Genomic bases of insularity and ecological divergence in barn owls (*Tyto alba*) of the Canary Islands

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Abstract

Islands, and the particular organisms that populate them, have long fascinated biologists. Due to their isolation, islands offer unique opportunities to study the effect of neutral and adaptive mechanisms in determining genomic and phenotypical divergence. In the Canary Islands, an archipelago rich in endemics, the barn owl (*Tyto alba*) is thought to have diverged into a subspecies (*T. a. gracilirostris*) on the eastern islands, Fuerteventura and Lanzarote. Taking advantage of 40 whole-genomes and modern population genomics tools, we provide the first look at the origin and genetic makeup of barn owls of this archipelago. We show that the Canaries hold diverse, long-standing and monophyletic populations with a neat distinction of gene pools from the different islands. Using new method, less sensitive to structure than classical F_{ST}, to detect regions involved in local adaptation to the insular environment, we identified a haplotype-like region likely under positive selection in all Canaries individuals. Genes in this region suggest morphological adaptations to insularity. In the eastern islands, where the subspecies *T. a. gracilirostris* is present, genomic traces of selection pinpoint signs of locally adapted body proportions and blood pressure, consistent with the smaller size of this population living in a hot arid climate. In turn, genomic regions under selection in the western barn owls from Tenerife showed an enrichment in genes linked to hypoxia, a potential response to inhabiting a small island with a marked altitudinal gradient. Our results illustrate the interplay of neutral and adaptive forces in shaping divergence and early onset speciation.

Key words – Local adaptation; Niche analysis; Population genomics; *Tyto alba gracilirostris*; Whole genome sequencing

Introduction

Due to the often-peculiar organisms that inhabit them, islands have always fascinated naturalists and scientists alike. Since Darwin's first visit to the Galapagos in 1835, the study of insular populations has been crucial to the development of evolutionary theory (MacArthur and Wilson 1967; Grant 1998; Warren et al. 2015). Labelled nature's test tubes, islands are home to a myriad of endemic (sub)species. Moreover, the combination of their relatively small size, discrete borders, geographical isolation and natural replication provides an excellent setting to study the evolutionary forces underlying population divergence and speciation (Losos and Ricklefs 2009). The divergence of insular populations from their founders and surrounding islands is the result of neutral and selective forces. Disentangling the respective impacts of these two forces is a challenging task, as they are interconnected and can both contribute to genetic and phenotypic differentiation.

Isolated and small populations, such as those frequently found on islands, are under a markedly strong influence of genetic drift. This process will alter the genetic makeup of the population by randomly removing rare alleles and fixating common ones, hence decreasing genetic diversity (Frankham 1997). This is a common occurrence on islands which, coupled with low gene flow, can lead to inbreeding (Keller and Waller 2002) and accelerate neutral divergence. Conversely, the absence of regular gene flow, and the often distinctive ecological conditions of the islands, can facilitate the action of local adaptation on beneficial alleles (Lenormand 2002; Tigano and Friesen 2016). This process can lead to the emergence of ecomorphs via ecological divergence as populations adapt to unfilled insular niches (Losos and Ricklefs 2009), particularly so in remote islands that are colonized less often (MacArthur and Wilson 1963). Ecomorphs can occur in different islands or in the same one (Gillespie et al. 1997; Losos et al. 1998; Gillespie 2004), a concept mirrored in inland lakes (Malinsky et al. 2015), the aquatic homologous of islands. Eventually, ecomorphs can become new subspecies or even species and, in extreme cases, result in adaptive radiations as illustrated by Darwin's finches (Grant 1999; Lamichhaney et al. 2015).

86   The Afro-European barn owl (*Tyto alba*) is a non-migratory, nocturnal raptor present from

87   Scandinavia to Southern Africa. It is also found on numerous islands and archipelagos where

88   subspecies have often been described (Uva et al. 2018). A recent study of the species' genetic

89   structure in the Western Palearctic (Cumer et al. 2021) described two main lineages occupying

90   this region: the eastern lineage in the Levant and the western in Europe. In addition, Cumer et

91   al. (2021) showed that barn owls from Tenerife (Canary Islands) were very distinct from both

92   lineages. The Canaries are a volcanic archipelago that was formed several million years ago

93   (Anguita and Hernán 2000) about 100 km from the coast of north-western Africa and was never

94   connected to the mainland. This long-term isolation (Norder et al. 2019), along with its

95   subtropical climate and elevation gradients (Steinbauer et al. 2016), has resulted in a high level

96   of endemicity, for example in plants (Carine et al. 2009), reptiles (Thorpe and Baez 1993;

97   Nogales et al. 1998; Nogales et al. 2001; Molina-Borja 2003; Mateo et al. 2011), mammals

98   (Hutterer et al. 1987; Pestano et al. 2003; Firmat et al. 2010; Masseti 2010) and birds (Illera et

99   al. 2016; Lifjeld et al. 2016; Rodríguez et al. 2020; Senfeld et al. 2020). Among them, an

100   endemic barn owl subspecies, *T. a. gracilirostris* (Hartert, E, 1905), has been described based on

101   its morphological traits, especially for its smaller size and darker coloration (Bannerman 1963;

102   Clements et al. 2019). This subspecies is recorded in the eastern Canary Islands of Lanzarote

103   and Fuerteventura, as well as in its surrounding islets (Lobos, Alegranza, Montaña Clara and La

104   Graciosa), and is the only barn owl in this sector of the archipelago (Siverio 2007).

105   The presence of this subspecies on the eastern islands is surprising however, given that it is

106   sandwiched between the western islands and the mainland which both harbour the nominal

107   species *T. alba*. Lacking any evidence of different colonization origins or timing, this could

108   suggest that selection to local conditions acting on the eastern population has accelerated

109   divergence in comparison to the western one. In both cases, neutral and adaptive

110   microevolutionary processes promoting divergence of insular populations would leave traces on

111   their genomic makeup. The advances in sequencing technology, and its decreasing costs, now

112   allow to sequence the entire genomes of individuals. With the parallel development of

113   sophisticated tools, it is possible to analyse changes in allelic frequencies at a high resolution to

114   investigate the history of populations and inspect the genomic landscape for signals of local

115   adaptation.

116   Here, we investigate the genomic bases of differentiation of barn owls from the Canary Islands.

117   Making use of the whole-genome sequences from 40 individuals, we first describe the neutral

118   genetic structure and diversity of the Canaries populations in contrast to the mainland, in order

119   to retrace their history. Second, we employ a new relatedness-based method to probe the

120   genomic landscape of these isolated populations for signals of local adaptation to the insular

121   environment in regards to the mainland. Third, we characterize the climatic niches barn owls

122   occupy on eastern and western islands, and explore how each population is diverging to adapt

123   to their niches from a genomic perspective. Our results elucidate the genomic bases of the

124   differentiation of insular populations, thus enlightening the classification of the Canaries barn

125   owls.

126

Materials & Methods

Whole-genome sequencing, SNP calling and identification of coding regions

For this study, 40 individual barn owls were sampled from four populations (Figure 1;

Supplementary Table 1): Eastern Canaries (EC, Fuerteventura and Lanzarote), Western Canary

(WC, Tenerife), Morocco (MA), Portugal (PT) and Israel (IS). All but the EC and MA populations

were published in previous work, including a North American owl that was used as an outgroup

for some analyses (Genbank accession JAEUGV000000000 (Cumer et al. 2021; Machado et al.

2021). For EC and MA, we followed the same molecular and sequencing protocol as in the

aforementioned publications. Succinctly, genomic DNA was extracted using the DNeasy Blood &

Tissue kit (Qiagen, Hilden, Germany) and individually tagged 100bp TruSeq DNA PCR-free

libraries (Illumina) were prepared according to manufacturer's instructions. Whole-genome

resequencing was performed on multiplexed libraries with Illumina HiSeq 2500 high-throughput

paired-end sequencing technologies at the Lausanne Genomic Technologies Facility (GTF,

University of Lausanne, Switzerland).

The bioinformatics pipeline used to obtain analysis-ready SNPs from the 40 individuals plus the

outgroup was the same as in (Machado et al. 2021), adapted from the Genome Analysis Toolkit

(GATK) Best Practices (van der Auwera et al. 2013) to a non-model organism following the

developers' recommendations. Briefly, reads were trimmed with Trimommatic v.0.36 (Bolger et

al. 2014) and aligned with BWA-MEM v.0.7.15 (Li and Durbin 2009) to the barn owl reference

genome (GenBank accession JAEUGV000000000; Machado et al. 2021). Base quality score

recalibration (BQSR) was performed in GATK v.4.1.3 using high-confidence calls obtained from

two independent callers: GATK's HaplotypeCaller and GenotypeGVCF v.4.1.3 and ANGSD v.0.921

(Korneliussen et al. 2014). Following BQSR, variants were called with GATK's HaplotypeCaller

and GenotypeGVCFs v.4.1.3 from the recalibrated bam files. Genotype calls were filtered using

GATK and VCFtools (Danecek et al. 2011) if they presented: low individual quality per depth (QD

< 5), extreme coverage (600 > DP > 1000), mapping quality (MQ < 40 and MQ > 70), extreme

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153   hetero or homozygosity (ExcessHet > 20 and InbreedingCoeff > 0.9) and high read strand bias

154   (FS > 60 and SOR > 3). We filtered further at the level of individual genotype for low quality (GQ

155   < 20) and extreme coverage (GenDP < 10 and GenDP > 40). Lastly, we kept only bi-allelic sites

156   with less than 5% of missing data across individuals resulting in 7'283'516 SNP. For analyses of

157   neutral population structure and demography, an exact Hardy-Weinberg test was used to

158   remove sites that significantly departed (p<0.05) from the expected equilibrium using the R (R

159   Development Core Team 2016) package HardyWeinberg (Graffelman and Morales-Camarena

160   2008; Graffelman 2015) yielding 6'827'220 SNP with a mean coverage of 19.9X (4.6 SD).

161

162   **Population structure and genetic diversity**

163   To investigate population structure among our samples, sNMF v.1.2 (Frichot et al. 2014) was run

164   for K 2 to 5 in 25 replicates to infer individual clustering and admixture proportions. For this

165   analysis, singletons were excluded and the remaining SNPs were pruned for linkage

166   disequilibrium in PLINK v1.946 (Purcell et al., 2007; parameters -indep-pairwise 50 10 0.1) as

167   recommended by the authors, retaining 288'775 SNP. The same dataset was used to perform a

168   Principal Component Analysis (PCA) with the R package SNPRelate (Zheng et al. 2012). A

169   second PCA was performed by merging the data in this study with that of (Cumer et al. 2021)

170   that includes European populations (total of 2'036'320 SNP with no missing data) to assess

171   where the Eastern Canary population (unsampled in Cumer et al. 2021) falls among the larger

172   sampling.

173   Individual observed heterozygosity and population-specific private alleles were estimated using

174   custom R scripts for each population. Individual-based relatedness (β; (Weir and Goudet 2017;

175   Goudet et al. 2018), inbreeding coefficients for whole genome SNP data (F_{IS} and F_{IT}), overall,

176   population specific and pairwise F_{ST} (Weir and Goudet 2017) were calculated with hierfstat v.0.5-

177   9 (Goudet 2005).

178

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179   **Demographic history**

180   To investigate the demographic history of the insular populations and potential admixture

181   events we used Treemix (Pickrell and Pritchard 2012). Using the LD-pruned dataset filtered

182   further to include no missing data (228'980 SNP), Treemix was run for 10 replicates with 0 to 5

183   migration events, rooting the tree on the IS population, given its position on the PCA and what is

184   known of the region from previous work (Cumer et al. 2021). The function get_f was used to

185   estimate the variance explained by adding migration events.

186

187   **Detection of genomic regions under selection**

188   *Insular vs mainland barn owls*

189   In this study, we aimed to identify genomic regions potentially under selection at two different

190   levels. First, to detect signatures of selection specific to barn owls of the Canary Islands, we

191   grouped insular individuals (EC and WC) and compared them to the mainland ones (MA, PT and

192   IS). A script by Simon Martin

193   (https://github.com/simonhmartin/genomics_general/blob/master/popgenWindows.py) was

194   used to estimate genome wide patterns of relative (F_{ST}^{ILvsML}) and absolute (d_{xy}) divergence

195   between the insular and mainland groups, and to calculate nucleotide diversity (π) per group, in

196   windows of 100kbp with 20kbp steps.

197   SNPrelate was used to calculate a pairwise matrix of linkage disequilibrium (r) from SNPs with

198   over 5% minor allelic frequency (MAF) over all insular individuals (EC and WC) on one hand and

199   all mainland individuals (PT, MA and IS) in the other, which was then squared to obtain r^2. For

200   plotting, we estimated the mean of non-overlapping 100 SNP windows.

201   The topology weighting method implemented in Twisst (Martin and Van Belleghem 2017), was

202   used to quantify the relationships between the five populations in our dataset and visualize how

203   they change along the genome. Twisst estimated the topology based on trees produced using

204   Randomized Axelerated Maximum Likelihood (RAxML) v8.2.12 (Stamatakis 2014). RAxML

205   inferred trees in sliding windows (100kb of length, 20kb of slide) using a generalized time-

206   reversible (GTR) CAT model with Lewis ascertainment bias correction. Twisst then estimated the

207   weighting of each taxon topology (defined as the fraction of all unique population sub-trees) per

208   window.

209   Finally, we calculated population specific F_{ST} from allele sharing matrices (β; (Weir and Goudet

210   2017; Goudet et al. 2018) in sliding windows of 100kbp with 20kbp steps, using hierfstat. For

211   each matrix, we calculated i) the mean allele sharing for pairs of individuals from islands and ii)

212   the mean allele sharing for pairs of individuals, one from an island and the other from the

213   mainland, from which we obtain the islands specific F_{ST}. We shall refer to this estimate as F_{ST}

214   island-specific (F_{ST}^{Can}; see Sup. Fig. 1 for a schematic representation). This method allowed us to

215   identify genomic regions of high differentiation exclusively on the islands with no confounding

216   effect from the mainland (see also Weir et al. 2005).

217   From the genome wide scans, we identified peaks of differentiation with at least two

218   overlapping windows of F_{ST}^{Can} higher than 5 standard deviations (SD) from the mean (threshold:

219   0.377), and extracted the genes in these regions from the NCBI's annotation of the reference

220   genome (RefSeq accession: GCF_018691265.1). The gene list was then fed to ShinyGO v0.61

221   (Ge et al. 2020) to investigate potential enrichment of molecular pathways.

222

223   *Eastern vs Western Canary Islands*

224   On a second stage, to investigate potential genomic signals of differentiation, putatively linked

225   with ecological adaptation to their distinct niches, we contrasted the two insular lineages (EC

226   against WC). We estimated pairwise F_{ST}, d_{xy} and π as for the island-mainland comparison

227   described above.

228   Then, as for the island-mainland comparison above, we used hierfstat to calculate population

229   specific F_{ST} in sliding windows of 100kbp with 20kbp steps based on a dataset including only

230   the insular individuals. For each island, we consequently identified genomic regions with at least

231   two overlapping windows of pairwise F_{ST} higher than 5 SD from the mean (regions highly

232   differentiated between islands, threshold: 0.157) and above the 99th quantile of each

233   population's F (regions highly similar within each island, respective threshold for F_{ST}^{EC}= 0.404

234   and for F_{ST}^{WC} =0.393) and extracted the genes in these regions as described above. This yielded

235   two genes lists, one per island, which were input to ShinyGO as above.

236

237   **Climatic niche analysis**

238   To assess whether the barn owl populations of eastern and western Canaries occupy different

239   climatic niches, we used the Outlying Mean Index (OMI) approach (Dolédec et al. 2000) as

240   implemented in the R package ade4 v.1.7-16. Observation points for barn owls were compiled

241   from three different sources: Global Biodiversity Information Facility (GBIF), samples sequenced

242   in this study and in Burri et al. (2016). We kept records only from the islands sampled in this

243   study, namely Tenerife (*T. alba*; N=79) and Lanzarote and Fuerteventura (*T. a. gracilirostris;*

244   N=34 and N=39, respectively).

245   Climatic variables for the Canary Islands were extracted from the WorldClim database (Hijmans

246   et al. 2005) at 30 sec resolution (approximately 1 km^2) using the R package rbioclim (Exposito-

247   Alonso 2017). Redundant variables (correlation of 1) were trimmed and the final model was run

248   with the following 13 variables: Mean Diurnal Range (BIO2), Isothermality (BIO3), Temperature

249   Seasonality (BIO4), Max Temperature of Warmest Month (BIO5), Min Temperature of Coldest

250   Month (BIO6), Temperature Annual Range (BIO7), Mean Temperature of Driest Quarter (BIO9),

251   Annual Precipitation (BIO12), Precipitation of Driest Month (BIO14), Precipitation Seasonality

252   (BIO15), Precipitation of Warmest Quarter (BIO18), Precipitation of Coldest Quarter (BIO19).

253

254 # Results

255 **Population structure and genetic diversity**

256 The overall F_{ST} in our dataset was 0.0698. Individual ancestry analyses with sNMF distinguished

257 four genetic clusters, separating each population into its own cluster, except Morocco (MA) and

258 Portugal (PT) that clustered together (Fig. 1a). Similarly, PCA clustering clearly grouped

259 individuals according to their population, except PT and MA (Fig. 1c). The first axis opposed the

260 insular populations to the mainland, as did sNMF K=2 (Sup. Fig. 2), with Eastern Canary (EC) and

261 Israel (IS) at each extreme. The second axis contrasted the two insular populations EC and

262 Western Canary (WC), as in K=3 (Sup. Fig. 2), and finally the third axis segregated the mainland

263 groups with PT and MA opposed to IS, as in K=4 (Fig. 1a, 1c). Three individuals from EC (one

264 from Fuerteventura and two from Lanzarote) showed small ancestry levels from both WC and PT

265 in sNMF and were placed intermediately on axes 1 and 2 of the PCA. In the PCA including the

266 European individuals, the first axis remained qualitatively the same with EC and WC together in

267 opposition to IS (Sup. Fig. 3). Axes 2 and 3 switched positions, with MA, PT and the rest of

268 Europe being first isolated from the rest and only then the two Canary split from each other

269 (Sup. Fig. 3). In terms of differentiation, pairwise F_{ST} were highest between both islands and IS

270 (EC-IS 0.092; WC-IS 0.088) as well as between islands (WC-EC 0.084). The mainland

271 populations were overall less differentiated (all below 0.04), with PT and MA having the lowest

272 F_{ST} with all other populations in accordance with their central position on the PCA (all below

273 0.06 for PT and 0.061 for MA), and the lowest between themselves (0.007) (Table 1).

274 Treemix yielded a population tree highly resembling the first PCA axis, with two main branches

275 splitting from the IS root, one towards PT and MA and the second to WC and EC (Sup. Fig. 4).

276 Most of the variance was explained by the tree with no migration (0.993). Nonetheless, the tree

277 with two migration events displayed the highest likelihood (162.284), with one migration edge

278 from the base of WC towards the tip of PT (edge weight 0.33) and the other from the base of PT

279   towards the tip of EC (edge weight 0.13). Adding more than two migration events to the tree did

280   not improve its fit to the data.

281   Overall, mainland populations presented higher genetic diversity than the insular ones (Table 1).

282   Nonetheless, both insular populations showed over 280'000 private polymorphic sites (Table 1).

283   Accordingly, individual relatedness was higher within and between insular populations (Sup. Fig.

284   5), and PT had the lowest within population relatedness. All populations showed signs of

285   random mating with F_{IS} close to zero but slightly negative as expected of dioecious species

286   (Balloux 2004), while the inbreeding levels of insular barn owls relative to the whole set of

287   populations (F_{IT}) were higher than those on the mainland (Table 1), a reflection of their isolation

288   from the continent.

289

290   **Island vs mainland genomic comparisons**

291   In order to measure the differentiation between islands and mainland individuals, we computed

292   two distinct F_{ST} along the genome (see methods for details). F_{ST}^{Can} allowed the detection of

293   regions of high similarity in the islands as a whole, whereas F_{ST}^{ILvsML} produced less clear results

294   with population-specific allelic frequencies driving the overall signal instead of the defined

295   groups. For example, F_{ST}^{ILvsML} yielded a peak of differentiation between the islands and the

296   mainland which, upon closer inspection of pairwise comparisons of the populations, turned out

297   to be due to differences between EC and the mainland only, whereas WC did not produce the

298   same signal (Sup. Fig. 6). The genomic comparisons of diversity and divergence between insular

299   and mainland barn owls based on the F_{ST}^{Can} yielded 48 regions (478 100kb overlapping

300   windows) of high differentiation including 100 genes (Fig. 2a). ShinyGO analyses identified an

301   enrichment of five functional categories related to morphogenesis in humans (Sup. Table 2). The

302   largest enriched pathway – anatomical structure morphogenesis – included 25 of the genes in

303   regions of high genomic differentiation. The remaining three categories – anatomical structure

304   formation involved in morphogenesis, tube morphogenesis and blood vessel morphogenesis –

305   were subsets of the largest pathway, including 15, 14, 12 and 10 of the 25 genes, respectively.

13

306   The largest of the peaks encompassed 15Mb of Super-Scaffold_1000006. Of all the genes

307   found in peaks of differentiation, 87 out of 100 were within this region. Here, insular owls

308   showed a strong decrease in relative diversity compared to the mainland (F_{ST}^{Can}), as well as a

309   drop of absolute divergence (d_{xy}) between each other and nucleotide diversity (π). The region

310   showed strong LD (r^2) in all insular owls between neighbouring variants compared to the rest of

311   the scaffold (Fig. 2b), which was not the case among continental ones (Sup. Fig. 7). In addition,

312   F_{ST} was higher between island and mainland owls (Sup Fig. 6). Twisst showed roughly similar

313   proportions of each tree along the genome, except for this region where there was a higher than

314   average proportion of trees that joined EC and WC (Sup. Fig. 8). Of the 25 genes of the

315   morphogenesis pathway, 18 were found in this closely-linked region of

316   Super_Scaffold_1000006 (21% of the total 87 genes of the region).

317

318   **Eastern vs Western Canary Islands**

319   *Climatic niche analysis*

320   To investigate the genomic and ecological differentiation between island populations (EC and

321   WC), we first depict different climate in the two set of islands based on barn owl observations in

322   the Canary Islands. The climatic niche analyses (OMI) yielded two axes that explained the

323   climatic variability in our study area (Fig. 3b), with the first axis (OMI1) explaining nearly all of it

324   (99.3%). OMI1 was positively correlated with temperature and negatively correlated with

325   precipitation (Sup. Fig. 10). The eastern population *T. a. gracilirostris* occupied a narrow niche of

326   high temperature, low precipitation and low seasonal and daily variability. *Tyto alba* in Tenerife

327   occupied a broader niche that covered most of OMI1, including some of the niche of *T. a.*

328   *gracilirostris*. OMI2 explained little of the variability (0.7%), spreading slightly each population's

329   niche without segregating them.

330

331   *Detection of differentially selected genomic regions*

332   We then searched for regions under selection in each island, yielding to a total of 33 putatively

333   adaptive regions (14 in EC and 19 in WC), with high differentiation (F_{ST}) between island and

334   increased relatedness within each island (F_{ST}^{EC} and F_{ST}^{WC}), from which we obtained two lists of

335   genes (Fig. 3c, 3d). For EC, there were 30 such genes (Sup. Table 3) while for WC there were 25

336   genes (Sup. Table 4). Enrichment analyses found no link to a specific GO pathway for either

337   island population. Nonetheless, in each island there were clusters of genes with similar

338   identified functions, namely body proportions and blood pressure in EC, and cellular response to

339   hypoxia in WC.

340   # Discussion

341   Islands offer unique conditions for organisms to adapt and expand their niches. In the Canaries,

342   an archipelago rich in endemics, the barn owl is one of the few raptors present and is thought to

343   have diverged into a subspecies on the easternmost islands. Taking advantage of whole-

344   genome sequences, we first investigate the origin of the population of barn owls in the Canary

345   Islands, revealing that the latter are long-standing populations and allowing us to address their

346   taxonomic classification. Using a new, more sensitive method based on excess of allele sharing

347   within the islands, we detect 58 putatively locally adapted genomic segments, many of them

348   grouped in a haplotype-like region seemingly under positive selection in the Canary Islands. A

349   quarter of the tightly linked genes in this genomic region are enriched for genes contributing to

350   a pathway of anatomical morphogenesis suggesting morphological adaptations to insularity. We

351   also identify scattered genomic regions putatively locally adapted to either the eastern and

352   western islands. For eastern Canaries, the identified genes in regions under positive selection

353   belong to pathways linked to body proportions and blood pressure, consistent with the smaller

354   owl size of this population living in a hot arid climate. In the western Canaries, barn owls from

355   Tenerife display a potential signal of selection of genes related to hypoxia, a potential response

356   to inhabiting an island with a steep elevation gradient.

357

358   **Barn owls from the Canary Islands and Mediterranean Basin**

359   Our work shows that, while each population in the study area has its own unique genetic

360   composition (Fig. 1), barn owls from the Canary Islands are distinct from those on the mainland

361   surrounding the Mediterranean Basin. Indeed, clustering methods constantly opposed insular

362   individuals to mainland ones (Fig. 1c; Sup. Fig. 2) and were supported by the drift-based trees of

363   Treemix. Thus, overall, our current results indicate that the two insular lineages – Eastern and

364   Western Canaries – have a common origin.

16

365   In terms of genetic diversity, the islands were less diverse than the mainland as expected and

366   showed slightly higher levels of inbreeding relative to the whole set (Frankham 1997). However,

367   they presented nearly 10-fold higher levels of private alleles than those reported for other

368   islands in the Atlantic (British Isles; Machado et al. 2021) and in the Mediterranean Sea (Cyprus

369   and Greek islands; Machado et al. 2021). Notably, the two Canaries insular populations, about

370   165 km apart, were more distant genetically from each other than either was from Portugal,

371   over 1000 km away. Furthermore, they were more distant from each other even than WC was

372   from any population in continental Europe in a recent genomic study (Cumer et al. 2021), as

373   well as in an earlier one with microsatellites (Burri et al. 2016). The high private diversity could

374   be partially explained by the small number of samples in north-western Africa, which may be

375   masking any shared polymorphisms between the islands and the nearest mainland as private to

376   the former. However, as we did sample PT and IS, the most diverse populations in the Western

377   Palearctic assumed to meet in northern Africa (Cumer et al. 2021), much of this insular diversity

378   is likely indeed private. Therefore, the Canaries appear to have been colonized much earlier than

379   the other studied insular populations and have thus had the time for *in situ* mutations to

380   accumulate in spite of genetic drift, which is supported by their higher divergence as well. These

381   populations may also reflect a more ancient lineage from northern Africa that would have been

382   replaced or simply evolved in a different direction and only the addition of samples from African

383   mainland (on top of the three MA samples) would allow to fully depict the neutral history of

384   these populations.

385

386   **Insularity**

387   We found multiple evidence of adaptation common to both barn owl lineages of the Canary

388   Islands. To do so, we used an estimator of population specific F_{ST} (Weir and Goudet 2017;

389   Goudet et al. 2018) to identify genomic regions with an excess of shared ancestry in all insular

390   individuals relatively to the mean shared ancestry between islands and mainland individuals.

391   Being a moment estimator, it can process efficiently a large amount of genomic loci, compared

392　　to maximum likelihood or Bayesian estimators (e.g. Foll and Gaggiotti 2008). More importantly,

393　　it does not rely on the F-model, which assumes independent populations. This island specific F_{ST}

394　　(F_{ST}^{Can}) identified regions of increased relatedness between insular individuals compared to the

395　　averaged relatedness along the genome (i.e. regions in which all insular individuals resemble

396　　each other more than expected). This population specific, moment based and model-free

397　　estimator of F_{ST} provides a clearer result than classical pairwise F_{ST} scan, as it focuses on the

398　　diversity in the target population rather than taking an average over the set of populations, and

399　　should be a useful addition to the population genomic toolbox to detect nested signals of local

400　　adaptation, especially when there is substructure in the groups one wishes to compare. We thus

401　　considered regions highly similar in insular individuals as putatively under selection on the

402　　islands. The genomic landscape of F_{ST}^{Can} differentiation between insular and mainland owls

403　　yielded 58 windows putatively under selection (Fig. 2a). Among these, a particularly large and

404　　clear peak of differentiation stood out. This region approximately 15 Mb in length was highly

405　　similar among insular individuals (Sup. Fig. 9) as shown by the accompanying drop in d_{XY} and π

406　　(Fig. 2b). Furthermore, the increased linkage between alleles in this region suggests that it is

407　　transmitted in a haplotype-fashion. Crucially, the fact that we do not see the slightest surge of

408　　LD in mainland individuals confirms that it is not a by-product of a region of low-recombination

409　　in this species (Sup. Fig. 7). Overall, we provide strong evidence of positive selection in this

410　　genomic region in Canary Islands owls, suggesting an adaptation to insularity (Fig. 2).

411　　A fifth of the genes in this haplotype (18 out of 87), in conjunction with 7 other genes in

412　　potentially adaptative regions, significantly enriched the anatomical structure morphogenesis

413　　pathway (Sup. Table 2), a biological process related to the organisation and generation of

414　　anatomical structure during development. This suggests positive selection on some

415　　morphological trait on insular individuals. Given that there is evidence of gene flow from the

416　　mainland into both islands (see admixed individuals in Fig. 1, Sup Fig, S2), we propose two

417　　hypotheses to explain how selection might act on this haplotype. First, it could confer a

418　　significant advantage to individuals carrying it on the island and prevent those that do not carry

419　　it from reproducing or surviving. In this scenario, immigrants from the mainland not carrying this

420   haplotype would reproduce less in both islands. In the second scenario, selection would happen

421   on the migrants themselves before reaching the island if, for example, the haplotype facilitates

422   long flight over large spans of water. It is widely accepted that, given how dispersal capacity is

423   highly variable across species, even among birds, some are more prone to colonizing islands

424   than others. Therefore, it is also conceivable that, within a species or population, some

425   individuals are morphologically more predisposed or have better dispersal abilities than others.

426   Since the barn owl generally avoids flying over open water, as demonstrated by its consistently

427   higher differentiation on islands (Cumer et al. 2021; Machado et al. 2021, n.d.), this seems

428   plausible. The absence of phenotypic measurements from the sequenced birds prevents us from

429   establishing a link between phenotypes and genotypes on this data set, and we hence remain

430   cautious on the speculation regarding the functional implications of this haplotype. Future work

431   should verify the frequencies of this haplotype in a larger cohort as we only had 19 insular

432   individuals in this study and, if possible, include detailed morphometric measurements to allow

433   a GWAS-like approach.

434

435   **Ecological divergence**

436   In the Canary archipelago, both the eastern islands and Tenerife have many specific endemic

437   species across multiple taxa. This is generally attributed to their intrinsic characteristics driving

438   ecological speciation, namely the arid and windy conditions of Lanzarote and Fuerteventura, and

439   the elevation gradient of the Teide volcano (up to 3'718m a.s.l.) in Tenerife. We quantified the

440   climatic differences between the two environments with a niche analysis based on reported

441   barn owl observations, and show that indeed barn owls occupy significantly different niches on

442   each group of islands (Fig. 3b). In the east, they are found on unvaryingly hot and dry locations,

443   whereas Tenerife covers a wide range of temperature and precipitation (Fig. 3b).

444   From the genomic data, we found evidence of local adaptation on both insular populations (Fig.

445   3c, 3d). The eastern population had more genomic regions, and more genes, potentially under

446   selection compared to the west (30 and 25 genes, respectively). Although no significant

19

447   pathway enrichment was detected in either population, there were clear groups of genes with

448   similar known functions in the putatively adapted regions. In the eastern population there were

449   two such groups. The first, composed of 7 genes, has significant links to body size and

450   proportions in humans (see Sup. Table 3 and references therein). Among these, a specific set of

451   4 genes – *HIP1R*, *CCDC62*, *VPS37B* and *ABCB9* – is tightly clustered in the barn owl genome

452   (Fig. 3c). These four genes have been linked to body height, body-mass-index and other body

453   measurement ratios (Turcot et al. 2018; Kichaev et al. 2019; Vuckovic et al. 2020; Zhu et al.

454   2020), and may thus play a role in the smaller size of barn owls in the eastern population, which

455   would then be adaptive. The second group of genes in regions potentially under selection,

456   includes 11 genes related to numerous blood parameters (Sup. Table 3), a similar signal to that

457   seen in chickens adapted to hot arid environments (Gu et al. 2020). In particular, the gene

458   *MTHFR* has extensive connections to blood pressure (Newton-Cheh et al. 2009; Ehret et al.

459   2016; Liu et al. 2016; Surendran et al. 2016; Hoffmann et al. 2017; Wain et al. 2017; Kulminski

460   et al. 2018; German et al. 2020), a trait known to vary with environmental temperature in

461   mammals (Halonen et al. 2011) and birds (Darre and Harrison 1987), potentially suggesting

462   barn owls have circulatory systems adapted to the hot and dry conditions of the eastern

463   Canaries.

464   In the western island population, regions putatively under selection contained an interesting

465   group of 4 genes - *EPAS1*, *PRKCE*, *MCFD2* and *FZD8* - with links to red blood cells, haemoglobin

466   density and cellular response to hypoxia (i.e. low levels of oxygen; Sup. Table 4; Astle et al.

467   2016; Kichaev et al. 2019; Chen et al. 2020; Oskarsson et al. 2020; Vuckovic et al. 2020). Red

468   blood cells, and the haemoglobin within, are responsible for transporting oxygen in the body and

469   are direct targets of selection at high elevation (O'Brien et al. 2020). The gene *EPAS1* in

470   particular, is well known for being involved in adaptation to high altitude environments across

471   vertebrates (Witt and Huerta-Sánchez 2019). These genes hints at a possible adaptation of barn

472   owls to higher altitude in Tenerife. On this small island, barn owls are mostly concentrated at

473   lower altitude (i.e. along the coast – 0 to 300m a.s.l.) and their repartition is limited in the

474   central part of the island due to the presence of the high mountains at about 2000m a.s.l., that

475   culminates with the colossal peak of Teide at 3715m a.s.l. (Siverio 1998). This is consistent with

476   the known limited ability of this bird to live at high altitudes (Machado et al. 2018; Cumer et al.

477   2021). However, the observation of individuals up to 1200m a.s.l. and the presence of breeding

478   couples at moderate altitudes (600 to 1200m a.s.l., Siverio 1998), support the hypothesis of an

479   ongoing adaptation to higher altitude in this insular population. This hypothesis, which deserves

480   further investigations, is also consistent with observations made in other populations in warm

481   climates; where local barn owl populations expand their range by adapting to slightly higher

482   altitudes (Romano et al. 2020).

483   Considering its wide distribution, even accounting for phenotypic plasticity, barn owls' capacity

484   to adapt to a variety of prey and environments is unquestionable. As such, detecting signals of

485   local adaption in the Canary Islands is not surprising. Indeed, with islands generally being

486   species-poor, the species that do inhabit them have to adapt to different or broader niches via

487   ecological divergence (Losos and Ricklefs 2009). This is especially true of volcanic islands that

488   arise isolated and uninhabited, in contrast to those intermittently connected to the mainland

489   and more easily colonized. Moreover, the community of birds of prey in the Canary archipelago

490   includes less than half the species found in the nearby mainland (8 diurnal and 2 nocturnal

491   species; Martín and Lorenzo, 2001; Rodríguez et al. 2018), likely due to the lack of suitable

492   habitat, preys and/or the limited surface. A by-product of this is the reduction of inter-specific

493   competition, which could have allowed the barn owl to maintain population sizes just large

494   enough on the islands through time for selection to act and potentially expand its niche to better

495   exploit the insular environment. Our results suggest this is happening in parallel on each island

496   (Fig. 3c, 3d), consistent with their different niches (Fig. 3b) and relative genetic isolation,

497   producing two distinct ecomorphs, adapted to distinct ecosystems.

498

499   **Insular subspecies**

500   The eastern islands of Lanzarote and Fuerteventura, and adjacent islets (Fig. 3a) are home to

501   the barn owl subspecies *T. a. gracilirostris*. This classification is based on its smaller size and

21

502   even on colouration pattern, although the latter is contested by ornithologists and inconsistent

503   with reported phenotypical measurements (Burri et al. 2016). The reduction in size is actually a

504   common pattern in insular barn owls (Romano et al. 2021), and could be an adaptation to

505   nesting in very small cavities (i.e. cracks in lava walls) and/or to better navigate the strong

506   winds in the eastern islands (Siverio 2007). The genomic data presented here is consistent with

507   this population forming an endemic subspecies. It has diverged considerably from the mainland,

508   with higher differentiation levels than barn owls from any other studied island in the Western

509   Palearctic (Machado et al. 2021, n.d.). Moreover, we show it carries high levels of private genetic

510   diversity and multiple genomic regions showing signs of local adaptation (Fig. 3c).

511   In contrast, barn owls from Tenerife and the remaining islands are considered to belong to the

512   nominal *T. alba* found also on the mainland surrounding the Mediterranean Basin (Fig. 3a).

513   However, it too has considerably diverged from the mainland and shows signs of potential

514   ongoing adaptation in Tenerife and its elevation gradient (see previous section). Furthermore, it

515   clusters with the other insular Canary population rather than the mainland (Fig. 1). While it is

516   not the aim of this study to evaluate what constitutes a subspecies, we provide evidence that

517   the Tenerife population is diverging significantly from its founding population, both neutrally and

518   adaptively, albeit at a slower pace than the eastern population.

519   The reasons why the eastern population is more divergent than the western, a puzzling fact

520   considering it is closer to the mainland, are not yet fully resolved. Neutral divergence in F_{ST}

521   between these two insular populations suggest they are the result of two independent

522   colonisation events rather than a strict east-to-west progression as described for other taxa

523   (Juan et al. 2000). Although the islands themselves emerged from east to west, Tenerife is at

524   least 11 million years old, twice the inferred time of formation of the *T. alba* species (Uva et al.

525   2018) and thus available for colonisation at the time. Nonetheless, an earlier settlement of the

526   eastern islands would have given more time for both genetic drift and selection to promote

527   divergence. Alternatively, a very small population size in the east, consistent with current census

528   data (Palacios 2004; Siverio 2007), could account for the stronger drift in a scenario of

22

529   simultaneous colonization. However, it would strongly hinder local adaptation, making it a less

530   likely hypothesis since we identified more regions putatively under selection in this population.

531   Further work, including an extensive sampling of all island populations, as well as demographic

532   modelling, would be needed to resolve this intriguing pattern and refine the history of the barn

533   owl in the Canary archipelago.

534

535   **Conclusion**

536   Due to their intrinsic characteristics, islands house numerous endemics making them ideal

537   systems to study the bases of ecological divergence. We provide empirical evidence that both

538   neutral and adaptive evolutionary mechanisms shaped divergence from the mainland in barn

539   owls from the Canary archipelago. Our results show clear signs of genome-wide differentiation

540   (i.e. neutral), a combination of mutations (high private diversity; Table 1) and drift (high F_{ST} and

541   F_{IT}), consistent with theoretical expectations for populations established and isolated long ago

542   despite some admixture. We also identify signals of local adaptation to common insular

543   conditions (Fig. 2), as well as to each island's niche, creating ecomorphs (Fig. 3). While the

544   history and functional effect of the putatively adapted genomic regions identified here deserve

545   further investigation, these observations highlight how selection can still act on small isolated

546   populations. This study illustrates the capacity of a widespread bird to adapt to the local

547   ecological conditions of small islands, an adaptative capacity which may prove essential in

548   facing a changing global climate.

549

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Data Accessibility

The raw Illumina reads for the whole-genome sequenced individuals are available in BioProjects PRJNA700797, PRJNA727977 and PRJNA774943. Sampling locations used for niche modelling are given in appendix 1.

Author Contributions

APM, TC, AR, JG designed this study; FS, MC, IR, RL provided samples; APM produced whole-genome resequencing libraries; TC and APM conducted the analyses; APM and TC led the writing of the manuscript with input from all authors.

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Tables & Figures

Table 1 – Genetic diversity and population differentiation of barn owls from the Mediterranean Basin and the Canary Islands. Right-hand-side of the table shows the matrix of population pairwise F_{ST}.

Population	Abbrev.	N	#PA	#rPA	H_O	F_{IS}	F_{IT}	F_{ST}	EC	WC	MA	PT	IS
Eastern Canary	EC	10	324458	265175 (3829)	0.161 (0.013)	-0.015 (0.08)	0.10 (0.07)	EC	0.112	0.081	0.061	0.060	0.088
Western Canary	WC	9	288313	288313	0.167 (0.006)	-0.030 (0.04)	0.07 (0.03)	WC	0.081	0.105	0.055	0.054	0.083
Morocco	MA	3	234524	692508 (13287)	0.190 (0.001)	-0.04 (0.01)	-0.06 (0.01)	MA	0.061	0.055	-0.013	0.007	0.034
Portugal	PT	9	669889		0.182 (0.008)	-0.013 (0.04)	-0.01 (0.04)	PT	0.060	0.054	0.007	0.014	0.039
Israel	IS	9	703392	703392	0.180 (0.002)	-0.036 (0.04)	-0.004 (0.01)	IS	0.088	0.083	0.034	0.039	0.050

N – number of sampled individuals; #PA – private alleles in each population; #rPA – private alleles (SD) rarefied to 9 individuals per population (note that PT and MA were merged); H_O – mean observed heterozygosity (SD); F_{IS} - population level inbreeding coefficient (SD); F_{IT}: mean individual inbreeding coefficient relative to the meta-population (SD). F_{ST}: pairwise and population specific FST.
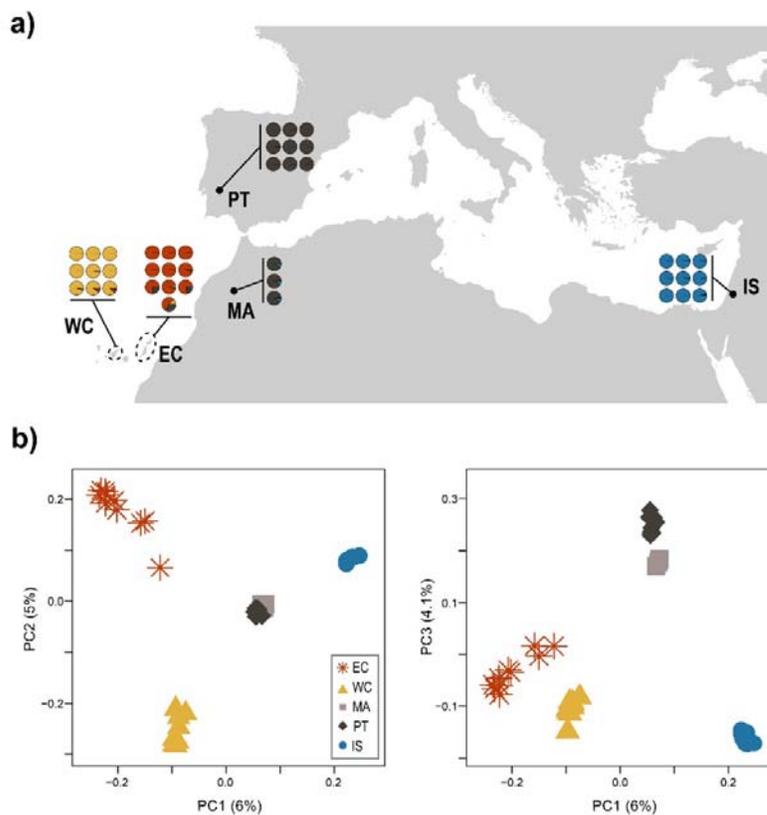
Figure 1 – Population structure of barn owls from the Mediterranean Basin and the Canary Islands. **a)** Individual admixture proportion of each of K=4 lineages as determined by sNMF. Black dots are located at the approximate centroid of each sampled population. Dashed lines encircle the island(s) sampled for each Canary population. **b)** PCA of the 40 individuals. Point shape and colour denote populations according to the legend. Axes one to three are shown and values in parenthesis indicate the percentage of variance explained by each axis.

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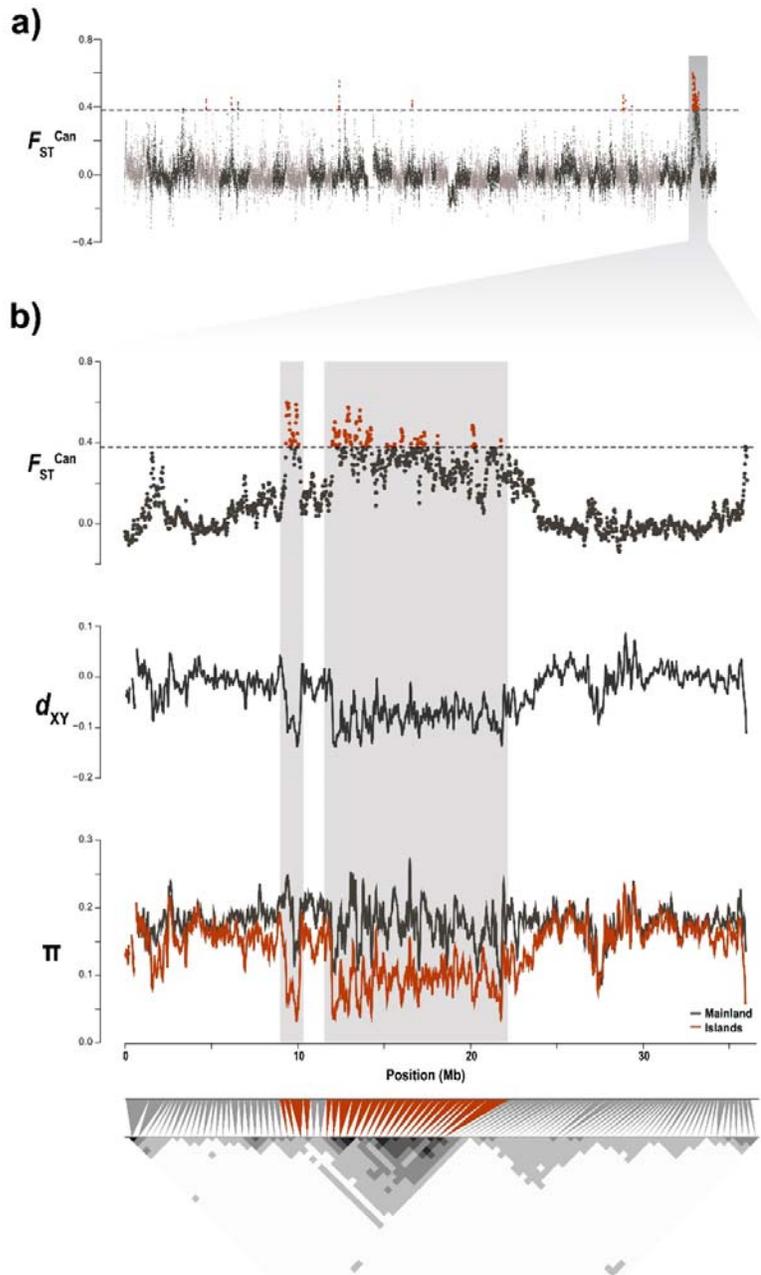
Figure 2 – Genomic landscape of differentiation between insular and mainland barn owls. **a)** Genome-wide beta comparison between individuals from the Canary Islands (EC & WC) and from the mainland (PT & IS). Each dot represents a 100kb window. Dashed line indicates the 5 SD threshold used to identify genomic regions of high differentiation, emphasised in red. Alternating grey colours denote different scaffolds. Shaded vertical bar highlights Scaffold 100006. **b)** Zoom on Scaffold 100006 and, in particular, the ~15 Mb long highly differentiated genomic region (background shading) over windows of 100 kb. From top to bottom, we see in this region a high F_{ST}^{Can} between insular and mainland barn owls, low absolute distance (d_{XY}) between both islands (scaled with mean=0) and reduction of nucleotide diversity (π) among insular individuals (red line) compared to the mainland (black line). The bottom triangular matrix shows pairwise LD (r^2) between groups of 100 SNP along the chromosome in insular owls. Darker pixels show higher LD. Grey triangles match each
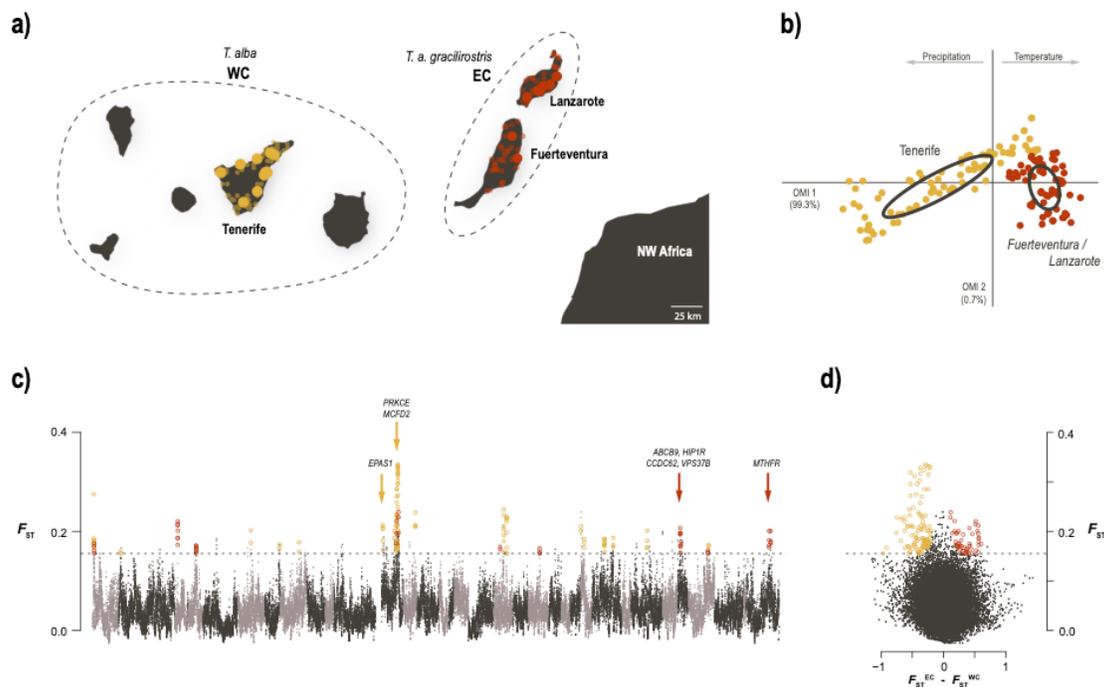
1147   pixel in the matrix diagonal to the region it spans on the chromosome above. Red triangles indicate
1148   pixels that overlap the region of high differentiation.

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1154   **Figure 3 –** Ecological divergence in barn owls from the Canary Islands. **a)** Sampling location of
1155   Western (WC; yellow) and Eastern (EC; red) Canary individuals, off the coast of north-western Africa.
1156   Sampled islands are named. Large dots indicate individuals sampled for WGS and population
1157   genomics analyses; small transparent dots are barn owl observations used in niche analysis. Dashed
1158   lines group islands according to barn owl taxonomy. **b)** Climatic niche occupied by the two Canary
1159   populations. The first axis varies from cold and wet to hot arid environments. **c)** Genome-wide F_{ST}
1160   comparison between individuals from each Canary population. Each dot represents a 100kb window.
1161   Alternating grey colours denote different chromosomes. Dashed line indicates the 5 SD F_{ST} threshold
1162   used to identify genomic regions of high differentiation overlaid with F_{ST}^{WC}, highlighted in yellow and
1163 F_{ST}^{EC} in red. Arrows denote the location of genes linked with response to hypoxia in WC; and the
1164   cluster of 4 genes linked to morphological ratios and the main gene related to blood pressure in EC.
1165   **d)** Same F_{ST} windows and threshold as in **c** plotted against the difference between F_{ST}^{WC} and F_{ST}^{EC},
1166   clearly highlight the two sets of windows putatively under local adaptation.

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