

**Convergent evolution on oceanic islands: comparative genomics reveals species-specific processes in birds**

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Declarations of interest: none

## Abstract

Understanding the factors driving phenotypic and genomic differentiation of insular populations is of major interest to gain insight into the speciation process. Comparing patterns across different insular taxa subjected to similar selective pressures upon colonizing oceanic islands provides the opportunity to study parallel evolution and identify shared patterns in their genomic landscapes of differentiation. We selected four species of passerine birds (common chaffinch *Fringilla coelebs/canariensis*, red-billed croucher *Pyrhacorax pyrrhacorax*, house finch *Haemorrhous mexicanus* and dark-eyed/island junco *Junco hyemalis/insularis*) that have both mainland and insular populations. For each species, we sequenced whole genomes from mainland and insular individuals to infer their demographic history, characterize their genomic differentiation, and identify the factors shaping them. We estimated the relative ( $F_{ST}$ ) and absolute ( $d_{xy}$ ) differentiation, nucleotide diversity ( $\pi$ ), Tajima's D, gene density and recombination rate. We also searched for selective sweeps and chromosomal inversions along the genome. Changes in body size between island and mainland were consistent with the island rule. All species shared a marked reduction in effective population size ( $N_e$ ) upon island colonization. We found highly differentiated genomic regions in all four species, suggesting the role of selection in island-mainland differentiation, yet the lack of congruence in the location of these regions indicates that each species adapted to insular environments differently. Our results suggest that the genomic mechanisms involved, which include selective sweeps, chromosomal inversions, and historical factors like recurrent selection, differ in each species despite the highly conserved structure of avian genomes and the similar selective factors involved.

**Keywords:** Comparative genomics, island rule, parallel evolution, speciation.

## Introduction

The colonization of oceanic islands by mainland individuals has been a major engine of biological diversification, resulting in the evolution of thousands of new species across the world (Schluter, 2000; Grant, 2001; Price, 2008; Warren et al., 2015; Gillespie et al., 2020). These colonization events have also provided valuable research models to study processes like evolutionary divergence and local adaptation (Grant & Grant, 2002; Losos & Ricklefs, 2009; Brown et al., 2013). Upon colonization of oceanic islands, individuals across taxonomic groups have often been subjected to similar demographic and selective factors, like population bottlenecks, strong selection for local adaptation, and reduced dispersal (Woolfit & Bromham, 2005; Whittaker et al., 2017). Shared patterns of phenotypic evolution of insular populations across taxonomic groups has led to general biogeographic rules, like Foster's rule, also known as the "island rule", which postulates that on islands small animals tend to become larger, and large animals tend to become smaller (Foster, 1964; Clegg & Owens, 2002; Benítez-López et al., 2021). These patterns suggest the possibility of parallel evolution across species, and provide the opportunity to test whether the selective mechanisms acting during island colonization are shared across species, and whether selection acts on the same or different genomic loci.

The genomic underpinnings of divergence in oceanic islands are poorly understood, yet an increasing number of studies are addressing this topic thanks to the recent advances in high-throughput DNA sequencing (reviewed in Sackton & Clark, 2019). Both selection and drift can drive phenotypic changes in islands, yet patterns of parallel phenotypic change are more likely to be driven by selection than by random drift (Clegg, 2009; Rosenblum et al., 2014). Parallel phenotypic changes on islands could be promoted by similar selective pressures due to their particular features relative to the mainland, such as simplified ecosystems, reduced trophic resources, the availability of new ecological niches, a reduction in predation which often leads to an increase in intraspecific competition, and a reduction in interspecific competition (Blondel, 2000; Losos & Ricklefs, 2009). These insular selective pressures usually result in predictable changes in body size (Benítez-López et al., 2021), usually attributed to the absence of predators and the shifts in competition, and also result in diet shifts in order to adapt to the new trophic resources, leading to behavioral (Sayol et al., 2018; Lapiedra et al., 2021), morphological (Glor et al., 2004; Campana et al., 2020) and physiological adaptations (Blanco et al., 2014; Tattersall et al., 2018). The molecular basis of convergent phenotypic traits across species could be entirely species-specific, or instead show evolutionary convergence among species. The degree of molecular parallelism can range from sharing the same mutation on the same gene, to changes at different nucleotides within

the same gene, to changes in different genes within the same pathway (Manceau et al., 2010; Sackton & Clark, 2019). The probability of molecular parallelism is determined by several factors, increasing when selective pressures are similar and genomic constraints such as demography and phylogenetic history are shared (Rosenblum et al., 2014). The genetic basis of the phenotypic traits under selection is also important: single-locus traits have been often involved in repeated convergent evolution (e.g., Reed et al., 2011; Colosimo et al., 2005), yet for polygenic traits, which can be modified through multiple pathways, molecular parallelism becomes less likely (Rosenblum et al., 2014; Boyle et al., 2017; Sendell-Price et al. 2021) resulting instead in heterogeneous, species-specific patterns of differentiation.

Understanding the factors that generate heterogeneous patterns of differentiation across the genome is one of the main goals of population genomics (Cruickshank & Hahn, 2014; Burri, 2017; Ravinet et al., 2017; Feng et al., 2020; Chase et al., 2021). The main factors shaping differentiation patterns are drift and selection, but demographic history and genomic features such as recombination rate and gene content also affect the distribution of the differentiated regions (Ravinet et al., 2017). Recent advances in sequencing technologies have allowed studying the genomic landscapes of variation, which show the distributional pattern of genomic variation across the entire genome (Ellegren et al., 2012; Nadeau et al., 2012; Poelstra et al., 2014; Meier et al., 2018). When comparing differentiated populations, regions that are highly divergent relative to the genomic background are known as “islands of differentiation” (Turner et al., 2005; Ellegren et al., 2012) and are usually detected as regions of high relative divergence ( $F_{ST}$ , Weir & Cockerham, 1984). Early genome scans interpreted  $F_{ST}$  peaks as signatures of strong selection surrounded by valleys homogenized by gene flow (Nosil et al., 2009), where those  $F_{ST}$  peaks were caused by marked differences in allele frequencies at locally adapted sites and the neutral loci linked to them (Charlesworth et al., 1997; Feder & Nosil, 2010). However, when considering patterns of absolute divergence ( $d_{xy}$ ) and within-population diversity ( $\pi$ ) besides  $F_{ST}$ , new interpretations of how these islands of differentiation originate have been put forward.  $F_{ST}$  peaks could also appear when population diversity is low in either of the populations compared, while  $d_{xy}$  is less affected by this pattern. Several processes such as positive and/or background selection can reduce within population nucleotide diversity and generate “islands” of relative divergence, while absolute divergence remains unchanged (Cruickshank & Hahn, 2014; Burri et al., 2015; Irwin et al., 2018). Four models have been proposed to explain the underlying cause of islands of differentiation (Irwin et al., 2016; Irwin et al., 2018) and in order to differentiate these models it is crucial to understand the relationship between  $F_{ST}$ ,  $d_{xy}$  and  $\pi$  (Cruickshank & Hahn, 2014; Irwin et al., 2016; Han et al., 2017; Irwin et al., 2018). Two of those



models account for speciation in the presence of gene flow (“divergence-with-gene-flow” and “sweep-before-differentiation”) and the other two involve allopatric speciation (“Selection in allopatry” and “Recurrent selection”) (Irwin et al., 2016). Moreover, other factors such as demographic history, mutation rate heterogeneity, and recombination rate across the genome, as well as gene density, could modify the genomic landscape (Ravinet et al., 2017). Therefore, to correctly interpret the genomic landscapes of differentiation it is important to understand the demographic and evolutionary history of the target taxa (Ravinet et al., 2017). Variations in effective population size ( $N_e$ ) can produce different genomic signatures. For instance, marked reductions in  $N_e$  such as those caused by population bottlenecks at founder events, can modify levels of background selection and therefore the baseline for the detection of outlier loci (Ferchaud & Hansen, 2016; Leroy et al., 2021).

Covariation of genomic patterns of differentiation among different avian species has been shown across broad evolutionary timescales (Van Doren et al., 2017; Delmore et al., 2018; Vijay et al., 2017, Carbeck et al., 2023) and the coincident location of differentiation peaks has been of special interest to understand the process of convergent molecular evolution where similar loci evolve independently in several species (Seehausen et al., 2014). Bird genomes show high synteny (Zhang, 2014), a relatively stable number of chromosomes (Ellegren, 2010), similar recombination landscapes (Singhal et al., 2015; Kawakami et al., 2017), and across species microchromosomes show higher density in gene content than macrochromosomes (Dutoit et al., 2017; Singhal et al., 2015). The similarity in genomic landscapes of differentiation across closely related and diverged avian species could be due to the non-random distribution of gene content across the genome and the coincidence of low recombination areas along with linked selection (Van Doren et al., 2017; Irwin et al., 2018), since it has been shown that the recombination landscape in birds can be maintained across species over long evolutionary time periods (Singhal et al., 2015).

Here we use a comparative approach to examine patterns of genome-wide differentiation in avian species that have colonized oceanic islands, with the goal of assessing the relative roles of demographic history, time of divergence, and directional selection in driving divergence and potentially evolutionary convergence upon island colonization. We selected four passerine species that have mainland populations and have also colonized oceanic islands; two species from mainland Europe that have colonized the island of La Palma in the Canary Islands, Atlantic Ocean, the common chaffinch (*Fringilla coelebs/canariensis*) and the red-billed chough (*Pyrrhocorax pyrrhocorax*), and two species from North

America that have colonized Guadalupe Island on the Pacific Ocean, the house finch (*Haemorrhous mexicanus*) and the dark-eyed junco (*Junco hyemalis/insularis*). The red-billed chough and the house finch have diverged from mainland populations within the last 100,000 years, whereas the common chaffinch and the junco have been separated from their mainland relatives for over 500,000 years (Aleixandre et al., 2013; Morinha et al., 2020; Recuerda et al., 2021). Given that all four species have colonized oceanic islands and have been subjected to potentially similar selective pressures, we first analyzed if the differences phenotype between insular and mainland counterparts affected the same traits across species. Changes in morphological traits are expected upon colonization of the new insular environment (Warren et al., 2015; Whittaker et al., 2017) and those changes are likely to generate detectable genomic signatures. Therefore, we also asked if the genomic landscapes of differentiation are similar among species when taking divergence time into account.

We performed whole-genome resequencing of 9-12 individuals per treatment per species in order to determine whether the four species showed similar patterns of differentiation in their genomic landscapes, and whether these patterns have been shaped by similar processes. We studied the demographic history and performed genomic scans of  $F_{ST}$ ,  $d_{xy}$ ,  $\pi$ , Tajima's D, recombination rate, gene content and selective sweeps. We also scanned the genomes looking for putative chromosomal inversions, which have been shown to underlie major phenotypic polymorphisms in birds (Tuttle et al., 2016). We detected regions under selection among insular and mainland counterparts as  $F_{ST}$  outliers and selective sweeps, and identified shared candidate genes among the four species. Comparing the genomic signatures of island colonization in four different species that have been exposed to similar selective pressures and that differ in colonization time (which can be considered as a proxy for different stages along the speciation continuum), can provide useful understanding for the mechanisms shaping the genomic landscapes through the divergence process over time.

## Methods

### *Study Area and fieldwork*

We sampled mainland populations of the common chaffinch (Fringillidae: *Fringilla coelebs*) and the red-billed chough (Corvidae: *Pyrrhocorax pyrrhocorax*) in the Iberian Peninsula at Segovia and Los Monegros, respectively (see Recuerda et al. 2021, Morinha et al. 2020). The insular populations from both species were sampled in La Palma, the most north-western island of the Canary Islands archipelago (Fig. 1A,

Table S1). The common chaffinch lineage in the Canary Islands has recently been raised to species status (Billerman et al. 2022), and we use its current name, Canary Islands chaffinch (*Fringilla canariensis*). The mainland populations of the house finch (Fringillidae: *Haemorhous mexicanus*) and dark-eyed junco (Passerellidae: *Junco hyemalis oreganus*) were sampled in California, and two house finch individuals were sampled in Sierra Juarez (Baja California, Mexico). Insular populations for both species were sampled in Guadalupe Island, Mexico, in the Pacific Ocean (Fig. 1B, Table S1). The junco on Guadalupe Island, until recently a subspecies of *J. hyemalis*, has been raised to species status, and we use its current name, island junco (*Junco insularis*).

All individuals were captured in the field using mist nets, and also mesh traps in the case of red-billed choughs. All individuals were marked with uniquely numbered aluminum bands, sexed, aged and measured. A blood sample was obtained by venipuncture of the sub-brachial vein and stored in absolute ethanol at -20°C in the laboratory for DNA extraction. After processing, birds were released unharmed at the site of capture. We determined the sex of choughs by the amplification of the *Chd1* gene following Griffiths et al. (1996).

### ***Morphological data and analysis***

We compared the morphological traits of adult males from mainland and insular populations for all species using principal components analysis (PCA) of all variables and univariate analysis of variance (ANOVA) to compare the means among treatments for each species. For the common chaffinch, the junco and the house finch a wing ruler was used to measure unflattened wing length to the nearest 0.5 mm, and dial callipers of 0.1-mm precision were used to measure tail length, tarsus length, bill culmen, total bill length, bill width and bill depth, following Milá et al. (2008). All measurements were taken by a single observer (BM). For the red billed chough, the same traits were measured by a single observer (GB) following standard methods described previously (Blanco et al., 1996).

The PCA including all morphological variables was computed using the *prcomp* function in *stats R* package.

### ***Genome resequencing***

Genomic DNA was extracted with a QIAGEN Blood and Tissue kit following the manufacturer's protocol. Resequencing at 18x coverage of 24 individuals per species (12 per treatment, but only 9 for the

mainland common chaffinch) was conducted on a SE50 Illumina™ platform at Novogene™. Reads were trimmed with *Trim Galore* (Krueger, 2015) and mapped to their respective reference genomes using BWA (Burrows-Wheeler Aligner, Li & Durbin, 2009). For the common chaffinch and the house finch we used the common chaffinch reference genome (GCA\_015532645.2, Recuerda et al., 2021); for the junco we used the *Junco hyemalis* reference genome (GCA\_003829775.1, Friis et al., 2022); and for the red-billed croucher we used the *Corvus moneduloides* reference genome (GCA\_009650955.1, bCorMon1.pri). SNPs were called using BCFTOOLS v.1.3.1 (Danecek et al., 2021) including invariant sites. Filtering was performed with VCFTOOLS v. 0.1.15 (Danecek et al., 2011) separately for variant and invariant sites, using the following criteria for variant sites: (i) Indels and sites with more than two alleles were removed; (ii) a number of reads per site between 10 and 40; (iii) a minimal genotype quality of 30; (iv) a minor allele frequency of 0.01; and (v) 25% maximum missing data and for invariant sites a minimal genotype quality of 30. Variant and invariant sites were then merged using BCFTOOLS concat. The reference genomes from all four species were aligned to the zebra finch genome (*Taeniopygia guttata*, bTaeGut2.pat.W.v2) using nucmer from the MUMmer package (v.4.0, ‘-b 400’ and filtering with ‘delta-filter -1’; Marçais et al., 2018) and chromosomes were numbered accordingly (see Table S2, Fig. S1).

### ***Inference of demographic history***

The change in effective population size ( $N_e$ ) across time for each species was estimated using Pairwise Sequentially Markovian Coalescent (PSMC) analysis (Li & Durbin, 2011). The PSMC model infers demographic history based on genome-wide heterozygous sequence data. We used SAMTOOLS (Li et al., 2009) to obtain diploid consensus sequences from BAM files generated with BWA-mem (Li & Durbin, 2009). Sites with sequencing depth lower than 10 and higher than 35 were removed. Because sex chromosomes can show different rates and patterns of evolution than autosomes (reviewed by Irwin, 2018; Wright & Mank, 2013), we focused our comparisons of differentiation statistics on autosomes only. We converted the diploid consensus sequence to PSMC input files (psmcfa) using the tool fq2psmcfa included in the PSMC software. Then, the program PSMC was used to infer the population history with the options ‘-N25 -t5 -r1 -p “4+30\*2+4+6+10’’, except for the mainland common chaffinch, and for both populations of the house finch, where the upper time limit was set to 1 (-t1) to achieve convergence. We performed 100 bootstraps for one genome per species and treatment. The atomic time interval was set following Nadachowska-Brzyska et al., (2016). We used a mutation rate of 4.6 e-9 mutations/site/generation (Smeds et al., 2016), which has been used in other avian systems for PSMC

analysis (e.g., Ericson et al., 2017; Hanna et al., 2017; Sato et al., 2020; Campana et al., 2020). Generation time was set to two years for all species (Baker & Marshall, 1999; Reid et al., 2003; Møller, 2006; Friis et al., 2016).

### ***Inference of recombination rate***

In order to determine the effect of recombination rate on the genomic landscapes of differentiation, we estimated recombination rates across the genome for insular and continental populations for the four species using LDhat software (Mcvean & Auton, 2007). First, we created a modified likelihood lookup table based on the LDhat precomputed tables using a sample size of 12 per treatment (9 for the continental common chaffinch) and a population mutation rate parameter estimate of 0.001. Then vcf files were split into chunks of 10,000 SNPs and converted to ldhat format using VCFTOOLS v. 0.1.15 (Danecek et al., 2011). The input files generated were used in LDhat “interval” to estimate the effective recombination rate by implementing a Bayesian MCMC sampling algorithm with five million iterations, sampling every 5,000 steps and a block penalty of 10. Finally, the results were summarized using the LDhat module “stat”, discarding 20% of the samples as burn-in.

### ***Genome scans and detection of selective sweeps***

In order to detect genomic signatures of selection among the island and mainland counterparts from the four different species, we estimated two different statistics, the fixation index ( $F_{ST}$ , Weir & Cockerham, 1984) and the cross-population extended haplotype homozygosity (XP-EHH) (Sabeti et al., 2007). First,  $F_{ST}$ ,  $d_{xy}$  and  $\pi$  using were calculated in non-overlapping windows of 10Kb using pixy v. 2 (Korunes & Samuk, 2021). Pixy takes into account the invariant sites for  $\pi$  and  $d_{xy}$  calculations, thus overcoming the problem of most programs that use VCF files to calculate those statistics but do not distinguish among invariant and missing sites, resulting in deflated estimates (Korunes & Samuk, 2021). We also computed Tajima’s D (Tajima, 1989) in non-overlapping 10-Kb windows with VCFTOOLS (Danecek et al., 2011). The averaged values of each variable were then transformed to Z-scores using the “scale” command in R. To detect  $F_{ST}$ , outliers we corrected for multiple testing setting the false discovery rate (FDR) to 0.05 (Benjamini & Hochberg, 1995).

To detect selective sweeps, we computed the cross-population extended haplotype homozygosity (XP-EHH, Sabeti et al., 2007) using the R package *rehh* (Gautier et al., 2017). First, we phased the vcf files

containing only the variant sites in 50-Kb windows using Shapeit v2.r904 (Delaneau et al., 2013). The XP-EHH is based on the comparison of haplotype lengths between populations and has most detection power when the selected haplotype is near fixation in one population and still polymorphic in the other. The genomic regions showing a  $-\log_{10}(\text{p-value}) \geq 3$  were considered to be under selection. Then, we looked for overlapping regions between the  $F_{ST}$  and the XP-EHH outliers. We generated Manhattan plots for all the statistics using the R package *qqman* (Turner, 2018) in R v. 3.6 (R Core Team, 2018).

### ***Detecting putative chromosomal inversions***

In order to detect potential chromosomal inversions, we examined how patterns of population structure varied along the genome using the R package *lostruct* (Li & Ralph, 2019). SNP data for each species including only variant sites was converted to BCF format using BCFTOOLS version 1.9 (Li et al., 2009). We implemented the script provided by Huang et al. (2020), dividing the genome into 1,000-SNP non-overlapping windows and applying a principal components analysis (PCA) to each window. Euclidian distances between the two first principal components (PCs) between windows were calculated and mapped using multidimensional scaling (MDS) into a 40-dimensional space in order to see the similarity of the relatedness patterns between windows. To identify genomic regions with extreme MDS values, windows with absolute values greater than 4 SD over the mean across all windows were selected for each MDS coordinate. We performed 1,000 permutations of windows over chromosomes to test if outlier regions were randomly distributed across chromosomes. The putative inversion coordinates were the start position of the first outlier window and the end position of the last outlier window. The script included additional analyses to check if the MDS outliers were detecting inversions or instead other processes such as linked selection. First, a PCA was performed using the SNPs from each putative inversion with *SNPRelate* (Zheng et al., 2012). Inversions in the PCA would split the samples into three different groups (i.e., the two orientations and the heterozygotes in an intermediate cluster). The R function *kmeans* with the Hartigan & Wong (1979) method was used to identify the composition of groups of genotypes by performing clustering on the first PC, setting the initial cluster centers as the maximum, minimum and middle of the PC score range. Then, another test was performed averaging the individual heterozygosity per group detected by the k-means clustering. Inversions would show a pattern of higher heterozygosity of the central group relative to the other two groups. Finally, only MDS outlier regions that clustered into three groups in the PCA and showed higher heterozygosity in the middle group were considered as putative inversions.

297

## 298 ***Candidate genes and GO-term enrichment analysis***

299 We extracted the candidate genes of the genomic regions detected to be under selection by both  
300 methods separately ( $F_{ST}$  and XP-EHH outliers) using bedtools intersect and the annotation of their  
301 respective reference genomes. We checked their functions in *genecards* (Rappaport et al., 2017). We  
302 obtained the GO terms using the zebra finch dataset in *biomaRt* in R. We then performed a Gene  
303 ontology (GO) enrichment analysis for each set of outliers in the category “biological function” using the  
304 *TopGO* R package (Alexa & Rahnenfuhrer, 2016). To estimate the statistical significance, we used the  
305 Fisher exact test implementing the *weight01* method. As recommended by the *TopGO* authors, we did  
306 not implement corrections for multiple testing and presented raw p-values for the top-10 GO terms  
307 related to biological processes.

308

## 309 **Results**

### 310 ***Morphological differences***

311 The morphological analysis revealed marked differences in most traits between insular and continental  
312 populations for all species. The small species (common chaffinch, junco and house finch), shared a  
313 pattern of significantly larger values for most traits in the insular populations compared to mainland,  
314 except for the junco wing length, which was longer in the continent (Table S3). In the larger sized red-  
315 billed chough, we detected the opposite pattern, with significantly smaller values for most  
316 morphological traits in the insular populations, except for bill width, which was smaller in the continent  
317 (Table S3). The PC1 for all species showed significant differences among insular and mainland  
318 populations, explaining over 39% of the variance in all cases (Fig. 2).

319

### 320 ***Whole-genome resequencing***

321 The total number of sites obtained in the variant calling was close to the length of the reference  
322 genomes. The number of variant sites (40-50 million) was similar for all species except for the red-billed  
323 chough, which was lower (~13 million), and the same pattern was maintained after filtering (Table S4).  
324 The lower number of variants of the red-billed chough is consistent with its recent divergence, although

the house finch shows a high level of polymorphism, comparable to the other two species that diverged a longer time ago.

### ***Inference of demographic history***

PSMC-based demographic inference revealed a consistent pattern for the four species, showing stable or growing effective population sizes for mainland populations and a sharp reduction in effective population size in insular populations following colonization. The island-mainland divergence time estimates obtained from the PSMC analysis are around 900,000 years for the common chaffinch, 100,000 years for the house finch, 400,000 years for the dark-eye junco, and 30,000 years for the red-billed chough (Fig. 3, S2). The continental population of the red-billed chough showed the smallest effective population size, and the smallest difference between the continental and insular populations among the study species.

### ***Inferring parallel evolution from genome-wide scans***

Genome-wide scans of genetic differentiation showed high heterogeneity across the four target species. The  $F_{ST}$  genomic landscapes varied strongly among species (Fig. 4-7). Mean  $F_{ST}$  was higher in the common chaffinch, followed by the dark-eyed junco, as expected for relatively longer island-mainland divergence times. The red-billed chough showed a slightly higher mean  $F_{ST}$  than the house finch (Table 1). The red-billed chough's genetic diversity was one order of magnitude lower than the rest, both for insular and mainland populations. The insular common chaffinch population showed the second lowest genetic diversity while the continental population showed the highest diversity value (Table 1). All species showed consistently higher gene content and recombination rates at microchromosomes, and in general, recombination rates were higher at chromosome extremes (Fig. 4-7).

The red-billed chough genomic landscape shows high levels of relative differentiation across the whole genome with few outlier regions. Mean genetic diversity in both populations is one order of magnitude lower than in the other three species (Table 1), showing very low values across the entire genome except in the microchromosomes, where genetic diversity and divergence show higher values at regions of high gene content. However, the XP-EHH analysis revealed evidence of selective sweeps, showing a few clear peaks along the genome that coincide with drops in Tajima's D (Fig.4).



The common chaffinch genome landscape is characterized by several  $F_{ST}$  peaks that coincide with valleys in  $d_{xy}$  and  $\pi$ , and peaks in Tajima's D mainly in the continent (i.e., peaks in chromosomes 1, 1A, 2, 3, 4, 4A, 6, Fig. 5). This pattern is consistent with the model of recurrent selection, which states that selection in the ancestor previous to the mainland-island split, generates a pattern of low  $d_{xy}$  and subsequent selection after divergence reduces genetic diversity, generating  $F_{ST}$  peaks. XP-EHH detected selective sweeps mostly concentrated in the microchromosomes and the Z chromosome; few of them coincided with  $F_{ST}$  peaks.

The dark-eyed junco genomic landscape is highly differentiated across the entire genome, and there are few outlier genomic regions, which often coincide with chromosomal extremes (Fig. 6). The XP-EHH scans did not detect significant selective sweeps across the genome, with only three small regions detected.

The house finch genomic landscape is characterized by a large, highly differentiated region in the middle of chromosome 3, representing 47 million base pairs, suggesting a large chromosomal inversion. It coincides with high values of Tajima's D in the continental population and a region of low recombination, while  $d_{xy}$  and  $\pi$  show regular values (Fig. 7). At the end of the same chromosome and at the beginning of chromosome 4, there are two  $F_{ST}$  peaks that coincide with a valley in  $d_{xy}$  and  $\pi$ , and a peak in Tajima's D. This pattern is consistent with the recurrent selection model. The microchromosomes show high relative differentiation along with high recombination rates and enriched gene content. The XP-EHH scan showed a relatively flat landscape with no evidence for significant selective sweeps.

### ***Detecting putative chromosomal inversions***

After combining all possible evidence, the analysis to detect inversions revealed that the red-billed croun genome has no putative inversions. The dark-eyed junco genome showed two possible inverted regions in chromosomes 6 and 7 (Table S5, Fig. S3A) but neither of them coincided with an  $F_{ST}$  outlier region. The common chaffinch genome showed two possible inversions in chromosomes 2 and 4, and both coincided with  $F_{ST}$  outlier regions (Table S5, Fig. S3B). The house finch genome revealed five putative inversions, a large one in chromosome 3, one in chromosome 1A, and three in chromosome 1. (Table S5, Fig. S3C). Only the large inversion in chromosome 3 coincides with an  $F_{ST}$  outlier region (Fig. 7).

386

387 ***Detection of candidate genes and GO-term enrichment analysis***

388 Sharing of candidate genes among species was limited. There were only two genes putatively under  
389 selection that were shared between two species: the *morc2* gene was shared between the house finch  
390 and the dark-eyed junco, and the *spef2* gene was shared between the dark-eyed junco and the common  
391 chaffinch. The *morc2* gene is associated with Marie-Tooth Disease, Axonal, Type 2z (CMT2Z) and  
392 Developmental Delay, Impaired Growth, Dysmorphic Facies, and Axonal Neuropathy (DIGFAN) diseases  
393 in humans. CMT2Z is characterized by distal lower limb muscle weakness and sensory impairment  
394 (Vujovic et al., 2021) and DIGFAN by impaired motor and intellectual development, poor overall growth,  
395 usually short body height and microcephaly and subtly dysmorphic facial features in humans (Sacoto et  
396 al., 2020). The *spef2* gene is involved in sperm development and also plays a role in osteoblast  
397 differentiation, being required for normal bone growth (Lehti et al., 2018).

398

399 In the red-billed chaough, the  $F_{ST}$  outliers mapped to 19 genes and the XP-EHH outliers detected  
400 selective sweeps in 14 genes, without overlap between the two methods. Due to the high relative  
401 differentiation across the genome and the absence of clear  $F_{ST}$  peaks, the clear selective sweeps along  
402 the genome could be a better approach to detect candidates for the red-billed chough. However, most  
403 of the genes among the 14 outlier genes found within sweeps have unknown functions, and only five  
404 genes have known functions and associated GO terms. From the 20,580 available genes from the *Corvus*  
405 *moneduloides* genome, only 8,632 from the gene universe (including the five significant genes) could be  
406 used for the analysis. Among the top-10 GO terms for the XP-EHH outliers we found several related to  
407 chromatin cohesion (i.e., regulation of cohesion loading and negative regulation of sister chromatid  
408 cohesion) (Table S6).

409

410 In the common chaffinch, the genomic scan detected 85 genes in the  $F_{ST}$  outlier regions, and the XP-EHH  
411 revealed 1,724 outliers that mapped to 21 genes, 3 of which were shared with the  $F_{ST}$  candidates. Among  
412 the 16,563 genes available in the gene universe, the GO term analysis detected 9,065 feasible genes,  
413 including 48 out of the 85 significant genes detected as  $F_{ST}$  outliers. Among the top-10 GO terms we  
414 found several involved in transcription regulation such as “transcription-dependent tethering of RNA  
415 polymerase II gene DNA at nuclear periphery” and “histone H3-K4 acetylation”, and others affecting  
416 translation like “lysyl-tRNA aminoacylation” (Table S7). There were also two terms related to cell

adhesion “regulation of protein localization to cell-cell adherens junction” and “regulation of focal adhesion assembly”, as well as two terms associated with the organization of cellular components including: “positive regulation of endosome organization” and “lysosome localization”.

In the dark-eyed junco, the  $F_{ST}$  genome scan detected relatively few peaks distributed across the genome that mapped to 24 genes, and three regions were detected as sweeps by the XP-EHH scan but did not contain known genes. Among the 24 genes, only 16 had GO terms associated with them. The GO enrichment analysis performed with a gene universe of 17,038 genes found 9,220 feasible genes including 15 potential candidate genes. The top-10 GO terms revealed three terms related to the centrosome, including “negative regulation of protein localization to centrosome”, “protein localization to pericentriolar material” and “positive regulation of mitotic centrosome separation” (Table S8).

Finally, in the house finch, the  $F_{ST}$  genome scan detected 111 genes putatively under selection, while the XP-EHH scan detected no significant outliers. From the genes identified under selection, 20 were clustered in the middle region of chromosome 3, and two were at the end of the same chromosome. The remaining genes were mainly clustered within microchromosomes. From the 16,563 available genes in the gene universe, 9,065 including 83 significant genes could be used in the GO enrichment analysis. Within the top-10 significant GO terms (Table S9) we find “growth plate cartilage chondrocyte morphogenesis” which is involved in skeletal development and morphogenesis. Also involved in morphogenesis we found the term “zonula adherens maintenance” which is related to cell-cell adhesion. We also find several terms associated with transcription, including “negative regulation of telomerase RNA reverse transcriptase activity”, “glutaminyl-tRNA aminoacylation” and two histone acetylations (H2-K14 and H3-K23).

## Discussion

Our comparative analysis of mainland and insular populations of four passerine species yielded shared patterns of phenotypic divergence and demographic history, in contrast to species-specific patterns of related genome-wide variation. Relative to the mainland, all insular populations showed changes in body size, and suffered reductions in effective population size and genetic diversity, patterns that are consistent with previous findings (Frankham, 1997; Leroy et al., 2021; Benitez et al., 2021). Island colonizations are usually initiated by a small group of individuals, and the resulting genetic drift, combined with the small size of the island’s geographic area, leads to a small effective population size

and low genetic diversity (Leroy et al., 2021; Frankham, 1995). Among the four species, the red-billed chough showed the smallest effective population size in both insular and mainland populations, which corresponds to the lowest levels of genetic diversity. In the mainland, this species has shown marked levels of genetic structure in the absence of geographic barriers, suggesting that social barriers due to complex behavioral interactions may constrain gene flow and thus the effective size of local populations (Morinha et al., 2017); the insular population is unlikely to be an exception (Morinha et al., 2020).

Using PC1 and mean differences in tarsus length, as proxies for structural body size in birds (Jolicoeur, 1963; Rising & Somers, 1989; Freeman & Jackson, 1990; Senar & Pascual, 1997), we found that the three smaller passerines increased in size and the larger species suffered a size reduction upon island colonization. This is consistent with the island rule, which posits that small birds evolve towards a larger size and large birds towards a smaller size upon island colonization (Clegg & Owens, 2002; Benitez et al., 2021). However, the difference in the house finch tarsus length among insular and mainland populations was not significant probably due to the small sample size. Regarding beak size, we find that insular individuals from the small sized and short-billed species show longer bills than their mainland counterparts whereas the insular population of the long-billed chough species shows a reduction in bill length. All the species show also differences in at least other bill dimension; however, the red billed chough is the only one in which the change is in the opposite direction, showing shorter but wider bills on the island. The beak is both a feeding and thermoregulatory structure with great evolutionary potential that allows birds to quickly adapt to new environmental conditions (Grant & Grant, 2011) and therefore plays a fundamental role in avian fitness (Grant, 1999; Boag & Grant, 1981; Price et al., 1984; Gibbs & Grant, 1987; Tattersall et al., 2017; Gamboa et al., 2022).

A major question in evolutionary biology is whether shared phenotypic traits are the result of evolutionary convergence, and the degree to which traits under similar selective pressures share a common genetic basis (Morris, 2010; Blount et al., 2018). Finding shared patterns of genomic variation and common regions of divergence at the intra- or inter-specific levels has been of major interest to understand the mechanisms underlying local adaptation (Burri et al., 2015; Van Doren et al., 2017; Delmore et al., 2018). These shared divergent regions across taxa are particularly interesting when differentiation evolved independently in unrelated lineages (Seehausen et al., 2014). A striking result of our comparative analysis of island-mainland populations in four passerine species is the lack of parallelism in their respective genomic landscapes. We found highly differentiated genomic regions in all

four species that were often associated with reduced genetic diversity, suggesting the role of selection in island-mainland differentiation. Yet the lack of congruence in the location of these regions along the genome indicates that the four species adapted to insular environments in different ways, through genetic changes at different loci. Moreover, patterns of recombination rate in these regions suggest that the genomic mechanisms generating these patterns, which include selective sweeps caused by directional selection, chromosomal inversions, and historical factors like recurrent selection, differ in each of the four species.

According to our demographic analysis, the divergence between red-billed choughs on La Palma and the Iberian Peninsula took place around 30,000 years ago, considering a generation time of two years. A previous study (Morinha et al., 2020) estimated the divergence event in a similar time range, within the last 10,000 years using mitochondrial data and around 30,000 years using iMA2, however they used a generation time of 6 years based on mainland data. If we apply that value, the divergence time estimate changes to around 110,000 years. The red-billed chough also shows the smallest effective population size lowest genetic diversity. This reduced genetic diversity also results in an inflation of the relative divergence (Charlesworth, 1998; Cruickshank & Hahn, 2014), causing a high baseline to detect outliers while the absolute divergence remains low. The recent divergence of the red-billed chough is apparent due to the low divergence along the genome with a mean  $d_{xy}$  value of  $8.2 \cdot 10^{-4}$ . The regions of higher divergence and genetic diversity are located in the microchromosomes, which have relatively higher recombination rates and higher gene content (Burt, 2002). However, the scan for selective sweeps, which is more efficient in detecting recent divergence, revealed clear peaks along the genome. The red-billed chough is the species showing the strongest selective sweeps, which is also consistent with the low genetic diversity of the species due to genomic hitchhiking of the sites flanking selected loci (Kaplan et al., 1989). Among the top ten GO terms of the genes within the selective sweeps there were several related with chromatin cohesion. Specifically, the WAPL gene negatively regulates the association of cohesin with chromatin, having an opposing function to the NIPBL gene. Mutations in the NIPBL gene cause Cornelia de Lange syndrome (CdLS), therefore, mutations in WAPL gene could generate similar developmental deficits to CdLS (Dorsett & Krantz, 2009). CdLS can affect most organ systems, but typical characters include craniofacial structures, upper extremities, eyes and the gastrointestinal system (Jackson et al., 1993; Bhuiyan et al., 2006). The actual role of WAPL has not been properly tested, but it has been associated with Warsaw Breakage Syndrome (WABS) (Faramarz et al., 2019), which is a cohesinopathy that causes growth retardation, severe microcephaly, sensorineural hearing loss,

cochlear anomalies, intellectual disability and abnormal skin pigmentation (Alkhunaizi et al., 2018; Faramarz et al., 2019).

The common chaffinch of La Palma was found to have diverged from its mainland relatives around 0.8-0.9 my ago, which is in agreement with previous reconstructions of the species evolutionary history (Recuerda et al. 2021). A study of the entire common chaffinch radiation across the Atlantic archipelagos revealed that it first colonized Azores, then Madeira and finally the Canary Islands (Recuerda et al., 2021). This sequential colonization of isolated archipelagos has left a genomic signature of recurrent selection along the genome, leading to regions with low absolute divergence due to selection in the ancestor, that were subsequently selected in the daughter populations, reducing genetic diversity and generating  $F_{ST}$  peaks (Irwin et al., 2016). This recurrent-selection model fits well with the known colonization history, as the first selective episode probably occurred upon colonization of the Azores, and then at every subsequent colonization step between islands, where successive selective events at the same genomic regions likely led to a loss of genetic diversity. Among the genes associated with outlier loci there were several involved in metabolism (i.e., *fabp2*, *kars1*, *lipa*, *nfrkb*, *pdha1*), five involved in pigmentation and six related to singing. Among the genes related to pigmentation, there were several related to avian plumage coloration, *ap3b1* (Ren et al., 2021), *hps6* (Domyan et al., 2019) and *ric1* (Bruders et al., 2020), one was related to sexual dichromatism in birds (Gazda, 2019), and the *atrn* gene was related to melanin production and has also been associated with coat coloration in macaques (Bradley et al., 2013). Regarding the genes related to song, we detected, *chrm2* and *chrm5*, which have shown differential expression associated with song learning and production in zebra finch (Osogwa, 2018), the *mrps27* (Qi et al., 2012) and *upf3b* (Shi et al., 2021), which are involved in the song control system in the zebra finch, the *paip1* gene, which has been associated with song learning (Lovell et al., 2008), and the *ube2d3* gene, which was related to musical abilities using a convergent evidence method including data from humans, songbirds and other animals (Oikkonen et al., 2016). Interestingly, within the top-ten significant GO terms we detected “positive regulation of endosome organization” and endosomes play an important role in neural development (Yap & Winckler, 2012). We also find the term “regulation of focal adhesion assembly” and it has been shown that cell adhesion plays an important role in tissue morphogenesis (Harris & Tepass, 2010).

In the dark-eyed junco, the demographic inference revealed that the insular population on Guadalupe diverged around 400,000 years ago, which is similar to previous estimates (Aleixandre et al., 2013). The

differentiated regions were mainly distributed at the ends of chromosomes, coinciding with telocentric centromeres, as previously found in Swainson's thrushes (Delmore et al., 2015). Consistent with this pattern, among the top-ten GO terms we identified several that were related to the centrosomes, increasingly recognized as signaling machines capable of regulating many cellular functions (Doxsey et al., 2005).

In the house finch, the genomic landscape showed signatures of different processes. Despite the recent divergence time between mainland and Guadalupe Island populations, estimated at about 100,000 years before present, we did not detect signatures of significant selective sweeps. The large region showing high differentiation and very low recombination in chromosome 3 likely represents a major chromosomal inversion. Genomic islands of differentiation could be generated by chromosomal rearrangements that cluster highly differentiated loci together due to genomic hitchhiking (Yeaman, 2013; Huang et al., 2020). However, that could represent either a group of adaptive alleles or several neutral loci linked to a focal selected allele (Yeaman, 2013). Several studies have found regions highly diverged within chromosomal inversions (Hoffmann et al., 2004; Ayala et al., 2014; Christmas et al., 2019; Huang et al., 2020). In this case, 20 genes putatively under selection were found within the inversion. Two of those genes (*fam162b* and *fig4*) are related to facial morphology and related disorders. Little is known about the function of the *fam162b* gene, but it is expressed in mouse facial prominences (Feng et al., 2009), and *fig4* is associated with the Yunis-Varon syndrome, characterized by skeletal defects including cleidocranial dysplasia, digital anomalies and neurological impairment (Campeau et al., 2013). Another interesting candidate is the *lyd* gene, which is also found within an inversion in chromosome 2 in the white-throated sparrow (*Zonotrichia albicollis*) and has shown differences in expression between two morphs that differed in territorial aggression including song (Zinzow-Kramer et al., 2015). Within that inversion, they found mainly genes related to behavior and plumage color. Some genes within the inversion in the house finch are related to mental retardation in humans including FMN2 (Law et al., 2014; Gorukmez et al., 2020), or to behavior in mice, like *pnisr* (Moloney et al., 2019). Interestingly, within the house finch inversion we also found the gene *gtf3c6*, which was found to be a candidate involved in sexual selection in a comparison of 11 bird genomes (Jaiswal et al., 2021). Within the top-ten significant GO terms, we found "growth plate cartilage chondrocyte morphogenesis", which is involved in skeletal development and morphogenesis and regulated by multiple signaling pathways including, among others, the bone morphogenetic proteins (Bmp; De Luca et al., 2001), fibroblast growth factors (FGFs; Deng et al., 1996) and Wingless/int.1

molecules (Wnt; Yang et al., 2003). Among these pathways, the Bmp and Wnt signaling pathways are known to be involved in facial development in different organisms including beak morphology in birds (Abzhanov, 2004; Brugmann et al., 2010). We also found the term “zonula adherens maintenance” and it has been shown that the adherens junctions are also involved in tissue morphogenesis (Harris & Tepass, 2010).

Here we studied four cases of island-mainland divergence in passerine species that have colonized oceanic islands and share phenotypic modifications likely caused by similar selective pressures, and asked whether the underlying genetic mechanisms were also shared. Our general result in this respect is that the regions of the genome showing evidence of divergence under directional selection are lineage specific, suggesting that the genetic basis of phenotypic divergence is different in each case, so that evidence for convergence at the genomic level appears to be lacking (Van Doren et al., 2017). Even if the same regions had been detected as putatively under selection or with shared genomic features involved in genomic differentiation, such as the stable recombination landscape in avian lineages (Singhal et al., 2015), it would be difficult to determine whether that pattern is generated by directional selection or by background and linked selection. Despite examples showing that few loci of large effect can drive adaptive divergence in complex traits, such as the bill (e.g., Enbody et al., 2023), selection is likely to act on many loci of small effect due to the polygenic nature of most adaptive traits (Pritchard & Di Rienzo, 2010; Bosse et al., 2017). Consequently, convergent phenotypes could in fact be due to divergent genotypes. Several examples to date show that phenotypic change in a given trait can be driven by different sets of genes, such as mouth morphology in cichlid fishes (Elmer et al., 2014), or color pattern in mice (Hoekstra et al., 2006; Steiner et al., 2009) and flies (Wittkopp et al., 2003). Even though the outlier genes differ among species, there could be common significant GO terms because different genes share functions and pathways. Interestingly, between the common chaffinch and the house finch we found several similar GO terms related to tRNA aminoacylation, histone acetylations and cell adherens junctions. Remarkably, we found that in all four species, GO terms are mostly related to gene regulation, for instance by modifying histones or altering chromatin binding and chromosome condensation, which are essential for differentiation and development. Recently, Monroe et al. (2021) reported that mutations occur less often in functional regions of the genome, and that epigenomic and physical chromosomal features account for the position of the mutations. In our case, most of the terms related to outlier loci are involved in epigenetic modifications, suggesting that changes in gene regulation, instead of specific core genes, may be the main drivers of divergence. Currently, several



models are being developed to understand the role of gene regulation in the evolution of complex traits (Boyle et al., 2017; Liu et al., 2019), implying that regulatory regions are disproportionately targeted by polygenic selection, highlighting the key role of gene regulatory networks in evolution (Fagny & Austerlitz, 2021).

#### Data availability

Resequencing raw data is deposited at NCBI under the SRA data projects PRJNA661201 (for common chaffinch mainland population) with accession numbers SAMN16094451-SAMN16094459 and PRJNAXXXXX with accession numbers SAMNXXXXX-SAMNXXXXX, for the common chaffinch insular population and both populations from the rest of the species, see Table S1 for details) and the datasets, are deposited in Figshare (<https://doi.org/10.6084/m9.figshare.21590673>).

#### Acknowledgements

We are grateful to José Manuel González, Óscar Frías and Félix Medina for invaluable help in the field. This work was supported by grants CGL-2015-66381P and PGC-2018-098897-B-I00 from Spain's Ministry of Science and co-financed by the European Union's Regional Development Fund (ERDF). MR was supported by a doctoral fellowship from Spain's Ministry of Education, Culture, and Sport (FPU16/05724).

#### CRedit authorship contribution statement

MR carried out the molecular lab work, carried out the data curation and analysis, participated in the design of the study, collected field data and drafted the manuscript; GB conceived and designed the study, collected field data and critically revised the manuscript; BM conceived and designed the study, collected field data and critically revised the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

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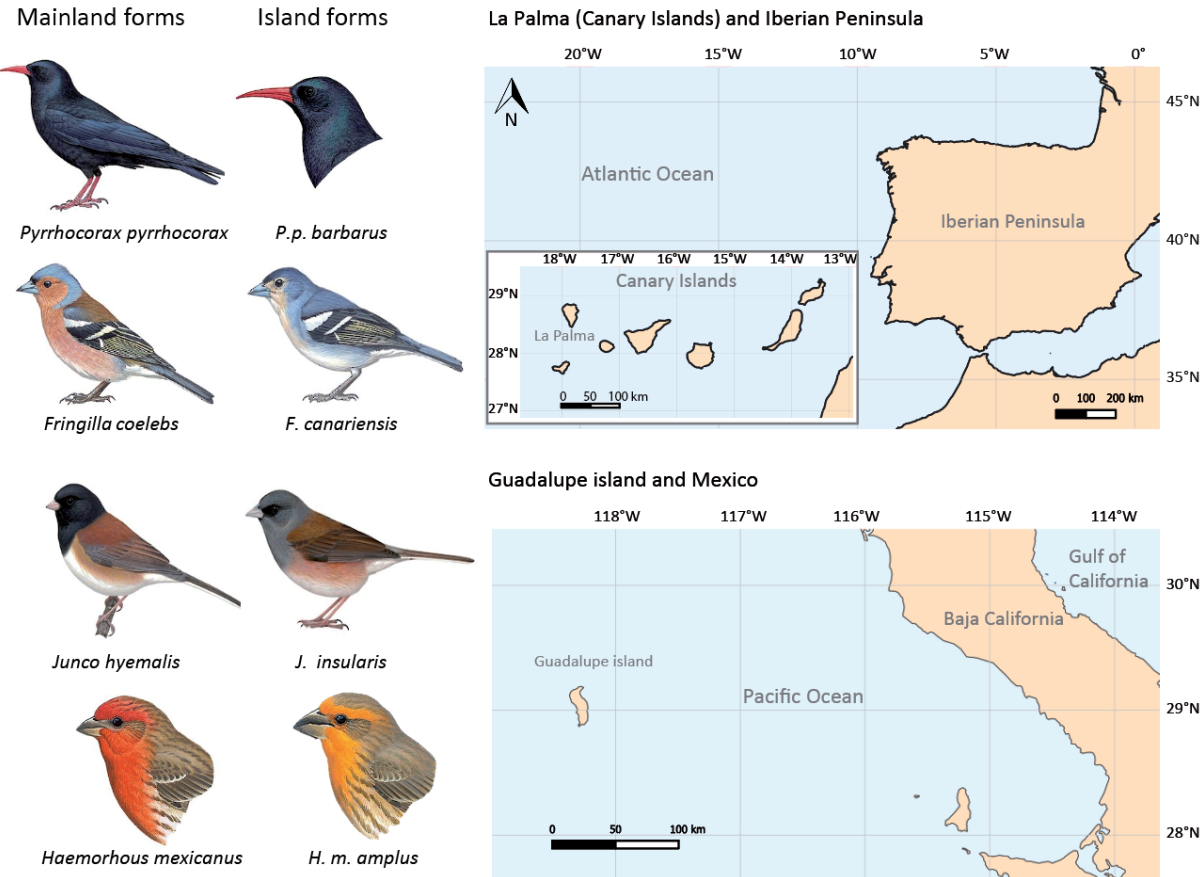


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**Tables**

**Table 1.** Divergence and diversity across the genome. Mean values, standard deviation and range of genomic summary statistics for the four species, including: Samples sizes for the continental and insular populations ( $N_{\text{cont}}$  and  $N_{\text{is}}$ ), fixation Index ( $F_{\text{ST}}$ ), absolute genomic divergence ( $d_{\text{xy}}$ ), and genetic diversity for the insular and the continental populations.

Species	$N_{\text{cont}}$	$N_{\text{is}}$	$F_{\text{ST}} \pm \text{sd}$	range	$d_{\text{xy}} \pm \text{sd}$	range	$\pi_{\text{island}} \pm \text{sd}$	range	$\pi_{\text{continent}} \pm \text{sd}$	range
Red-billed chough	12	12	$0.21 \pm 0.12$	[-0.055 - 0.89]	$0.0008 \pm 0.0004$	[0 - 0.15]	$0.0005 \pm 0.003$	[0 - 0.013]	$0.0008 \pm 0.0004$	[0 - 0.020]
House finch	12	12	$0.14 \pm 0.09$	[-0.45 - 0.66]	$0.006 \pm 0.002$	[0 - 0.017]	$0.0043 \pm 0.002$	[0 - 0.018]	$0.0052 \pm 0.002$	[0 - 0.016]
Dark-eyed junco	12	12	$0.26 \pm 0.07$	[0.006 - 0.68]	$0.005 \pm 0.002$	[0 - 0.023]	$0.0022 \pm 0.001$	[0 - 0.023]	$0.0049 \pm 0.002$	[0 - 0.022]
Common chaffinch	9	12	$0.40 \pm 0.05$	[-0.033 - 0.88]	$0.009 \pm 0.003$	[0 - 0.022]	$0.0016 \pm 0.001$	[0 - 0.021]	$0.0091 \pm 0.003$	[0 - 0.023]



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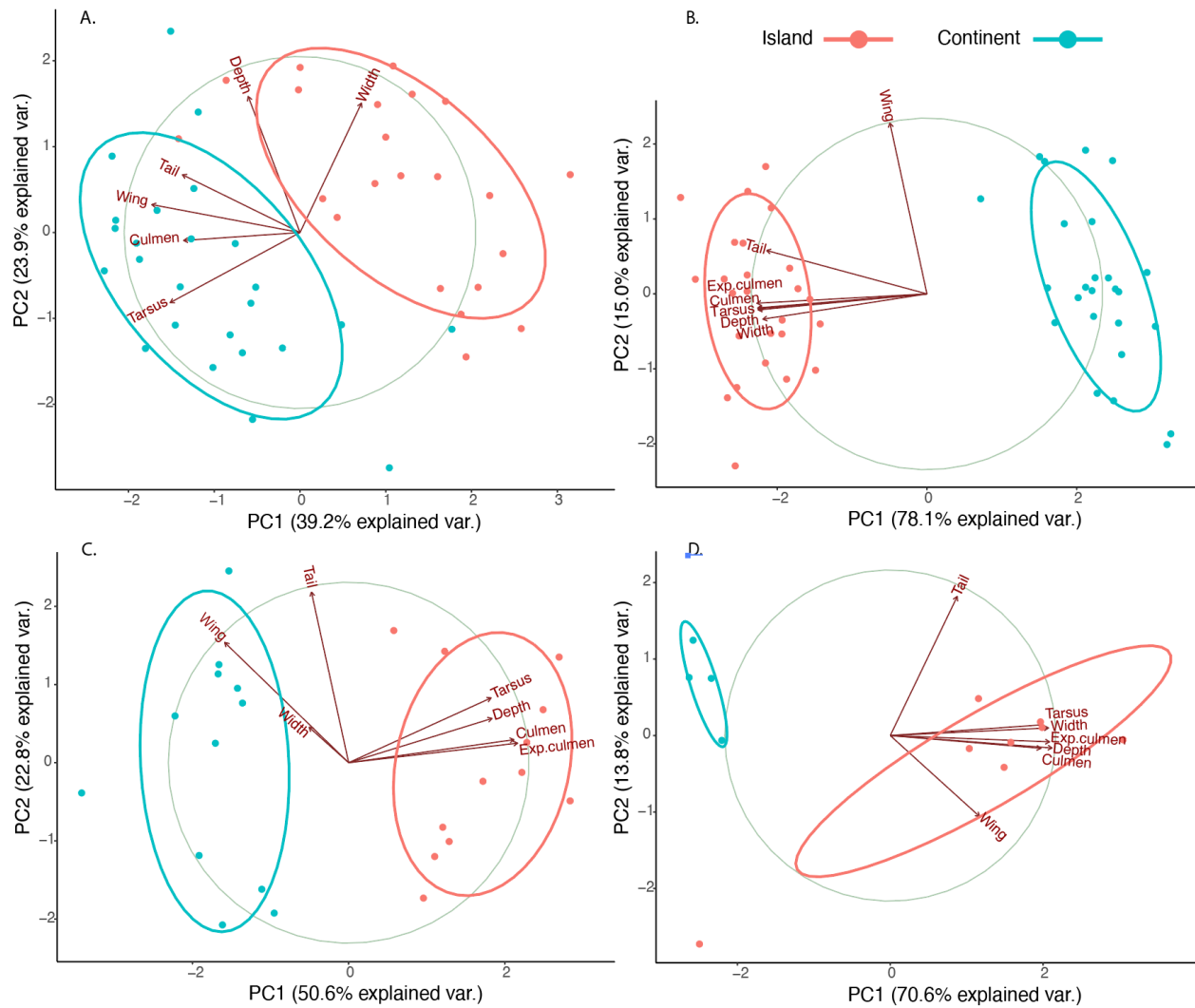
1140   **Figure 1. Target taxa for comparative analysis.** (A) Species that have colonized La Palma in the Atlantic

1141   Ocean: the red-billed chough and the common chaffinch. (B) Species that have colonized Guadalupe

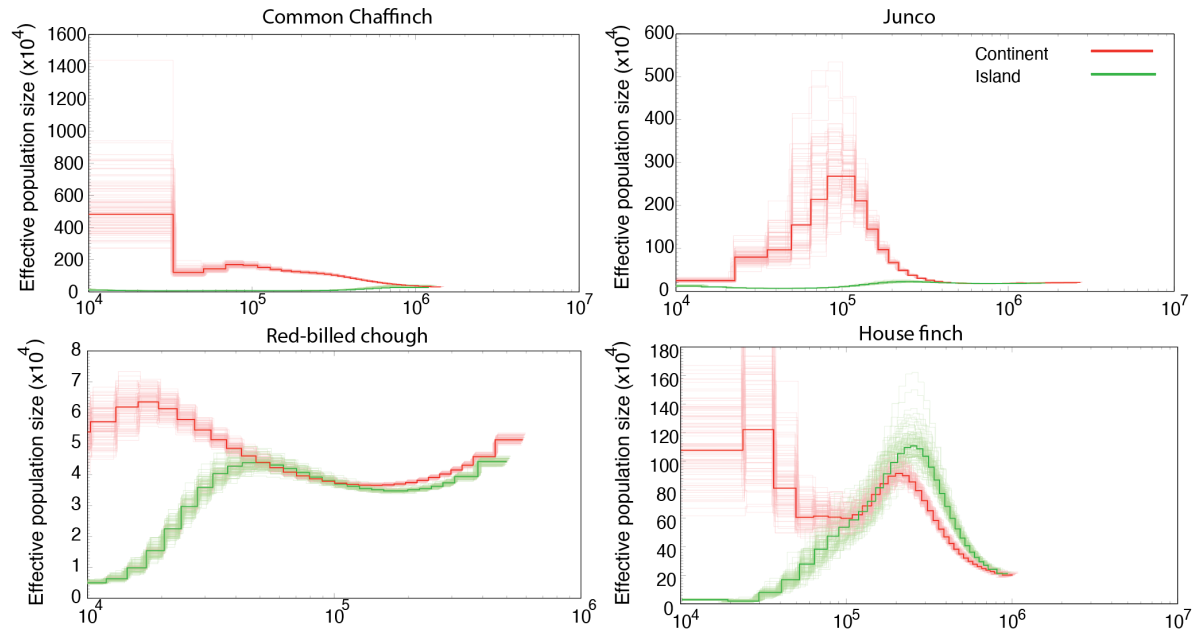
1142   island in the Pacific Ocean: the dark-eyed junco and the house finch. Bird species according to Clements

1143   et al., (2023). Bird illustrations from Billerman et al., (2022).

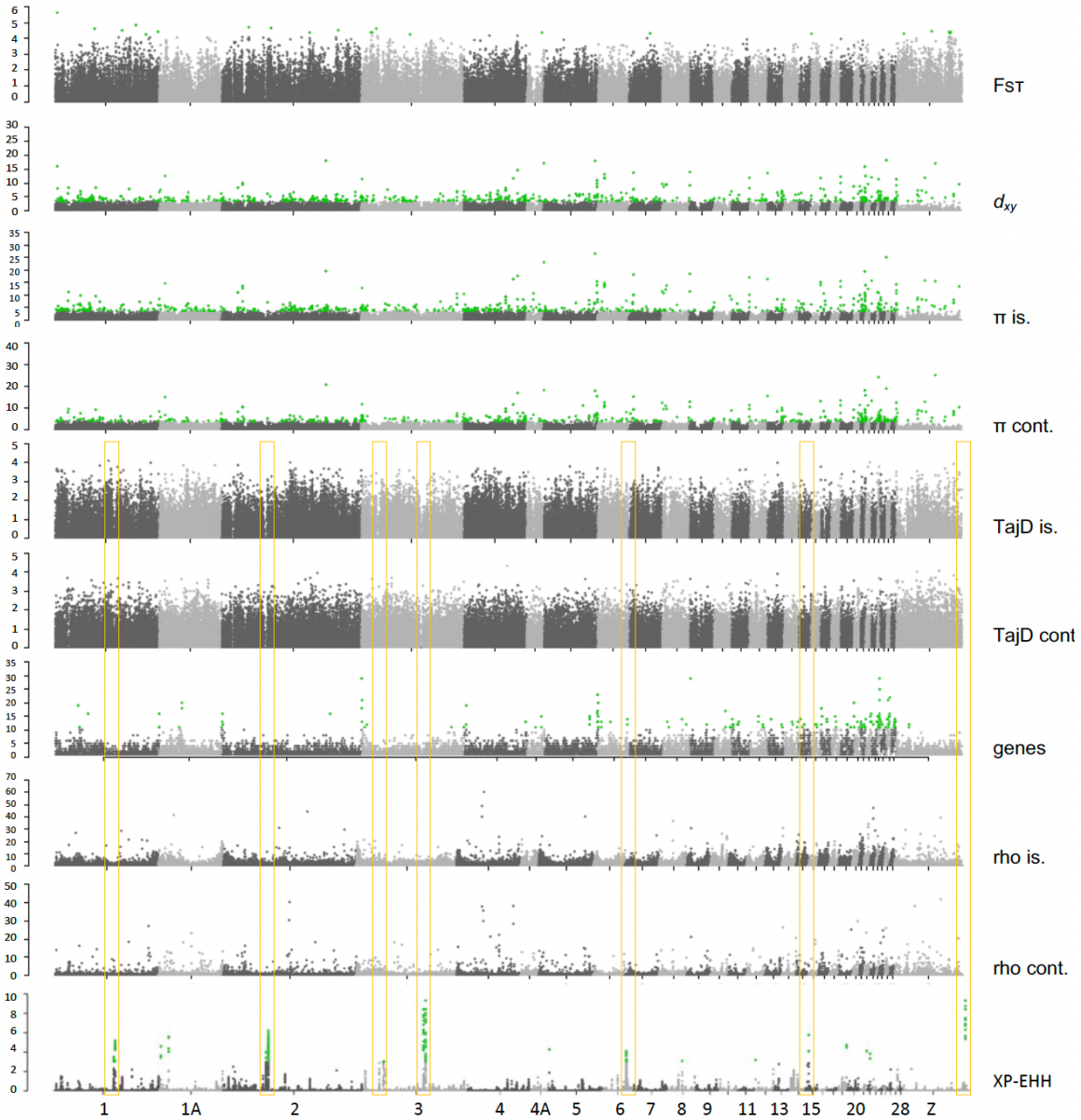
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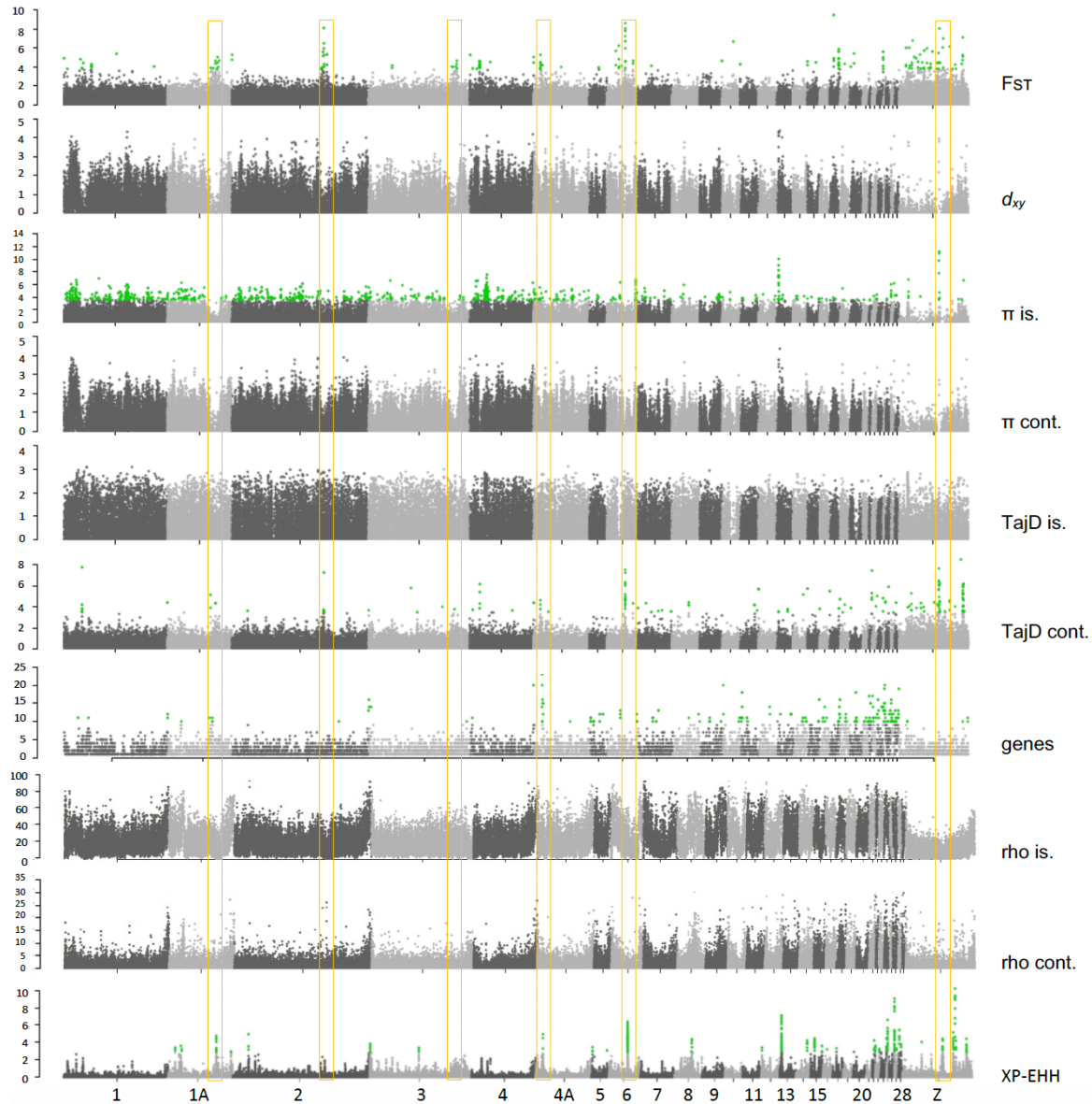
**Figure 2.** Principal Component Analysis (PCA) with morphological data per species A) Red-billed chough, B) Common/Canary Islands chaffinch, C) Dark-eyed/island junco, D) House finch. The variables included are wing, tail and tarsus length and bill depth, width, culmen and exposed culmen (the latter is not included for the red-billed chough). The correlation circle with radius 1 show the loadings of each variable that are represented by the arrows. The variables included are wing, tail and tarsus length and bill depth, width, culmen and exposed culmen (the latter is not included for the red-billed chough). Red and blue markers correspond to insular and mainland individuals, respectively.



**Figure 3.** Demographic history of insular and mainland populations. The analysis was performed using Pairwise Sequentially Markovian Coalescent (PSMC). Demographic inference for one individual per treatment and species, with the red and green dark lines corresponding to the continental and insular populations, respectively. The lighter red and green lines represent 100 bootstrap replicates. The point where both lines depart from each other corresponds to the time of colonization, which is around 40,000 y for the red-billed chough, 900,000 y for the common chaffinch, 100,000 y for the house finch and 400,000 y for the dark-eye junco. The mutation rate used was of 4.6e-9 mutation/site/generation for all species, and the generation time used in all cases was two years. See Fig. S2 for bootstrapped versions of the individual PSMC plots.

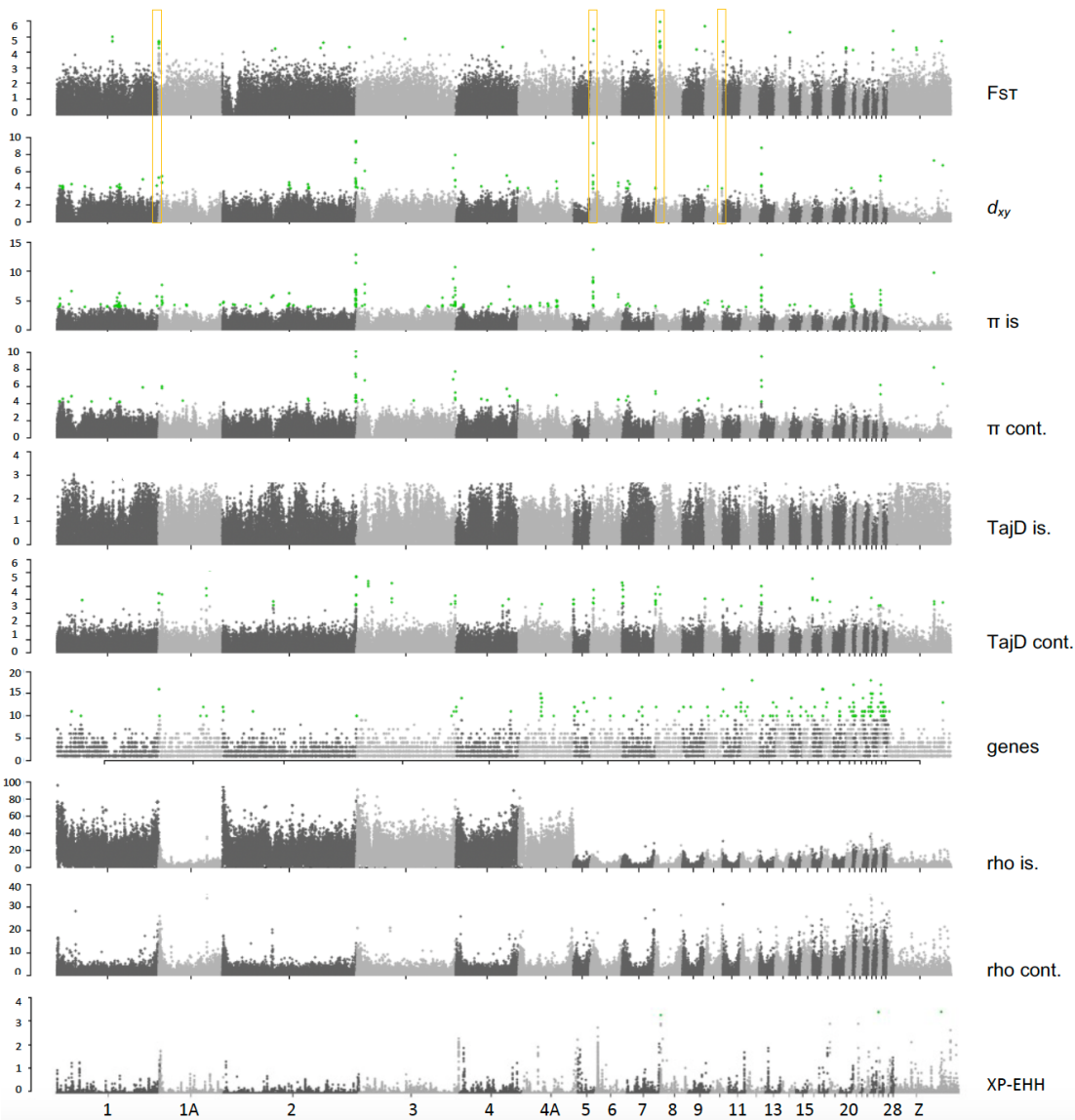


**Figure 4.** Genomic scans for several summary statistics for an island-mainland comparison in the red-billed cough (*Pyrrhonorax pyrrhonorax*). From top to bottom, fixation index ( $F_{st}$ ), genomic divergence ( $d_{xy}$ ), genetic diversity for insular and continental populations ( $\pi$ ), Tajima's D for insular and continental populations (TajD), number of genes, recombination rates for insular and mainland populations (rho) and Cross-populations Extended Haplotype Homozygosity (XP-EHH). Chromosome numbers correspond to the Zebra finch genome (*Taeniopygia guttata*). Green dots represent outliers with the false discovery rate (FDR) set at 0.05 after applying the Benjamini and Hochberg correction, except for the XP-EHH, where the threshold is set at  $-\log_{10}(p\text{-value}) \geq 3$ . The yellow boxes highlight the XP-EHH peaks coincident with drops in Tajima's D.



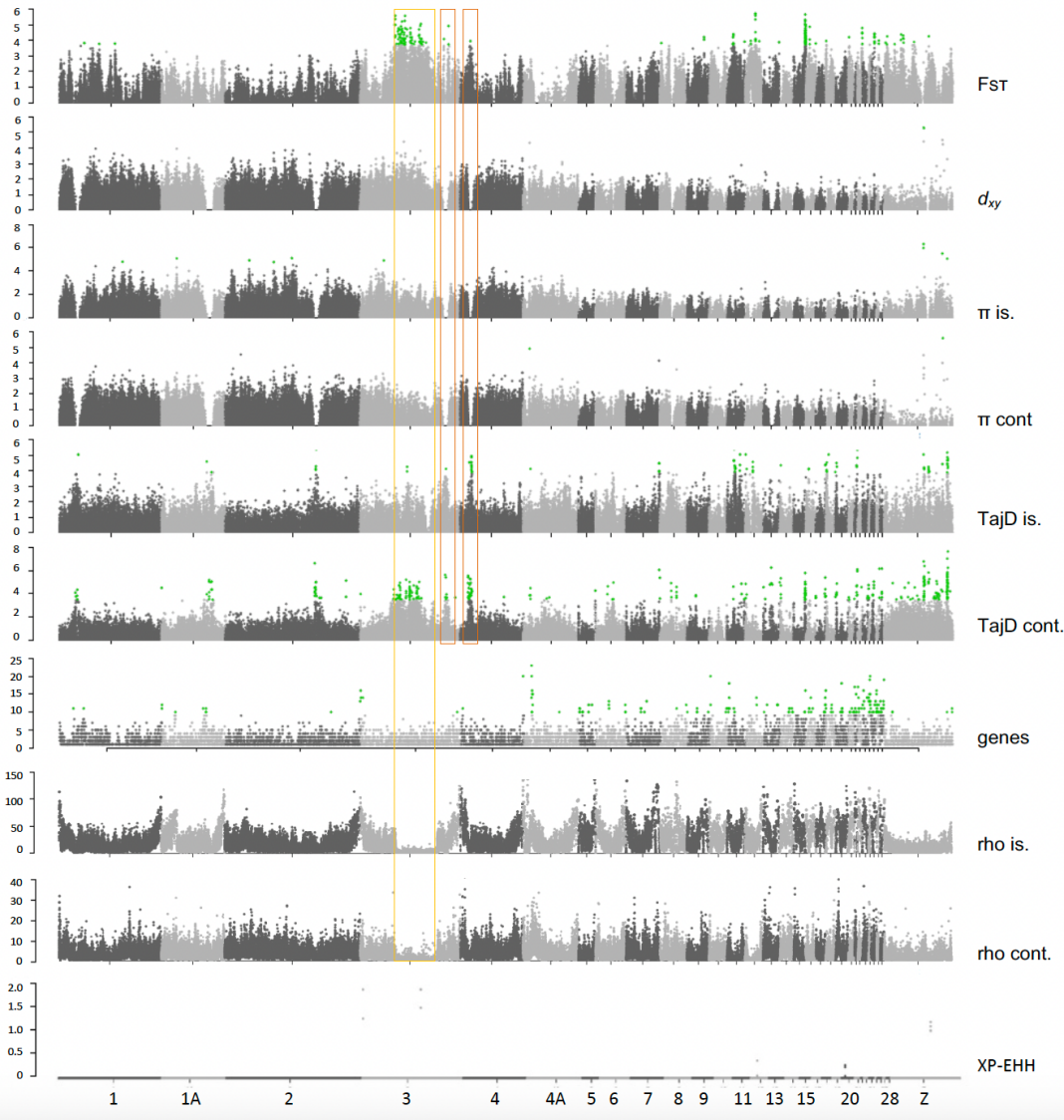
**Figure 5.** Genomic scans for several summary statistics for an island-mainland comparison in the common chaffinch (*Fringilla coelebs*). From top to bottom, fixation index ( $F_{ST}$ ), genomic divergence ( $d_{xy}$ ), genetic diversity for insular and continental populations ( $\pi$ ), Tajima's D for insular and continental populations (TajD), number of genes, recombination rates for insular and mainland populations ( $\rho$ ) and Cross-populations Extended Haplotype Homozygosity (XP-EHH). Chromosome numbers correspond to the Zebra finch genome (*Taeniopygia guttata*). Green dots represent outliers with the false discovery rate (FDR) set at 0.05 after applying the Benjamini and Hochberg correction, except for the XP-EHH, where the threshold is set at  $-\log_{10}(p\text{-value}) \geq 3$ . The yellow boxes highlight the signatures of recurrent selection ( $F_{ST}$  peaks coincident with drops in  $d_{xy}$  and  $\pi$ ). Some of them are also coincident with peaks in XP-EHH.





**Figure 6.** Genomic scans for several summary statistics for an island-mainland comparison in the dark-eyed junco (*Junco hyemalis*). From top to bottom, fixation index ( $F_{ST}$ ), genomic divergence ( $d_{xy}$ ), genetic diversity for insular and continental populations ( $\pi$ ), Tajima's D for insular and continental populations (TajD), number of genes, recombination rates for insular and mainland populations ( $\rho$ ) and Cross-populations Extended Haplotype Homozygosity (XP-EHH). Chromosome numbers correspond to the Zebra finch genome (*Taeniopygia guttata*). Green dots represent outliers with the false discovery rate (FDR) set at 0.05 after applying the Benjamini and Hochberg correction, except for the XP-EHH, where the threshold is set at  $-\log_{10}(p\text{-value}) \geq 3$ . The yellow boxes highlight the  $F_{ST}$  peaks in the chromosome extremes.





**Figure 7.** Genomic scans for several summary statistics for an island-mainland comparison in the house finch (*Haemorrhous mexicanus*). From top to bottom, fixation index ( $F_{ST}$ ), genomic divergence ( $d_{xy}$ ), genetic diversity for insular and continental populations ( $\pi$ ), Tajima's D for insular and continental populations (TajD), number of genes, recombination rates for insular and mainland populations (rho) and Cross-populations Extended Haplotype Homozygosity (XP-EHH). Chromosome numbers correspond to the Zebra finch genome (*Taeniopygia guttata*). Green dots represent outliers with the false discovery rate (FDR) set at 0.05 after applying the Benjamini and Hochberg correction, except for the XP-EHH, where the threshold is set at  $-\log_{10}(p\text{-value}) \geq 3$ . The yellow box highlights the putative inversion in chromosome 3 ( $F_{ST}$  peak that coincides with a drop in the recombination rate). The orange boxes highlight the signatures of recurrent selection ( $F_{ST}$  peak coincident with drops in  $d_{xy}$  and  $\pi$ ).