carel, 2013. The progressive loss of syntactical structure in bird song along an island colonization chain. Curr. Biol. 23 (19), 1896–1901. https://doi.org/10.1016/j.cub.2013.07.057.

Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T., Calcott, B., 2016. PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Mol. Biol. Evol. 34, 772–773. https://doi.org/10.1093/molbev/msw260.

Lawson, Daniel John, Hellenthal, Garrett, Myers, Simon, Falush, Daniel, Copenhaver, Gregory P., 2012. Inference of population structure using dense haplotype data. PLoS Genet. 8 (1), e1002453. https://doi.org/10.1371/journal.pgen.1002453.

Lerner, HeatherR.L., Meyer, Matthias, James, HelenF., Hofreiter, Michael, Fleischer, RobertC., 2011. Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian honeycreepers. Curr. Biol. 21 (21), 1838–1844. https://doi.org/10.1016/j.cub.2011.09.039.

Leroy, Thibault, Rousselle, Marjolaine, Tilak, Marie-Ka, Caizergues, Aude E., Scornavacca, Céline, Recuerda, María, Fuchs, Jérôme, Illera, Juan Carlos, De Swardt, Dawie H., Blanco, Guillermo, Thébaud, Christophe, Milá, Borja, Nabholz, Benoit, 2021. Island songbirds as windows into evolution in small populations. Curr. Biol. 31 (6), 1303–1310.

Li, H., Durbin, R., 2009. Fast and accurate short read alignment with Burrows-Wheeler transform. Bioinformatics 25 (14), 1754–1760. https://doi.org/10.1093/bioinformatics/btp324.

Lischer, H.E., Excoffier, L., 2012. PGDSpider: an automated data conversion tool for connecting population genetics and genomics programs. Bioinformatics 28, 298–299. https://doi.org/10.1093/bioinformatics/btr642.

Losos, Jonathan B., Ricklefs, Robert E., 2009. Adaptation and diversification on islands. Nature 457 (7231), 830–836. https://doi.org/10.1038/nature07893.

Lynch, Alejandro, Baker, Allan J., 1994. A population memetics approach to cultural evolution in chaffinch song: differentiation among populations. Evolution 48 (2), 351–359. https://doi.org/10.1111/evo.1994.48.issue-210.1111/j.1558-5646.1994.tb01316.x.

MacArthur, R.H., Wilson, E.O., 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J.

Malinsky, M., Trucchi, E., Lawson, D.J., Falush, D., 2018. RADpainter and fineRADstructure: population inference from RADseq data. Mol. Biology and Evolution, 35, 1284-1290. DOI: 10.1093/molbev/msy023.

Marshall, H.Dawn, Baker, Allan J., 1999. Colonization history of Atlantic island common chaffinches (*Fringilla coelebs*) revealed by mitochondrial DNA. Mol. Phylogenet. Evol. 11 (2), 201–212.

Martín, José L., 2009. Are the IUCN standard home-range thresholds for species a good indicator to prioritise conservation urgency in small islands? A case study in the Canary Islands (Spain). J. Nature Conserv. 17 (2), 87–98. https://doi.org/10.1016/j.jnc.2008.10.001.

Martín, A., Lorenzo, J.A., 2001. Aves del archipiélago canario. Francisco Lemus.Editor, La Laguna, Spain.

Matzke, N.J., 2013. Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. Front. Biogeogr. 5 https://doi.org/10.21425/F5FBG19694.

Matzke, N.J., 2014. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. Syst. Biol. 63, 951–970. https://doi.org/10.1093/sysbio/syu056.

McKenna, A., Hanna, M., Banks, E., Sivachenko, A., Cibulskis, K., Kernytsky, A., Garimella, K., Altshuler, D., Gabriel, S., Daly, M., DePristo, M.A., 2010. The Genome Analysis Toolkit: a MapReduce framework for analyzing next-generation DNA sequencing data. Genome Res. 20, 1297–1303. http://www.genome.org/cgi/doi/10.1101/gr.107524.110.

Meier, J.I., Marques, D.A., Wagner, C.E., Excoffier, L., Seehausen, O., 2018. Genomics of parallel ecological speciation in Lake Victoria cichlids. Mol. Biol. Evol. 35, 1489–1506. DOI: 10.1093/molbev/msy051.

Miller, M., Pfeiffer, W., Schwartz, T., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. New Orleans, LA, USA: Gateway Computing Environments Workshop (GCE). https://doi.org/10.1109/GCE.2010.5676129.

Morinha, Francisco, Milá, Borja, Dávila, José A., Fargallo, Juan A., Potti, Jaime, Blanco, Guillermo, 2020. The ghost of connections past: A role for mainland vicariance in the isolation of an insular population of the red-billed chough (Aves: Corvidae). J. Biogeogr. 47 (12), 2567–2583. https://doi.org/10.1111/jbi.v47.1210.1111/jbi.13977.

Nathan, R., 2006. Long-distance dispersal of plants. Science 313 (5788), 786–788. https://doi.org/10.1126/science:1124975.

Ödeen, A., Björklund, M., 2003. Dynamics in the evolution of sexual traits: losses and gains, radiation and convergence in yellow wagtails (*Motacilla flava*). Mol. Ecol. 12 (8), 2113–2130. https://doi.org/10.1046/j.1365-294X.2003.01883.x.

Padial, J.M., Miralles, A., De la Riva, I., Vences, M., 2010. The integrative future of taxonomy. Front. Zool. 7, 1–14. https://doi.org/10.1186/1742-9994-7-16.

Patiño, J., Whittaker, R.J., Borges, P.A., Fernández-Palacios, J.M., Ah-Peng, C., Araújo, M.B., Ávila, S.P., Cardoso, P., Cornuault, J., de Boer, E.J., de Nascimento, L., Gil, A., González-Castro, A., Gruner, D.S., Heleno, R., Hortal, J., Illera, J.C., Kaiser-Bunbury, C.N., Matthews, T.J., Papadopoulou, A., Pettorelli, N., Price, J.P., Santos, A.M.C., Steinbauer, M.J., Triantis, K.A., Valente, L., Vargas, P., Weigelt, P., Emerson, B.C., 2017. A roadmap for island biology: 50 fundamental questions after 50 years of The Theory of Island Biogeography. J. Biogeogr. 44, 963–983. https://doi.org/10.1111/jbi.12986.

Perktaş, Utku, Peterson, A. Townsend, Dyer, Dale, 2017. Integrating morphology, phylogeography, and ecological niche modeling to explore population differentiation in North African Common Chaffinches. J. Ornithol. 158 (1), 1–13.

Pritchard, J.K., Stephens, M., Donnelly, P., 2000. Inference of population structure using multilocus genotype data. Genetics 155, 945–959.

R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rambaut, A., Suchard, M.A., Xie, D., Drummond, A.J., 2014. Tracer v1. 6. Computer program and documentation distributed by the author, website http://beast.bio.ed.ac.uk/Tracer.

Rambaut, A., 2017. FigTree-version 1.4. 3, a graphical viewer of phylogenetic trees. Computer program distributed by the author, website: http://tree.bio.ed.ac.uk/software/figtree.

Recuerda, M., Vizueta, J., Cuevas-Caballé, C., Blanco, G., Rozas, J., Milá, B., 2021. Chromosome-level genome assembly of the common chaffinch (Aves: Fringilla coelebs): a valuable resource for evolutionary biology. Genome Biol. Evol. 13 (4), evab034. https://doi.org/10.1093/gbe/evab034.

Ree, R.H., Sanmartín, I., 2018. Conceptual and statistical problems with the DEC+ J model of founder-event speciation and its comparison with DEC via model selection. J. Biogeogr. 45, 741–749. https://doi.org/10.1111/jbi.13173.

Rodrigues, Pedro, Lopes, Ricardo Jorge, Reis, Sandra, Resendes, Roberto, Ramos, Jaime Albino, Tristão da Cunha, Regina, 2014. Genetic diversity and morphological variation of the common chaffinch *Fringilla coelebs* in the Azores. J. Avian Biol. 45 (2), 167–178. https://doi.org/10.1111/jav.2014.45.issue-210.1111/j.1600-048X.2013.00229.x.

Rundell, Rebecca J., Price, Trevor D., 2009. Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. Trends Ecol. Evol. 24 (7), 394–399. https://doi.org/10.1016/j.tree.2009.02.007.

Sackton, Timothy B., Grayson, Phil, Cloutier, Alison, Hu, Zhirui, Liu, Jun S., Wheeler, Nicole E., Gardner, Paul P., Clarke, Julia A., Baker, Allan J., Clamp, Michele, Edwards, Scott V., 2019. Convergent regulatory evolution and loss of flight in paleognathous birds. Science 364 (6435), 74–78. https://doi.org/10.1126/science:aat7244.

Salzburger, W., Ewing, G.B., Von Haeseler, A., 2011. The performance of phylogenetic algorithms in estimating haplotype genealogies with migration. Mol. Ecol. 20, 1952–1963. https://doi.org/10.1111/j.1365-294X.2011.05066.x.

Samarasin-Dissanayake, P., 2010. Population differentiation, historical demography and evolutionary relationships among widespread common chaffinch populations (Fringilla coelebs ssp.). Master's Thesis. University of Toronto, Canada.

Sangster, George, 2013. The application of species criteria in avian taxonomy and its implications for the debate over species concepts. Biol. Rev. 89 (1), 199–214. https://doi.org/10.1111/brv.12051.

Sangster, George, Rodríguez-Godoy, Felipe, Roselaar, C.S., Robb, Magnus S., Luksenburg, Jolanda A., 2016. Integrative taxonomy reveals Europe's rarest songbird species, the Gran Canaria blue chaffinch *Fringilla polatzeki*. J. Avian Biol. 47 (2), 159–166. https://doi.org/10.1111/jav.00825.

Sanmartín, Isabel, van der Mark, Paul, Ronquist, Fredrik, 2008. Inferring dispersal: a Bayesian approach to phylogeny-based island biogeography, with special reference to the Canary Islands. J. Biogeogr. 35 (3), 428–449. https://doi.org/10.1111/jbi.2008.35.issue-310.1111/j.1365-2699.2008.01885.x.

Schluter, D., 2000. The ecology of adaptive radiation. Oxford University Press, Oxford (UK).

Sequeira, A.S., Lanteri, A.A., Albelo, L.R., Bhattacharya, S., Sijapati, M., 2008. Colonization history, ecological shifts and diversification in the evolution of endemic Galápagos weevils. Mol. Ecol. 17, 1089–1107. https://doi.org/10.1111/j.1365-294X.2007.03642.x.

Shirihai, H., Svensson, L., 2018. Handbook of Western Palearctic Birds, Volume 1: Passerines: Larks to Warblers. Bloomsbury Publishing.

Sorenson, Michael D., Ast, Jennifer C., Dimcheff, Derek E., Yuri, Tamaki, Mindell, David P., 1999. Primers for a PCR-based approach to mitochondrial genome sequencing in birds and other vertebrates. Mol. Phylogenet. Evol. 12 (2), 105–114. https://doi.org/10.1006/mpev.1998.0602.

Stamatakis, A., 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30, 1312–1313. https://doi.org/10.1093/bioinformatics/btu033.

Stamatakis, A., Hoover, P., Rougemont, J., 2008. A rapid bootstrap algorithm for the RAxML web servers. Systematic Biol. 57, 758–771. https://doi.org/10.1080/10635150802429642.

Stange, M., Sánchez-Villagra, M.R., Salzburger, W., Matschiner, M., 2018. Bayesian divergence-time estimation with genome-wide single-nucleotide polymorphism data of sea catfishes (Ariidae) supports Miocene closure of the Panamanian Isthmus. Systematic Biol. 67, 681–699. https://doi.org/10.1093/sysbio/syy006.

Stervander, Martin, Illera, Juan Carlos, Kvist, Laura, Barbosa, Pedro, Keehnen, Naomi P., Pruisscher, Peter, Bensch, Staffan, Hansson, Bengt, 2015. Disentangling the complex evolutionary history of the Western Palearctic blue tits (*Cyanistes spp.*)–phylogenomic analyses suggest radiation by multiple colonization events and subsequent isolation. Mol. Ecol. 24 (10), 2477–2494. https://doi.org/10.1111/mec.13145.

Suárez, Nicolás M., Betancor, Eva, Klassert, Tilman E., Almeida, Teresa, Hernández, Mariano, Pestano, José J., 2009. Phylogeography and genetic structure of the Canarian common chaffinch (*Fringilla coelebs*) inferred with mtDNA and microsatellite loci. Mol. Phylogenet. Evol. 53 (2), 556–564. https://doi.org/10.1016/j.ympev.2009.07.018.

Svensson, L., 2015. A new North African subspecies of Common Chaffinch *Fringilla coelebs*. Bulletin of the British Ornithologists' Club 135, 69–76.

Thornton, I., 2007. Island colonization: the origin and development of island communities. Cambridge University Press.

Tobias, J.A., Seddon, N., Spottiswoode, C.N., Pilgrim, J.D., Fishpool, L.D., Collar, N.J., 2010. Quantitative criteria for species delimitation. Ibis 152, 724–746. https://doi.org/10.1111/j.1474-919X.2010.01051.x.

Tobias, J.A., Donald, P.F., Martin, R.W., Butchart, S.H., Collar, N.J., 2021. Performance of a points-based scoring system for assessing species limits in birds. Auk 138, ukab016. https://doi.org/10.1093/ornithology/ukab016.

Valente, Luis, Illera, Juan Carlos, Havenstein, Katja, Pallien, Tamara, Etienne, Rampal S., Tiedemann, Ralph, 2017. Equilibrium bird species diversity in Atlantic islands. Curr. Biol. 27 (11), 1660–1666.e5. https://doi.org/10.1016/j.cub.2017.04.053.

Valente, Luis, Phillimore, Albert B., Melo, Martim, Warren, Ben H., Clegg, Sonya M., Havenstein, Katja, Tiedemann, Ralph, Illera, Juan Carlos, Thébaud, Christophe, Aschenbach, Tina, Etienne, Rampal S., 2020. A simple dynamic model explains the diversity of island birds worldwide. Nature 579 (7797), 92–96. https://doi.org/10.1038/s41586-020-2022-5.

VanderWerf, Eric A., Young, Lindsay C., Yeung, Norine W., Carlon, David B., 2010. Stepping stone speciation in Hawaii's flycatchers: Molecular divergence supports new island endemics within the elepaio. Conserv. Genet. 11 (4), 1283–1298.

Warren, Ben H., Simberloff, Daniel, Ricklefs, Robert E., Aguilée, Robin, Condamine, Fabien L., Gravel, Dominique, Morlon, Hélène, Mouquet, Nicolas, Rosindell, James, Casquet, Juliane, Conti, Elena, Cornuault, Josselin, Fernández-Palacios, José María, Hengl, Tomislav, Norder, Sietze J., Rijsdijk, Kenneth F., Sanmartín, Isabel, Strasberg, Dominique, Triantis, Kostas A., Valente, Luis M., Whittaker, Robert J., Gillespie, Rosemary G., Emerson, Brent C., Thébaud, Christophe, Courchamp, Franck, 2015. Islands as model systems in ecology and evolution: prospects fifty years after MacArthur-Wilson. Ecol. Lett. 18 (2), 200–217. https://doi.org/10.1111/ele.2015.18.issue-210.1111/ele.12398.

Whittaker, R.J., Araújo, M.B., Jepson, P., Ladle, R.J., Watson, J.E., Willis, K.J., 2005. Conservation biogeography: assessment and prospect. Divers. Distrib. 11, 3–23. https://doi.org/10.1111/j.1366-9516.2005.00143.x.

Whittaker, R.J., Fernández-Palacios, J.M., 2007. Island biogeography: ecology, evolution, and conservation. Oxford University Press.

Whittaker, Robert J., Fernández-Palacios, José María, Matthews, Thomas J., Borregaard, Michael K., Triantis, Kostas A., 2017. Island biogeography: taking the long view of nature's laboratories. Science 357 (6354), eaam8326. https://doi.org/10.1126/science:aam8326.

Winker, K., 2010a. Chapter 1: Subspecies represent geographically partitioned variation, a gold mine of evolutionary biology, and a challenge for conservation. Ornithol. Monogr., 67, 6–23. DOI: 10.1525/om.2010.67.1.6.

Winker, K., 2010b. Is it a species? Ibis 152, 679–682.

Winker, K., 2021. An overview of speciation and species limits in birds. Auk 138, ukab006. https://doi.org/10.1093/ornithology/ukab006.

Wright, Natalie A., Steadman, David W., Witt, Christopher C., 2016. Predictable evolution toward flightlessness in volant island birds. Proc. Natl. Acad. Sci. 113 (17), 4765–4770. https://doi.org/10.1073/pnas.1522931113.

Yates, Andrew, Akanni, Wasiu, Amode, M. Ridwan, Barrell, Daniel, Billis, Konstantinos, Carvalho-Silva, Denise, Cummins, Carla, Clapham, Peter, Fitzgerald, Stephen, Gil, Laurent, Girón, Carlos García, Gordon, Leo, Hourlier, Thibaut, Hunt, Sarah E., Janacek, Sophie H., Johnson, Nathan, Juettemann, Thomas, Keenan, Stephen, Lavidas, Ilias, Martin, Fergal J., Maurel, Thomas, McLaren, William, Murphy, Daniel N., Nag, Rishi, Nuhn, Michael, Parker, Anne, Patricio, Mateus, Pignatelli, Miguel, Rahtz, Matthew, Riat, Harpreet Singh, Sheppard, Daniel, Taylor, Kieron, Thormann, Anja, Vullo, Alessandro, Wilder, Steven P., Zadissa, Amonida, Birney, Ewan, Harrow, Jennifer, Muffato, Matthieu, Perry, Emily, Ruffier, Magali, Spudich, Giulietta, Trevanion, Stephen J., Cunningham, Fiona, Aken, Bronwen L., Zerbino, Daniel R., Flicek, Paul, 2016. ensembl 2016. Nucleic Acids Res. 44 (D1), D710–D716. https://doi.org/10.1093/nar/gkv1157.

Zheng, X., Levine, D., Shen, J., Gogarten, S.M., Laurie, C., Weir, B.S., 2012. A high-performance computing toolset for relatedness and principal component analysis of SNP data. Bioinformatics 28 (24), 3326–3328. https://doi.org/10.1093/bioinformatics/bts606.