

Ancient genomics reveals lost giant chaffinch ecomorphs in the Azores

Juan Carlos Illera

`jcillera@csic.es`

Instituto Mixto de Investigación en Biodiversidad

B. Karina Montero

Instituto Mixto de Investigación en Biodiversidad

Juan Carlos Rando

Universidad de La Laguna

Josep Antoni Alcover

Mediterranean Institute for Advanced Studies

Carles Lalueza-Fox

Museu de Ciències Naturals de Barcelona

Martin Irestedt

Swedish Museum of Natural History

Carmen N Hernández-Flores

Universidad de Las Palmas de Gran Canaria

Erik Sandertun

University of Oslo

Bezawit Tesfa

University of Oslo

Jens Hering

German Ornithological Society

Mark Ravinet

University of Oslo

Pere Bover

Universidad de Zaragoza

Research Article

Keywords: Anthropogenic impacts, directional selection, ecological plasticity, island biogeography, island finches, island rule, Macaronesia

Posted Date: August 18th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-10624936/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.
[Read Full License](#)

Additional Declarations: No competing interests reported.

Abstract

Background Islands harbour exceptional concentrations of endemic biodiversity, yet their biotas have been profoundly reshaped by human colonisation. In the Azores, deforestation and the introduction of invasive mammals drove major ecological transformations, and the fossil record reveals that the archipelago once supported avian communities far more diverse than those of today. During palaeontological expeditions conducted between 2011 and 2018, we recovered cranial and postcranial remains from several islands that were unambiguously assigned to the genus *Fringilla*, but exhibited substantially enlarged cranial morphology relative to the extant Azorean common chaffinch (*F. moreletti*). Remarkably, skull and beak proportions closely resembled those of the Canary Islands blue chaffinches (*F. teydea* and *F. polatzeki*), raising the possibility of a shared evolutionary origin.

Results Using endogenous DNA extracted from fossil remains, we reconstructed complete or near-complete mitochondrial genomes from seven individuals. Combined with dense taxonomic sampling and whole-genome resequencing across *Fringilla*, these data enabled reconstruction of the evolutionary history of the Azorean forms. Contrary to expectations based on morphology, phylogenetic analyses unequivocally placed the extinct giant morphotypes within the clade of extant Azorean common chaffinches.

Conclusions These findings reveal an extraordinary degree of ecological plasticity in passerines and demonstrate that pronounced morphological divergence can evolve without substantial genome-wide divergence. More broadly, our results highlight the importance of integrating genomic and morphological evidence when reconstructing the evolutionary history of extinct island taxa.

Background

Approximately 99.9% of all known species and evolutionary lineages are now extinct (Raup 1991). Although extinction is a natural process, the majority of extinction events since the onset of the Holocene can be attributed to direct and indirect human activities (Ceballos and Ehrlich 2023), with island ecosystems being disproportionately affected (Fernández-Palacios et al. 2021; Wiens and Saban 2025). Paleontological, archaeological, and historical records provide compelling evidence of substantial impacts on island biotas and community composition following human colonization (Steadman 2006; Crowley 2010; Szabo et al. 2012; Nogué et al. 2021; Cook et al. 2023; Illera et al. 2024). The extinction of species has not only resulted in the loss of unique taxa but has also led to significant reductions in both functional and phylogenetic diversity (Matthews et al. 2024; Llorente-Culebras et al. 2025). Importantly, the loss of ecological and evolutionary functions has not been mitigated or compensated by the introduction of non-native species (Baiser et al. 2018; Sayol et al. 2021). Consequently, species disappearance disrupts ecological interactions, undermining species functionality and jeopardizing the long-term maintenance of ecosystem services (Mortensen et al. 2008; Rogers et al. 2017; Piquet and Darias 2021). Moreover, extinction patterns observed on oceanic islands do not appear to be stochastic. For instance, among birds, taxa characterized by larger body size, ground-nesting behaviour, and

flightlessness are particularly vulnerable to extinction (Boyer 2008; Illera et al. 2016; Sayol et al. 2020, 2024). The resulting ecological consequences include the establishment of novel ecological equilibria, typically characterised by communities impoverished in both species richness and functional diversity (Baiser et al. 2018; Triantis et al. 2022; Ali et al. 2023).

The pace of extinction in island ecosystems depends on the magnitude and persistence of environmental perturbations, as well as the resilience and resistance of the affected species. Additionally, the island size and the capacity to receive immigrants are also key factors determining the rate and pace of extinction processes (MacArthur and Wilson 1969; Valente et al. 2020). It is widely acknowledged that many extinct species remain undiscovered due to the idiosyncrasies and biases of fossil preservation (Cooke et al. 2023). For example, smaller bird species tend to be underrepresented in the fossil record compared to larger ones, and warmer climates generally favour fossil preservation over colder or drier environments (Gardner et al. 2016). Nonetheless, oceanic archipelagos composed of relatively small islands may offer especially favourable conditions for identifying previously undocumented extinctions, as these settings eventually promote the rapid accumulation and preservation of fossil remains at rich paleontological sites.

The Azores islands exemplify the profound transformations that island landscapes can undergo after human arrival. This volcanic archipelago, located in northern Macaronesia, lies approximately 1,400 km from mainland Europe, 1,500 km from mainland Africa, and 1,900 km from North America (Fig. 1). It comprises nine main islands, with São Miguel being the largest, covering an area of approximately 750 km² (Florencio et al. 2021). Although the Azores were officially colonized by the Portuguese crown in the 15th century (Bach, 2025), there is growing evidence suggesting the possible presence of Viking visitors predating Portuguese settlement (Rull et al. 2017; Raposeiro et al. 2021, 2022; Elias et al. 2022). However, the extent of their impact on the Azorean landscape and its biota remains contentious. Palaeoecological records indicate that prior to Portuguese colonization, the Azorean plant communities were dominated by dense, evergreen laurel forests. These forests primarily consisted of *Laurus azorica*, *Juniperus brevifolia*, *Prunus azorica* and *Morella faya* with additional species such as *Frangulla azorica*, *Picconia azorica* and *Erica azorica* also present (Rull 2023). Following colonisation, the islands experienced a progressive land clearing and impoverishment of native forests, culminating in extensive deforestation by the 18th century (Rull 2023; Rull et al. 2017).

Habitat deforestation and the introduction of invasive mammal species (e.g., rats, mice, and cats), have had severe consequences for native animal communities in the Azores (Illera et al. 2012; Fernández-Palacios et al. 2025). Over the past decade, these islands have emerged as a dramatic example of vertebrate biodiversity loss, as revealed by fossil material recovered from volcanic caves. Several newly recognized extinct endemic bird species have been identified, including quails (*Coturnix* sp.), owls (*Otus frutuoso*), rails (*Rallus montivagorum* and *R. carvaoensis*), petrels (*Pterodroma zinorum*), and passerines (*Pyrrhula crassa*) (Alcover et al. 2015, 2016; Rando et al. 2013, 2017, 2020, 2024). There is no evidence of major climate changes occurring during the early and mid-Holocene in the Azores that could account for these extinctions, nor of widespread volcanic activity affecting most of the archipelago during the same

period. Instead, radiocarbon dating of selected fossil remains suggests that the extinction of these bird species occurred at a similar time period as Portuguese settlement (Alcover et al. 2015; Rando et al. 2013, 2017, 2024). Collectively, these findings suggest that, prior to European colonization, the Azores hosted more diverse avian communities than present today. Furthermore, this supports the hypothesis that the disruption of multiple ecological processes likely led to both primary and secondary extinctions, resulting in severe ecological consequences for Azorean ecosystems.

Island taxa are well known for exhibiting distinctive adaptations such as gigantism, dwarfism, increased longevity, and flightlessness. These traits, collectively referred to as the “island syndrome” (Whittaker et al. 2023), are generally viewed as adaptive responses to insular environments, driven primarily by natural selection (Bunce et al. 2005; Losos and Ricklefs 2009; Baeckens and Van Damme 2020). However, pronounced morphological differences observed between fossil remains and extant taxa do not necessarily provide unequivocal evidence of distinct extinct lineages. In some cases, these differences may instead reflect extreme expressions of morphological plasticity (e.g., Prost et al. 2013; Froese et al. 2017). In this context, ancient DNA techniques have become invaluable for clarifying phylogenetic relationships between extinct and extant taxa, thereby improving our understanding of morphological evolution and informing conservation and management strategies (e.g., Oswald et al 2019; Rawlence et al. 2024; Souilmi et al. 2024).

During several paleontological expeditions in the Azores between 2011 and 2018, we recovered cranial and postcranial avian remains from the islands of Pico, Terceira, São Miguel, and Graciosa. Some of these bones were morphologically and unambiguously assigned to the genus *Fringilla* (see section 3.1) but exhibited significantly larger cranial dimensions than those of the extant Azorean common chaffinch (*Fringilla moreletti*). Notably, the skull and beak sizes resembled those of the blue chaffinches (*F. teydea* and *F. polatzeki*), which are endemic to the Canary Islands. This morphological similarity raised the possibility that these extinct chaffinches might have a common ancestor with the Canarian blue chaffinches, suggesting a sequential colonisation pathway through the Azores, similar to hypotheses proposed for the expansion of common chaffinches across Macaronesia (Marshall and Baker 1999; Recuerda et al. 2021; Condori et al. 2025). In the present study, we (1) conducted a comparative morphological analysis of cranial and postcranial elements from both extinct and extant Macaronesian *Fringilla* taxa; (2) performed radiocarbon (^{14}C) dating of selected bone collagen using accelerator mass spectrometry (AMS) to approach the timing of the extinction event; and (3) employed ancient DNA techniques to determine the phylogenetic placement of the newly recovered paleontological material.

Results

Morphology

Extinct versus extant chaffinches

The collected materials were assigned to the genus *Fringilla* based on the following combination of characteristics: a granivorous beak; well-developed zygomaticus and postorbitalis processi; processus palatine premaxillaris longer and narrow, fused to the palatine; a foramen venae occipitalis externa located at the posterior border of the foramen magnum; an interorbital septum strong, with a fenestra septi developed with two fonticula orbitalia; and a simple foramen orbitonasale (Moreno 1985; Ujhelyi 1992). In many cases, the cranial and postcranial elements were found together, allowing the postcranial bones to be confidently assigned to this genus.

Extinct individuals from Graciosa and Pico Islands were significantly larger than extant birds in cranial ($W_d^* = 39.36$, $p < 0.001$), mandibular ($W_d^* = 66.54$, $p < 0.001$), and hindlimb ($W_d^* = 50.08$, $p < 0.001$) measurements, with no difference in forelimb size ($W_d^* = 0.42$, $p = 0.702$). Skull length in extinct birds was 18% greater on Graciosa and 13% greater on Pico. The largest reduction in extant birds occurred in maxilla height (beak depth), a key trait for processing large seeds (Price et al. 1984), declining by 30% on Graciosa and 5% on Pico. Mandible height and length were also reduced in extant birds, by 32% and 16% on Graciosa, and 17% and 12% on Pico, respectively (S-Table 3).

Postcranial measurements also showed reduced hindlimb size in extant birds. Compared with the fossil remains, femur length decreased by 9% on Graciosa and 7% on Pico, the tibiotarsus length by 8% in both islands, and the tarsometatarsus length by 12% and 10%, respectively (S-Table 3). In contrast, forelimb reductions were largely absent, except for the humerus. Ulna and carpometacarpus lengths were greater in extant birds than in extinct individuals on both islands, and a similar pattern was observed for the scapula on Pico (no scapula remains were identified from Graciosa).

Morphological groups in Macaronesia

Normal Mixture Model analyses revealed distinct morphological groups in both anatomical regions examined (Fig. 2). For mandible measurements, the best-supported model identified four morphological groups (BIC = 302.65), although support for models with three to four groups was comparable (S-Fig. 2). For skull measurements, the best-supported model identified five morphological groups (BIC = 598.79), with similarly close support for alternative models with five to six groups (S-Fig. 3). These results strongly rejected the hypothesis of a single morphologically homogeneous population across the archipelago.

The distribution of modern specimens among morphological groups showed clear taxonomic patterns. In the mandible dataset, most specimens were assigned to two major clusters (K1 and K4), corresponding to the common chaffinch and blue chaffinch species complexes, respectively (Fig. 2D). In the skull dataset, the five clusters represented both inter-archipelago differentiation among common chaffinches (Azores vs. Madeira and Canary Islands) and separation between the two blue chaffinch species (Fig. 2E). The morphological distinctiveness of these groups, particularly the blue chaffinch species and the extinct Graciosa morphotype, was evident in both ordination space (Figs. 2B, 2C) and in the predicted cluster assignments (Figs. 2D, 2E), indicating robust phenotypic discontinuities.

Notably, fossil specimens showed two distinct patterns of morphological affinity. Graciosa fossils formed a unique morphological cluster in the skull dataset, not represented by any modern population (Fig. 2E), suggesting the presence of a now-extinct morphotype on this island. In contrast, most fossil specimens in the mandible dataset clustered with both modern blue chaffinch species (Fig. 2D), indicating morphological convergence with the largest-bodied extant finches in Macaronesia.

Genetic diversity and phylogenetic relationships

We successfully extracted endogenous DNA from 10 extinct individuals (Pico: $n = 4$; Graciosa: $n = 6$), and from 213 extant *Fringilla* individuals (GenBank and ENA accession numbers are provided in S-Table 1). Complete or near-complete ($> 95\%$) mitochondrial genomes were recovered from seven extinct specimens (three from Pico and four from Graciosa), whereas the remaining three samples yielded lower-coverage consensus sequences ($\sim 70\text{--}93\%$). These latter samples were excluded from downstream analyses owing to the high proportion ($> 69\%$) of ambiguous (N) positions. Mean coverage depth among the best-preserved extinct specimens ranged from $1.9\times$ to $56.6\times$. Partial nuclear genomes were also recovered from all extinct individuals. However, only the best-preserved specimen (F224), which achieved 29% nuclear genome coverage at $\geq 3\times$ depth, was included in phylogenetic analyses to evaluate concordance between mitochondrial and nuclear signals. DNA damage profiles were consistent with a partially repaired ancient DNA library (Rohland et al. 2015) (Fig. S4).

Mitochondrial

Mitochondrial genetic diversity levels were similar between extinct and extant populations from Pico and Graciosa, although the extant chaffinches exhibited slightly higher values in haplotype diversity (S-Table 4). Neutrality tests were largely non-significant across groups, with the exception of Azorean chaffinches, which showed significant Tajima's D (-2.366) and R_2 (0.094) values, consistent with population expansion following a bottleneck (Fu's $F_s = 4.07$; Table S4). The remaining common chaffinch groups showed patterns consistent with demographic equilibrium at mitochondrial loci.

Bayesian (BEAST/Mr. Bayes) and Maximum Likelihood phylogenetic inferences were concordant, with most clades receiving strong nodal support (Fig. 3, S-Fig. 5). The inferred relationships are consistent with previous mitochondrial studies, recovering a monophyletic genus with the Brambling as sister to all other species (Marshall & Baker, 1998). The blue and common chaffinches form a fully supported clade [Maximum Likelihood Bootstrap (MLB) = 100, Posterior Probability (PP) = 1] and shared a common ancestor 4.26 My ago (Node A; 95% highest posterior density, 3.92–4.62 My). All Macaronesian common chaffinch taxa shared a common ancestor with the European and North African clade (Node B; MLB = 100; PP = 1) about 1.49 My ago (95%, 1.37–1.62 My), likely marking the Azores colonisation event. Colonisation of Madeira occurred 1.34 My ago (Node C; 95%, 1.22–1.46; MLB = 100; PP = 0.99/1), and the Canary Islands 1.06 My ago (Node D; 95%, 0.96–1.17 My; MLB = 100; PP = 1). Extinct Pico and Graciosa populations grouped with high nodal support (Node E; MLB = 100; PP = 0.99/1) within the

extant Azorean chaffinches but they did not form a distinct clade (Fig. 3, S-Fig. 5). Strikingly, one Azorean individual (F112) carried a European mitochondrial genome (Fig. 3), whereas its nuclear genome grouped unambiguously within the *moreletti* clade (see section 2.3.2 in supplementary material, Fig. 4). Finally, the basal clade for all common chaffinches was defined by North African individuals, suggesting a common origin for all common chaffinches in this continent, with relict haplotypes found in Tunisia and Libya (Fig. 3; S-Fig. 5).

Nuclear

Whole-genome analyses corroborated the mitochondrial results, placing the extinct chaffinch within the clade of extant Azorean chaffinches. Strong genetic structure was recovered in the Canary Islands, with maximal nodal support for all populations. In contrast, within the Azores, only the Graciosa extant population received maximal support, whereas relationships among the remaining islands were less well resolved (Fig. 4).

Our gene flow analyses revealed a complex history of ancestral introgression among *Fringilla* lineages (Fig. 5; S-Table 2). Overall, 82% of trios (235 out of 286) have resulted in significantly non-zero D values (Z-scores > 3, S-Table 2) indicating widespread signals of introgression. We then used *f*-branch statistics to summarize these signals and capture branch specific estimates of excess allele sharing based on the maximum likelihood nuclear tree (Fig. 4).

Extensive pattern of excess allele sharing between mainland and all island common chaffinches was observed in our *f*-branch analysis. The strongest signal was detected between Azorean and European common chaffinches, consistent with the European mitochondrial haplotype recovered from an Azorean individual. Meanwhile signals between Azorean and North African chaffinches were present but less pronounced. The remaining islands chaffinches, Madeira and Canary, exhibited low levels of introgression with both European and African lineages.

Several significant signals of excess allele sharing were also observed within the island lineages indicating a complex history of gene flow among them. Unexpectedly, several Canarian populations showed excess of allele sharing with other island lineages and amongst each other. The strongest signals were consistently seen in comparisons involving La Palma where the highest overall signal was observed between La Palma and La Gomera followed closely by other Canarian populations like Gran Canaria and Tenerife. Additional introgression events were inferred between La Palma and Madeira, La Palma and the Azores, and Madeira and the Azores. Overall, geographically proximate island populations tended to exhibit the highest inferred levels of gene flow.

Finally, we also detected significant signals of excess allele sharing between mainland chaffinches, *F. spodiogenys* (North Africa) and *F. coelebs* (Europe) (Z-scores > 3, S-Table 2) In particular, the strongest signals involved *F. s. harterti* and *F. coelebs*, as well as *F. s. spodiogenys* and *F. coelebs*. *f*-branch however combined and placed these signals on the internal branch ancestral to *F. s. harteti* and *F. s. spodiogenys*

rather than to terminal branches (Fig. 5). These patterns are consistent with historical gene flow between *F. coelebs* and the common ancestor of the two African lineages (Fig. 5).

The blue chaffinches interestingly exhibited signals of introgression with several ancestral branches of all common chaffinches rather than terminal branches suggesting the possibility of historical episodes of gene flow between ancestral populations of common and blue chaffinches (Fig. 5).

Radiocarbon dating

Table 1 summarises the dating results, indicating that all samples are of Holocene age. The oldest sample dates to 1400 BCE (lower CI), whereas the most recent (1225 CE, upper CI) approaches the period of early Portuguese presence in the first half of the 15th Century (Elias et al. 2022).

Table 1. Radiocarbon dates of ancient *Fringilla* from Azores islands. Conventional radiocarbon years (BP) and 2σ calibration interval (cal BCE or cal CE) are given. CE: Common Era. BCE: Before Common Era.

Lab codes	Island	Site	Radiocarbon years (BP)	2σ (cal BCE/cal CE)
RICH-21443	Pico	Furna das Cabras	883 ± 31	1040-1225 CE
RICH-21754	Graciosa	Furna do Calcinhas	3029 ± 31	1400-1130 BCE
RICH-27083	Graciosa	Furna do Calcinhas	2746 ±2 8	980-815 BCE

Discussion

Contrary to our expectations, our molecular findings refute the hypothesis that the giant ecomorphs found in the Azores represent an extinct species, instead indicating substantial phenotypic plasticity within this taxon. Accordingly, our results do not elucidate the origin or colonisation pathway of blue chaffinches in Macaronesia, but they do revise previous estimates (Valente et al. 2017) by pushing the timing of colonisation back to the early Pliocene. We document a marked non-isometric reduction in cranial and hindlimb proportions in the extant individuals, without corresponding mitochondrial or nuclear differentiation. These morphological estimates are likely conservative. Because the sex of fossil specimens could not be determined, measurements from males and females were necessarily pooled. Given that females are smaller than males in *Fringilla* (Cramp and Perrins 1994), the inclusion of female specimens in the fossil sample would reduce the estimated mean size of the extinct population, potentially underestimating the true extent of size reduction between extinct and extant chaffinches.

The extinction of giant chaffinch ecomorphs in the Azores

According to our radiocarbon (¹⁴C) dating results these changes are likely associated with habitat deforestation initiated by Portuguese colonisers since the 15th century. This rapid morphological divergence may represent a case of strong directional selection, in which the decline in the availability of

large seeds favoured smaller phenotypes, a process potentially driven by human-mediated environmental change (De León et al. 2011; Sendell-Price et al. 2020). In this case, deforestation likely played a key role. Strong associations between body size and extinction risk due to anthropogenic pressures have been recorded since the late Quaternary. These processes have led to the extinction of both giant and dwarf species, contributing to a general reduction in body size (Bochaton et al. 2018; Smith et al. 2018; Rozzi et al. 2023), and to a broader homogenization of avian morphospace (Hughes et al. 2022).

Finches are widely regarded as paradigms of rapid evolutionary radiation, largely due to pronounced morphological changes in both beak and cranial shape and size. Among them, Darwin's finches of the Galápagos and the Hawaiian drepanidine finches are the most prominent examples from oceanic islands, having significantly contributed to our understanding of speciation theory (Enbody et al. 2023; Mosleh et al. 2023; Illera et al. 2024). These two passerine groups exemplify how natural selection drives divergence through conspicuous modifications in beak and skull shape and size, facilitating the evolution of novel feeding strategies. However, such changes tend to be more subtle within species. Darwin's finches provide one of the few well-documented cases where it has been possible to study how natural selection operates on population differentiation in both sympatry and allopatry, depending on environmental conditions (Boag and Grant, 1981; Grant and Grant, 2006). Azorean common chaffinches underwent morphological shifts that exceed those documented in Darwin's finches. Because cranial morphology is tightly linked to jaw musculature and bite force, which together determine the ability to process seeds of different sizes and hardness (Herrel et al. 2005, 2010; Mosleh et al. 2023; Andries et al. 2025), the extinct giant ecomorphs from Graciosa and Pico were probably capable of exploiting larger and harder seeds than extant birds. Their disappearance likely reflects the profound ecological transformation of the Azores following human colonisation. Native forests now persist only as highly fragmented remnants covering ~ 3% of their original extent (Terzopoulou et al. 2015), indicating a near-complete restructuring of island ecosystems over recent centuries. Such habitat loss would have drastically altered seed availability, favouring smaller resources. The introduction of rodents (e.g., *Rattus* spp. and *Mus musculus*) probably intensified these changes, as invasive mammals are highly effective competitors for large seeds (Schluter 1988). Under these altered trophic conditions, individuals with smaller beaks may have gained a selective advantage through more efficient exploitation of the remaining seed resources (Díaz 1994). Together, these observations suggest that rapid environmental change imposed strong directional selection favouring reduced cranial size, ultimately leading to the disappearance of giant chaffinch ecomorphs in the Azores (Andries et al. 2025).

Intriguingly, the extinction of these giant forms coincided with that of another large endemic finch on Graciosa, the Greater Azores Bullfinch (*Pyrrhula crassa*). Its only surviving relative, the Azores bullfinch (*P. murina*), now restricted to São Miguel Island, also exhibits a pronounced reduction in maxilla height. The magnitude of this reduction is remarkably similar in both lineages (30.6% in bullfinches and 30.3% in chaffinches), although extinct bullfinches, unlike chaffinches, also possessed enlarged forelimbs relative to extant birds (Rando et al. 2017).

Our findings reveal an exceptional degree of phenotypic plasticity in Azorean common chaffinches, far exceeding the scale of morphological change reported in Darwin's finches. More broadly, they illustrate how rapid ecological transformation on islands can generate dramatic phenotypic shifts without substantial genome-wide divergence. Integrating genomic, functional, and palaeoecological evidence will now be essential to resolve the mechanisms underlying this striking evolutionary flexibility (Illera et al. 2024).

Evolutionary history of *Fringilla coelebs* species complex

Mitochondrial and nuclear genome analyses revealed a pronounced pattern of differentiation within the *Fringilla coelebs* species complex, supporting the recognition of five species: *Fringilla coelebs* occurring in Eurasia, *F. spodiogenys* in North Africa, *F. moreletti* in the Azores, *F. maderensis* in Madeira, and *F. canariensis* in the Canary Islands (Recuerda et al. 2021). The mitochondrial basal clade of these five taxa occurs in North Africa, raising two alternative hypotheses regarding the biogeographic history of this species complex. Under the first hypothesis, Pleistocene glaciations led to the contraction of the ancestral population with the North African lineage persisting as a relict. As climatic conditions became more favourable, this emerging lineage expanded northwards, colonising Europe and subsequently diverging genetically and phenotypically. The European lineage then acted as the source for successive colonisation events across Macaronesia, first reaching the Azores and successively Madeira and the Canary Islands (Recuerda et al. 2021; Condori et al. 2025; Figs. 4 and 5). Alternatively, the basal position of the North African lineage (Fig. 3) may reflect long-term persistence in this region while European populations diverged independently. Following the Pleistocene glacial cycles, European populations may have recolonised North Africa, leading to secondary contact and admixture with resident populations that retained ancestral mitochondrial lineages (Marshall and Baker, 1999). The occurrence of a complete European mitochondrial genome in an Azorean chaffinch supports the European origin for this taxon and may represent a striking example of incomplete lineage sorting in an island bird radiation (DeRaad et al. 2023). Alternatively, it could reflect the recent accidental arrival of one or a few European common chaffinches to the Azores, followed by hybridisation with the resident population. Because mitochondrial DNA has a fourfold smaller effective population size than the nuclear genome, the nuclear contribution of such migrants could have been rapidly diluted through repeated backcrossing, leaving only the European mitochondrial genome as evidence of this event. Notably, the significant excess of allele sharing detected between European and Azorean populations by the ABBA–BABA analyses is consistent with historical gene flow, although these data do not allow us to distinguish unequivocally between ancient introgression and incomplete lineage sorting (see below).

Recurrent gene flow between European and North African populations during glacial periods likely contributed to the progressive erosion of ancestral mitochondrial variation, with only ~ 35% of relict haplotypes currently retained in North Africa. This evolutionary scenario is further supported by the significant results obtained from D and *f*-branch statistics performed with the nuclear genome (Fig. 5); and for the mitochondrial demographic inferences from the Azores, which indicate a bottleneck followed by population expansion, as well as comparable levels of genetic diversity between extinct and extant

chaffinch populations in this archipelago (S-Table 4). We must note that while D and related f statistics are robust to disentangling incomplete lineage sorting from gene flow (Durand et al., 2011), such a significant result could arise under other evolutionary scenarios. In particular, structure within the ancestral population followed by rapid divergence could lead to asymmetric sorting of ancestral polymorphism among the descendants which can produce significant D statistic results even in the absence of gene flow (Durand et al. 2011; Eriksson and Manica 2012). In addition, “ghost” (i.e., unsampled) lineages, and incorrect topology are also known to produce false positives while computing these statistics (Durand et al. 2011; Roger 2015).

Despite pronounced morphological divergence, giant phenotypes were not associated with significant mitochondrial or nuclear differentiation, nor with elevated genetic diversity in extinct individuals. This pattern suggests that ancestral populations experienced frequent inter-island dispersal, maintaining high gene flow, limiting genetic structuring, and buffering against diversity loss (Ramírez et al. 2013), consistent with patterns observed in contemporary populations (Rodrigues et al. 2013; this study). This interpretation is further supported by the absence of substantial forelimb reduction in the extinct ecomorphs, indicating that dispersal ability remained largely intact and facilitated recurrent connectivity among islands. This pattern contrasts sharply with that observed in the Canary Islands, where populations show substantial genomic differentiation among islands (Illera et al. 2018; Recuerda et al. 2021; Condori et al. 2025; this study), despite signatures of introgression among neighbouring islands (Fig. 5).

Conclusions

Island species often undergo rapid phenotypic change, driven by trophic specialisation, release from predation, and novel competitive interactions (Whittaker et al. 2023). Yet, such specialisation is frequently linked to reduced adaptive potential and increased extinction risk (Birskis-Barros et al. 2026). Pronounced morphological divergence in extinct taxa has traditionally been interpreted as evidence of deep phylogenetic distinctiveness (Phillips et al. 2018). However, several cases in Macaronesia have shown that molecular evidence does not support taxonomic hypotheses based exclusively on morphological evidence (Ramírez et al. 2010; Renom et al. 2021), a pattern also reported in other island systems (Bunce et al. 2005; Louchart et al. 2018). The extinct *Fringilla* remains analysed here exemplify this pattern, showing pronounced morphological divergence despite minimal genetic differentiation from extant populations. Despite their striking cranial resemblance to the Canary Islands blue chaffinches, genomic analyses unequivocally place these birds within the clade of extant Azorean common chaffinch lineage. These findings reveal that dramatic cranial and postcranial divergence can arise over short evolutionary timescales without corresponding species-level genomic differentiation. Finally, our results highlight the extraordinary evolutionary plasticity of island birds and caution against relying on morphology alone when reconstructing the evolutionary history of extinct taxa. Integrating genomic, morphological, and palaeoecological evidence will be essential for resolving the processes shaping island biodiversity and for avoiding inflated estimates of taxonomic and phylogenetic diversity in fossil assemblages.

Material and Methods

Study area and fieldwork

From 2011 to 2018, all Azorean islands with documented volcanic tubes were systematically surveyed, and fossil bones were collected from the floors of these lava caves. Bones identified as belonging to the genus *Fringilla* were separated and labelled for further analysis. The best-preserved material was recovered from Graciosa and Pico islands, whereas only fragmented remains were found on Terceira and São Miguel (Fig. 1). Due to their poor condition, the fragmented bones from the latter two islands were unsuitable for morphological analyses; however, we assessed DNA preservation in two samples from Terceira following the ancient DNA protocols applied to the other ones.

Pico and Graciosa are relatively young and small volcanic islands within the Azorean archipelago (Fig. 1). Pico covers an area of 436 km² and is estimated to be between 0.186 and 0.125 million years (Ma) old (Costa et al. 2015). Graciosa, by contrast, covers 62 km², and the age of its earliest subaerial rocks has been estimated at between 1.057 ± 0.028 Ma (Larrea et al. 2014) and 0.702 ± 0.010 Ma (Sibrant et al. 2014). The *Fringilla* bones used for morphological analyses were recovered from Furna das Cabras on Pico and Furna do Calcinhas on Graciosa (Fig. 1). The volcanic tube containing Furna das Cabras lies close to Pico Mountain, a stratovolcano with substantial Holocene volcanic activity (Nunes et al. 2006). In contrast, the volcanic formation hosting Furna do Calcinhas has been dated to $44,000 \pm 5,000$ – $23,000 \pm 3,000$ years ago (Sibrant et al. 2014), although the most recent eruptions in this volcanic system occurred 3,900 years ago (Larrea et al. 2014).

To study the phylogenetic relationships between extinct and extant taxa, we captured modern common and blue chaffinches during multiple bird-ringing sessions conducted across the Macaronesian archipelagos (see Montero et al. 2025 for further details). Briefly, individuals were captured using mist-nets at geographically distant localities within each island group to maximize genetic variability representation. All birds were banded using uniquely numbered metallic rings issued under the national ringing schemes of Portugal and Spain (S-Table 1). Approximately 40–50 µL of blood was collected from each individual via brachial venepuncture. Samples were preserved in 99.9% ethanol and stored at –20°C in the laboratory until further analysis. After sampling, all individuals were released at the site of capture. Additionally, we used 55 tissue samples provided by the Royal Ontario Museum (ROM) from Azores (Santa Maria, Sao Jorge, Pico, and Faial), North Africa (Morocco and Tunisia), and Europe (Finland and United Kingdom) (S-Table 1).

Morphometric data collection

We analysed morphological variation using cranial and postcranial measurements from modern specimens across Macaronesia (4–7 individuals across islands), and fossil material from two islands (Pico and Graciosa). The modern specimens were obtained on loan from the Royal Ontario Museum (ROM) in Ontario (Canada), and from the University of La Laguna in Tenerife (Canary Islands, Spain) (S-Table 2). Morphological measurements (S-Fig. 1; Fig. 2) were taken using a digital calliper (Mitutoyo)

with a precision of 0.01 mm. All modern measurements were taken from male specimens, since most of the museum specimens were male, while the sex of fossil samples measured was unknown.

Molecular procedures

Ancient DNA

A total of 16 *Fringilla* samples were processed at the Paleogenomics Laboratory of the University Institute for Research in Environmental Sciences of Aragón (IUCA, University of Zaragoza, Spain). These included seven bones from Furna do Calcinhas (Graciosa), seven from Furna das Cabras (Pico), one from Furna San Antonio, and one from Furna da Achada, the latter two deposits located on Terceira. Additionally, three *Fringilla* samples from Furna do Calcinhas (Graciosa) were independently processed at the Institute of Evolutionary Biology (IBE) in Barcelona (S-Table 1). See Supplementary Material for DNA extraction and library construction methods.

As the individuals were morphologically identified as *Fringilla* sp. (see section 3.1) the collapsed reads from one sequencing run of sample 230 were preliminarily mapped to the mitochondrial genomes of *Fringilla coelebs* (NC_025599) and *Fringilla moreletti* (A407506_Graciosa), the latter newly obtained in this study. We used BWA v.0.7.17 backtrack (aln) algorithm (Li and Durbin, 2009) applying the parameters accepted to map ancient data (e.g., Olah et al. 2026), that is, aln -n 0.01, -o 2, -l 1024, and removing reads with minimum mapping quality of 25 (-q 25) using SAMtools v.1.11 (Li et al. 2009). Duplicate reads were removed using FilterUniqueSAMCons.py (Kircher 2012). Although the number of reads mapped to each reference genome was similar (2,709 reads mapped to the *F. coelebs* mitogenome and 2,833 to *F. moreletti*) the number of mismatches and gaps was substantially higher when mapping to *F. coelebs* (360 mismatches and 6 gaps) than to *F. moreletti* (48 mismatches and 3 gaps). This result suggested that *F. moreletti* was likely phylogenetically closer to the *Fringilla* remains from the Azores and, therefore, served as a more suitable reference genome for mapping. Accordingly, all remaining samples were subsequently mapped iteratively to *F. moreletti*, and after each round of mapping, an intermediate 75% majority consensus sequence was generated in Geneious Prime v.2022.0.2 (Biomatters, <http://www.geneious.com>; Kears et al. 2012) calling the nucleotides with coverage depths < 3 and leaving the reference nucleotides otherwise. The mapping process was repeated until no more reads were mapped (two iterations in this case). A final 75% majority consensus sequence for each sample was finally obtained using Geneious calling nucleotides only at sites with read-depth $\geq 3\times$. All the mapping results (i.e., number of iterations and unique reads mapped) are listed in S-Table 1. Ancient DNA misincorporation and fragmentation patterns were assessed using mapDamage v.2.1.1 (Jónsson et al. 2013).

Modern DNA

We carried out DNA extractions of extant finch samples at IMIB's Ecological Molecular Laboratory, located on the Mieres Campus of the Oviedo University, Spain, using the ammonium acetate method (Illera 2023). Samples were sequenced to an average of 11.7x coverage on a NovaSeq 6000 Illumina

platform. Raw reads were processed using a custom Nextflow pipeline (https://github.com/EcoEvoGenomics/genotyping_pipeline/tree/main) version 2.2.4 as described in Montero et. al. (2025). Briefly, adapter-trimmed reads were mapped to the *Fringilla coelebs* reference genome (Grouw 2024), variants were called using the BCFtools pipeline, and SNPs were filtered based on genotype quality < 30, sequencing depth > 16X, and sites with > 50% missing data. The resulting final dataset consisted of 33,374,076 SNPs. For mitochondrial genome reconstruction, the aligned reads were then processed with bcftools mpileup (-a DP, AD) and bcftools call (-m) under haploid ploidy settings, normalized with bcftools norm, and filtered to retain sites with QUAL > 30 and depth ≥ 3X (bcftools filter, -IndelGap 5). Low-confidence positions were independently masked using samtools mpileup, requiring a minimum depth of 3X and a majority allele frequency ≥ 75%; masked and low-depth sites were converted to N. Consensus sequences were generated with bcftools consensus.settings, and the fasta sequences were extracted with samtools v1.19 (Montero et al. 2025). Additionally, we incorporated one sequence of the common chaffinch (OY740764.1), and one Brambling (*Fringilla montifringilla*; NC024048.1) available from GenBank.

Radiocarbon dating

To approach the extinction date of the fossils, we performed radiocarbon dating using accelerator mass spectrometry (AMS) on bone collagen at the Radiocarbon Dating Lab of the Royal Institute for Cultural Heritage (Brussels). We dated three bone samples from specimens from Pico and Graciosa. The sample from Pico Island (RICH-21443) consisted of bone fragments (hindlimbs, vertebrae, and ribs) from one individual (0.49 g). The other two samples, both from Graciosa, included pooled skull fragments from three specimens weighing 0.83 g (RICH-21754) and a mandible fragment of a single specimen (0.25 g; RICH-27083).

Radiocarbon years were calibrated using OxCal v.4.4 (Bronk Ramsey 2009) and the Incal20 calibration curve for Northern Hemisphere (Reimer et al. 2020). Dates calculated from calibration (cal) are expressed as 2σ intervals (i.e., p = 95.45%) were CE being 'Common Era' and BCE 'Before Common Era'.

Analyses

Mitochondrial genetic diversity and phylogenetic inference

We calculated mitochondrial genetic diversity metrics, including the number of haplotypes, haplotype diversity, nucleotide diversity, and theta ($\theta = 2N\mu$), for both extant and extinct chaffinch populations using the program DnaSP v6.0 (Rozas et al. 2017). Additionally, we used the same program to assess potential deviations from a constant population size in both groups, applying the statistics F_S (Fu 1997), R_2 (Ramos-Onsins and Rozas, 2002), and Tajima's D (Tajima 1989).

We retrieved a total of 223 *Fringilla* sequences (Table S2), which were aligned using MUSCLE v3.8.425 (Edgar 2004) implemented in Geneious. The dataset was partitioned in five partitions: three partitions for codon positions (1–3) of the protein coding genes (PCGs) using DAMBE v.7.0.5 (Xia 2017), one partition

for ribosomal RNA genes (12s and 16S) and transfer RNA (tRNA) genes, and one partition for control region.

The partitioned dataset was used to infer phylogenetic relationships among *Fringilla* individuals, using two *F. montifringilla* individuals as outgroups. We incorporated one sequence of the common chaffinch (OY740764.1), and one Brambling (*Fringilla montifringilla*; NC024048.1) available from GenBank. Maximum Likelihood (ML) inference was conducted using IQ-TREE2, with nodal support assessed through 1,000 ultrafast bootstrap replicates (Hoang et al. 2018). Bayesian Inference (BI) was performed in MrBayes v3.2.7a (Ronquist et al. 2012) using four independent runs of four Markov chains each, for a total of 5 million generations per run. Convergence of parameter estimates was assessed using Tracer v1.7.2 (Rambaut et al. 2018). For both analyses nucleotide substitution model was estimated with ModelFinder (Kalyaanamoorthy et al. 2017), implemented in IQ-TREE2 v2.2.0 (Minh et al. 2020) (option -m TESTMERGE). Divergence times between taxa were estimated using BEAST2 v2.7.7 (Bouckaert et al. 2019). The best-fitting nucleotide substitution model was selected using BEAST Model Test, with the mutation rate selected to be estimated. We applied a strict molecular clock with a mean substitution rate of 0.01 and a standard deviation of 0.0075 substitutions per site per million years (Illera et al. 2008). A birth–death speciation model was used, and two independent MCMC analyses were run for 10^8 steps each, with a burn-in of 10^7 steps. Convergence of the MCMC chains was assessed in Tracer, and a maximum clade credibility consensus tree was generated using TreeAnnotator v2.7.7 (Drummond and Rambaut, 2007). Two independent runs were performed to ensure that the posterior probabilities, phylogenetic relationships and estimated dates were consistent. The resulting tree was visualized in FigTree v1.4.4 (<https://github.com/rambaut/figtree/releases>).

Nuclear analyses

To assess concordance between mitochondrial and nuclear genomes, we used all modern nuclear genomes ($n = 213$) and the highest-quality extinct chaffinch genome (F224, ENA accession number ERS30392845) to perform a maximum-likelihood phylogenetic inference using IQ-TREE2 v2.3.1. We converted the filtered VCF to PHYLIP format using vcf2phylip.py (<https://github.com/edgardomortiz/vcf2phylip/blob/master/vcf2phylip.py>), and generated a subsampled dataset of $\sim 100,000$ SNPs to infer phylogenetic relationships in IQ-TREE v2.3.1. To build a maximum-likelihood tree we used the GTR substitution model with ascertainment bias correction (GTR + ASC) to account for the exclusion of invariant sites, and nodal support was assessed with 1,000 ultrafast bootstrap replicates.

In addition, D-statistics/ABBA-BABA tests (Green et al. 2010; Durand et al. 2011), f_4 ratio and f -branch statistics were conducted in Dsuite v0.5 (Malinsky et al. 2021) to identify ancestral episodes of gene flow among *Fringilla* lineages and to distinguish these signals from incomplete lineage sorting. We carried out 286 comparisons among 13 populations to test different hypotheses for gene flow according with our topologies (see Gene flow section in Supplementary Material, for further details).

Morphology

Extinct versus extant chaffinches in Graciosa and Pico

We tested for differences in size between extant and fossil bones from Pico and Graciosa islands using the W_d^* test. This analysis is based on Welch MANOVA test, which is robust to heteroscedasticity, and accounts for unbalanced number of observations (Hamidi et al. 2019). We used both cranial and postcranial traits (S-Table 2). Significance was assessed using 999 permutations.

Detection of morphological groups in Macaronesian chaffinches

We used Normal Mixed Models (NMMs) to test for the existence of distinct morphological groups across Macaronesian finches. NMMs conceptualize phenotypic variation as a combination (i.e., mixture) of distinct normal distributions (McLachlan and Peel 2000), where each distribution may represent a morphologically distinct group (Cadena et al. 2018). Due to the fragmentary nature of fossil remains, we conducted separate analyses for those morphological traits with sufficient data: (a) skull measurements (maxilla length, maxilla width, maxilla height, interorbital width, cranium width, cranium length, cranium height; $n = 85$ modern specimens (range: 4–9 specimens per island), 2 fossils from Pico, 2 fossils from Graciosa); and (b) mandible measurements (mandible length, mandible height, symphysis length, articular end width; $n = 89$ modern specimens (range: 4–11 specimens per island), 5 fossils from Pico, 6 fossils from Graciosa). We retained only specimens with measurements for all variables within each anatomical grouping.

We first conducted Principal Components Analysis (PCA) on the covariance matrix of log-transformed measurements for each anatomical region (Fig. 2B-C). To reduce dimensionality while retaining variables most useful for group discrimination, we used the R package *clustvars* (Scrucca and Raftery 2004) to select the optimal number of principal components for subsequent analysis. This approach selects variables that maximize separation among groups in NMMs without requiring a priori group assignments (Raftery and Dean 2006). For the mandible dataset, PC1 and PC2 were retained; for the skull dataset, PC1, PC2, and PC3 were retained.

We then fitted NMMs to the selected principal components using the R package *mclust* (Scrucca et al. 2016), testing models with 1–9 groups and various covariance structures. Model selection was based on the Bayesian Information Criterion (BIC).

All analyses were conducted in R version 4.5.1 (R Core Team, 2024).

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and materials

All original data and scripts required to reproduce the morphological and phylogenetic analyses presented in this study will be available from the Zenodo Digital Repository at:

<https://doi.org/10.5281/zenodo.21834896>

Complete mitochondrial genome sequences have been deposited in the National Center for Biotechnology Information (NCBI) under accession numbers PX424344–PX424423 and PZ779205–PZ779337 for extant individuals, and PX423606–PX423612 for fossil individuals. Nuclear genomic data have been deposited in the European Nucleotide Archive (ENA) under project accession PRJEB65290 (Table S1).

Competing interests

The authors declare that they have no competing interests.

Funding

This work was supported by the Spanish Ministry of Science, Innovation and Universities and the European Regional Development Fund (PGC2018-097575-B-I00 and PID2022-140091NB-I00 to JCI, PB, JCR, and CNH-F; CGL2012-38087 and CGL2016-79795R to JAA); the Spanish Ministry of Education (PRX23/00006 to JCI); and American Genetic Association (EECG award to BKM).

Authors' contributions

Juan Carlos Illera: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; funding acquisition; supervision; validation; visualization; writing – original draft; writing – review and editing. **B. Karina Montero:** Data curation; formal analysis; validation; visualization; investigation; writing – review and editing. **Juan Carlos Rando:** Data curation; validation; visualization; investigation; writing – review and editing. **Josep Antoni Alcover:** Data curation; validation; investigation; writing – review and editing. **Carles Lalueza-Fox:** Data curation; validation; investigation; writing – review and editing. **Martin Irestedt:** Data curation; validation; investigation; writing – review and editing. **Carmen N. Hernández-Flores:** Data curation; validation; investigation; writing – review and editing. **Erik Sandertun:** Data curation; validation; investigation; writing – review and editing. **Bezawit Tesfa:** Data curation; formal analysis; validation; investigation; writing – review and editing. **Jens Hering:** Data curation; validation; investigation; writing – review and editing. **Mark Ravinet:** Data curation; validation; investigation; writing – review and editing. **Pere Bover:** Conceptualization; data curation; formal analysis; investigation; methodology; supervision; validation; visualization; writing – review and editing.

Acknowledgements

S. Alberdi and L. Llovera assisted with the modern and ancient DNA extraction. E. Blanco, E. Nicolás, E. González, D.P. Padilla, F. Medina, Á.C. Moreno, E. Torres, F. Pereira, J. Navarrete, H. Pieper (†), O. Runze, and T. Rodrigues contributed to the fieldwork. P. Borges and J.P. Constança provided logistic support in Terceira and São Miguel, respectively. Chaffinch illustrations were produced by J. de la Torre. We thank M. Peck from the Royal Ontario Museum (ROM) for loaning *Fringilla* skeletons and providing tissue samples for this study, and for arranging the shipping. B. Llamas and K.J. Mitchell provided comments and suggestions to the whole genome analyses. We are grateful to Galicia Supercomputing Center (CESGA), where all whole-genome analyses were performed. We are also grateful for resources for D-statistics and gene flow analyses provided by Sigma2 – the National Infrastructure for High-Performance Computing and Data Storage in Norway. We also thank to B. Bauluz and G. Cuenca-Bescós (Universidad de Zaragoza, Spain), as well as to the Departamento de Ciencias de la Tierra and IUCA (Universidad de Zaragoza, Spain), for their support of the Paleogenomics Laboratory. We also thank the Laboratory of Sequencing and Functional Genomics and the Laboratory of Proteomics at the Servicios Científico-Técnicos of CIBA (IACS–Universidad de Zaragoza, Spain) for their assistance. We thank the Institut Mediterrani d'Estudis Avançats (CSIC–UIB) for technical support during the field cataloguing of the samples. The Direção Regional do Ambiente, Secretaria Regional da Agricultura e Ambiente of the Government of the Azores granted permission to conduct the palaeontological surveys and study several caves throughout the Azores. Permits for capturing, ringing, and bleeding birds were granted by the Regional Government of the Canary Islands (Exp.: 2019/11937 and 2020/16669), the Regional Government of the Azores (N. 5/2021/DRAAC), and the Regional Government of Madeira (N. 04/IFCN/2020). Additional permits to work within protected areas were issued by the Cabildo of Gran Canaria (Exp. FA 16/2020), La Palma (Ref: A/EST-012/2019), and Tenerife (Exp. AFF 141/19). The National Park of Garajonay also provided permits (Exp. 190.673, PTSS/3.129) and accommodation during fieldwork. Ethical approval for blood sampling was obtained from the Regional Government of Asturias (PROAE 45/2019).

References

1. Alcover J.A., Pieper H., Pereira F., Rando JC. 2015. Five new extinct species of rails (Aves: Gruiformes: Rallidae) from the Macaronesian Islands (North Atlantic Ocean). *Zootaxa* 4057: 151–190.
2. Alcover J.A., Pieper H., Pereira F., Rando J.C. 2016. *Rallus nanus* nomen novum: a replacement name for *Rallus minutus* Alcover et al. 2015. *Zootaxa* 4085: 141–142.
3. Ali J.R., Blonder, B.W., Pigot A.L., Tobias J.A. 2023. Bird Extinctions Threaten to Cause Disproportionate Reductions of Functional Diversity and Uniqueness. *Functional Ecology* 37: 162–175.
4. Andries T., Müller W., Van Wassenbergh S. 2025. Beak dimensions affect feeding performance within a granivorous songbird species. *J. Exp Bio.* 228: jeb249681.
5. Bach C.S. 2025. Discovery and Settlement of the Azores: Assumptions Regarding Medieval Viking Presence on the Archipelago. *Archaeologica Discovery* 13: 1-25.

6. Baeckens S., Van Damme R. 2020. The island syndrome. *Current Biology* 30: R329–R339.
7. Baiser B., Valle D., Zelazny Z., Burleigh J.G. 2018. Non-random patterns of invasion and extinction reduce phylogenetic diversity in island bird assemblages. *Ecography* 41: 361-374.
8. Birskis-Barros I., Assis A.P.A., James H., Kim S.L., Yeakel J.D. 2026. Morphological variability as a buffer against extinction: insights from Hawaiian honeycreepers. *Proc. R. Soc. B* 293: 20252594.
9. Boag P.T., Grant P.R. 1981. Intense Natural Selection in a Population of Darwin's Finches (Geospizinae) in the Galapagos. *Science* 214: 82–85.
10. Bochaton C., Bailon S., Herrel A., Grouard S., Ineich I., Tresset A., Cornette R. 2017. Human impacts reduce morphological diversity in an insular species of lizard. *Proc. R. Soc. B* 284: 20170921.
11. Bouckaert R., Vaughan T.G., Barido-Sottani J., Duchêne S., Fourment M., Gavryushkina A., et al. 2019. BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLoS Comput Biol* 15(4): e1006650.
12. Bronk Ramsey C. 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon* 51(1): 337–360.
13. Bunce M., Szulkin M., Lerner H.R.L., Barnes I., Shapiro B., Cooper A., Holdaway R.N. 2005. Ancient DNA Provides New Insights into the Evolutionary History of New Zealand's Extinct Giant Eagle. *PLoS Biol* 3(1): e9.
14. Cadena C.D., Iván Jiménez F.Z. 2018. Issues and perspectives in species delimitation using phenotypic data: Atlantean Evolution in Darwin's finches. *Systematic Biology* 67: 81–194.
15. Ceballos G., Ehrlich P.R. 2023. Mutilation of the tree of life via mass extinction of animal genera. *Proc. Natl. Acad. Sci. U.S.A.* 120 (39): e2306987120,
16. Condori B., Recuerda M., Illera J.C., Milá B. 2025. The Relative Roles of Selection and Drift in the Chaffinch Radiation (Aves: *Fringilla*) Across the Atlantic Archipelagos of Macaronesia. *Ecol. Evol.* 15: e71307.
17. Cooke R., Sayol F., Andermann T. et al. 2023. Undiscovered bird extinctions obscure the true magnitude of human-driven extinction waves. *Nat. Commun.* 14: 8116.
18. Costa A.C.G., Hildenbrand A., Marques F.O., Sibrant A.L.R., Santos de Campos A. 2015. Catastrophic flank collapses and slumping in Pico Island during the last 130 kyr (Pico-Faial ridge, Azores Triple Junction). *Journal of Volcanology and Geothermal Research* 302: 33-46.
19. Cramp S., Perrins C.M. (eds) 1994. *Handbook of the birds of Europe, the Middle East, and north Africa: the birds of the western Palearctic. Vol. VIII. Crows to finches.* Oxford University Press.
20. Crowley B.E. 2010. A refined chronology of prehistoric Madagascar and the demise of the megafauna. *Quat. Sci. Rev.* 29: 2591–2603.
21. De León L.F., Raeymaekers J.A.M., Bermingham E., Podos J., Herrel A., Hendry, A.P. 2011. Exploring possible human influences on the evolution of Darwin's finches. *Evolution* 65: 2258-2272.
22. DeRaad D.A., McCullough J.M., DeCicco L.H., Hime, P.M., Joseph L., Andersen M.J., Moyle R.G. 2023. Mitonuclear discordance results from incomplete lineage sorting, with no detectable evidence for gene flow, in a rapid radiation of *Todiramphus* kingfishers. *Molecular Ecology* 32: 4844–4862

23. Díaz M. 1994. Variability in seed size selection by granivorous passerines: effects of bird size, bird size variability, and ecological plasticity. *Oecologia* 99: 1–6.
24. Drummond A.J., Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7: 214.
25. Durand E.Y., Patterson N., Reich D., Slatkin M. 2011. Testing for ancient admixture between closely related populations. *Molecular Biology and Evolution* 28: 2239-2252.
26. Edgar R.C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792-1797.
27. Enbody E.D., Sendell-Price A.T., Sprehn C.G., Rubin C.J., Visscher P.M., Grant B.R., Grant P.R., Andersson L. 2023. Community-wide genome sequencing reveals 30 years of Darwin's finch evolution. *Science* 381: eadf6218.
28. Elias R.B., Connor S.E., Góis-Marques C.A., Schaefer H., Silva L., Sequeira M.M., Moura M., Borges P.A.V., Gabriel R. 2022. Is there solid evidence of widespread landscape disturbance in the Azores before the arrival of the Portuguese? *Proc. Natl. Acad. Sci. U S A*. 119: e2119218119.
29. Eriksson A., Manica A. 2012. Effect of ancient population structure on the degree of polymorphism shared between modern human populations and ancient hominins. *Proc. Natl. Acad. Sci. U S A*. 109: 13956–13960.
30. Fernández-Palacios J.M., Kreft H., Irl S.D.H., Norder S. Ah-Peng C., Borges P.A.V., Burns K.C., de Nascimento L., Meyer J.-Y., Montes E., Drake D.R. 2021. Scientists' warning – The outstanding biodiversity of islands is in peril. *Global Ecology and Conservation* 31: e01847.
31. Fernández-Palacios J.M., Fructuoso M., Illera J.C., Rando J.C., De Nascimento L., Fernández-Palacios E., Patiño J., Otto R., Castilla-Beltrán A., Martín González E., Orihuela-Rivero R., Alcover J.A., Whittaker, R.J. 2025. A synthesis of terrestrial species extinctions in the Macaronesian Islands and their correspondence with human occupancy. *PNAS Nexus* 4: pgaf215.
32. Florencio M., Patiño J., Nogué S., Traveset A., Borges P.A.V., Schaefer H., Amorim I.R., Arnedo M., Ávila S.P., Cardoso P., De Nascimento L., Fernández-Palacios J. M., Gabriel S.I., Gil A., Gonçalves V., et al. 2021. Macaronesia as a fruitful arena for ecology, evolution, and conservation biology. *Frontiers in Ecology and Evolution* 9: 718169.
33. Froese D., Stiller M., Heintzman P.D., Reyes A.V., Zazula G.D., Soares A.E., Meyer M., Hall E., Jensen B.J., Arnold L.J., MacPhee R.D., Shapiro B. 2017. Fossil and genomic evidence constrains the timing of bison arrival in North America. *Proc Natl Acad Sci U S A*. 114: 3457-3462.
34. Fu Y.X. 1997. Statistical test of neutrality of mutations against population growth, hitchhiking, and background selection. *Genetics*, 147: 915–925.
35. Gardner E.E. Walker S.E., Gardner L.I. 2016. Palaeoclimate, environmental factors, and bird body size: A multivariable analysis of avian fossil preservation. *Earth-Science Reviews* 162: 177-197.
36. Grant P.R., Grant B.R. 2006. Evolution of character displacement in Darwin's finches. *Science* 313: 224–226.

37. Green R.E., Krause J., Briggs A.W., Maricic T., Stenzel U., et al. 2010. A Draft Sequence of the Neandertal Genome. *Science* 328: 710-722.
38. Hamidi B., Wallace K., Vasu C., Alekseyenko A.V. 2019. W_d^* -test: robust distance-based multivariate analysis of variance. *Microbiome* 7: 51.
39. Herrel A., Podos J., Huber S.K., Hendry A.P. 2005. Bite performance and morphology in a population of Darwin's finches: implications for the evolution of beak shape. *Functional Ecology* 19: 43-48.
40. Herrel A., Soons J., Aerts P., Dirckx J., Boone M., Jacobs P., Adriaens D., Podos, J. 2010. Adaptation and function of the bills of Darwin's finches: divergence by feeding type and sex. *Emu - Austral Ornithology* 110: 39-47.
41. Hoang D.T., Chernomor O., von Haeseler A., Minh B.Q., Vinh L.S. 2018. UFBoot2: Improving the ultrafast bootstrap approximation. *Mol. Biol. Evol.* 35:518-522.
42. Hughes E.C. Edwards D.P., Thomas G.H. 2022. The homogenization of avian morphological and phylogenetic diversity under the global extinction crisis. *Current Biology* 32: 3830-3837.e3
43. Illera J.C. 2023. DNA extraction using the ammonium acetate.
<https://doi.org/10.17504/protocols.io.knycvfw>.
44. Illera J.C., Rando J.C., Rodriguez-Exposito E., Hernández M., Claramunt S., Martín A. 2018. Acoustic, genetic, and morphological analyses of the Canarian common chaffinch complex *Fringilla coelebs* ssp. reveals cryptic diversification. *J. Avian Biol.* 49: e01885.
45. Illera J.C., Rando J.C., Richardson D.S., Emerson, B.C. 2012. Age, origins and extinctions of the avifauna of Macaronesia: a synthesis of phylogenetic and fossil information. *Quatern. Sci. Rev.* 50: 14-22.
46. Illera J.C., Rando J.C., Melo M., Valente L., Stervander M. 2024. Avian island radiations shed light on the dynamics of adaptive and non-adaptive radiation. *Cold Spring Harbor Perspectives in Biology* 16: a041451.
47. Illera J.C., Richardson D.S., Helm B., Atienza J.C., Emerson B.C. 2008. Phylogenetic relationships, biogeography and speciation in the avian genus *Saxicola*. *Molecular Phylogenetics and Evolution* 48, 1145-1154.
48. Illera J.C., Spurgin L.G., Rodriguez-Exposito E., Nogales M. Rando J.C. 2016. What are we learning about speciation and extinction from the Canary Islands? *Ardeola* 63: 15-33.
49. Jónsson H., Ginolhac A., Schubert, M., Johnson P., Orlando L. 2013. mapDamage 2.0: fast approximate Bayesian estimates of ancient DNA damage parameters. *Bioinformatics* 29:1682-1684.
50. Kalyaanamoorthy S., Minh B., Wong T., von Haeseler A., Jermini L.S. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* 14: 587-589.
51. Kearse M., Moir R., Wilson A., Stones-Havas S., Cheung M., Sturrock S., Buxton S., Cooper A., Markowitz S., Duran C., Thierer T., Ashton B., Meintjes P., Drummond A. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28:1647-1649.

52. Kircher M. 2012. Analysis of high-throughput ancient DNA sequencing data, p. 197–228. In (eds Shapiro, B. and Hofreiter, M. (eds.), *Ancient DNA: Methods and Protocols*. Methods in Molecular Biology, 840. Humana Press.
53. Larrea P., Wijbrans J., Galé C., Ubide T., Lago M., França Z., Widom E. 2014. ⁴⁰Ar/³⁹Ar constraints on the temporal evolution of Graciosa Island, Azores (Portugal). *Bulletin of Volcanology* 76: 796.
54. Li H., Durbin R. 2009. Fast and accurate short read alignment with Burrows Wheeler transform. *Bioinformatics* 25:1754–1760.
55. Li H., Handsaker B., Wysoker A., Fennell T., Ruan J., Homer N., Marth G., Abecasis G., Durbin R., and 1000 Genome project data processing subgroup. 2009. The sequence alignment/map (SAM) format and SAMtools. *Bioinformatics* 25: 2078–2079.
56. Llorente-Culebras S., Carmona C.P., Carvalho W.D., Menegotto A., Molina-Venegas R., Ladle R.J., Santos, A.M.C. 2024. Island biodiversity in peril: Anticipating a loss of mammals' functional diversity with future species extinctions. *Global Change Biology* 30: e17375.
57. Louchart A., Bastian F., Baptista M., Guarino-Vignon P., Hume J.P., Jacot-des-Combes C., Mourer-Chauviré C., Hänni C., Ollivier, M. 2018. Ancient DNA reveals the origins, colonization histories, and evolutionary pathways of two recently extinct species of giant scops owl from Mauritius and Rodrigues Islands (Mascarene Islands, south-western Indian Ocean). *Journal of Biogeography* 45: 2678–2689.
58. Losos J.B., Ricklefs R.E. 2009. Adaptation and diversification on islands. *Nature* 457: 830–836.
59. MacArthur R.H., Wilson E.O. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton.
60. Malinsky M., Matschiner M., Svardal H. 2021. Dsuite – fast D-statistics and related admixture evidence from VCF files. *Molecular Ecology Resources* 21: 584–595.
61. Malinsky M., Svardal H., Tyers A.M., Miska E.A., Genner M.J., Turner, G.F., Durbin R. 2018. Whole genome sequences of Malawi cichlids reveal multiple radiations interconnected by gene flow. *Nature Ecology & Evolution* 2: 1940–1955.
62. Marshall H.D. Baker A.J. 1998. Rates and patterns of mitochondrial DNA sequence evolution in Fringilline finches (*Fringilla* spp.) and the greenfinch (*Carduelis chloris*). *Molecular Biology and Evolution* 15: 638–646.
63. Marshall, H.D., Baker A.J. 1999. Colonization History of Atlantic Island Common Chaffinches (*Fringilla coelebs*) Revealed by Mitochondrial DNA. *Molecular Phylogenetics and Evolution* 11: 201–212.
64. Martin S.H., Dasmahapatra K.K., Nadeau N.J., Salazar C., Walters J.R., Simpson F., Blaxter M., Manica A., Mallet J., Jiggins C.D. 2013. Genome-wide evidence for speciation with gene flow in *Heliconius* butterflies. *Genome Research* 23(11): 1817–1828.
65. Matthews T.J., Triantis K.A., Wayman J.P., Martin T.E., Hume, J.P., Cardoso P., et al. 2024. The global loss of avian functional and phylogenetic diversity from anthropogenic extinctions. *Science* 386: 55–60.

66. McLachlan G., Peel D.A. 2000. *Finite mixture models*. Wiley Series in Probability and Statistics. John Wiley and Sons.
67. Minh B.Q., Schmidt H.A., Chernomor O., Schrempf D., Woodhams M.D., von Haeseler A., Lanfear R. 2020. IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution* 37:1530–1534.
68. Montero K.B., Gillingham M.A.F., Ravinet, M., Illera, J.C. 2025. Host filtering and biogeography structure island bird gut microbiomes. *bioRxiv* 2025.08.20.671302.
69. Moreno, E. 1985. Clave osteológica para la identificación de los Passeriformes Ibéricos. I. *Ardeola* 2: 295–377.
70. Mortensen H.S., Dupont Y.L., Olesen J.M. 2008 A snake in paradise: disturbance of plant reproduction following extirpation of bird flower-visitors on Guam. *Biol. Conserv.* 141: 2146-2154.
71. Mosleh S., Choi G.P.T., Musser G.M., James H.F., Abzhanov A., Mahadevan, L. 2023. Beak morphometry and morphogenesis across avian radiations. *Proc. R. Soc. B.* 290: 20230420.
72. Nunes J.C., Camacho A.G., França Z., Montesinos F.G., Alves M., Vieira R., Vélez E., Ortiz, E. 2006. Gravity anomalies and crustal signature of volcano-tectonic structures of Pico Island (Azores). *Journal of Volcanology and Geothermal Research* 156: 55-70.
73. Olah G., Bover P., Llamas B., Heiniger H., Segura Llanos R., Shimada I. 2026. Ancient DNA and spatial modeling reveal a pre-Inca trans-Andean parrot trade. *Nat. Comms.* 17: 2117.
74. Oswald A., Allen J.M., Witt K.E., Folk R.A., Albury N.A., Steadman D.W., Guralnick R.P. 2019. Ancient DNA from a 2,500-year-old Caribbean fossil places an extinct bird (*Caracara creightoni*) in a phylogenetic context. *Molecular Phylogenetics and Evolution* 140: 106576.
75. Phillips A.G., Töpfer T., Rahbek C., Böhning-Gaese K., Fritz S.A. 2018. Effects of phylogeny and geography on ecomorphological traits in passerine bird clades. *Journal of Biogeography* 45: 2337–2347.
76. Piquet J.C., López-Darias M. 2021. Invasive snake causes massive reduction of all endemic herpetofauna on Gran Canaria. *Proc. R. Soc. B* 288: 20211939.
77. Price T.D., Grant P.R., Gibbs H.L. Boag P.T. 1984. Recurrent patterns of natural selection in a population of Darwin's finches. *Nature* 309: 787–789.
78. Prost S., Klietmann J., van Kolfschoten T., Guralnick R.P. Waltari E., Vrieling K., Stiller M., Nagel D., Rabeder G., Hofreiter, M., Sommer R.S. 2013. Effects of late quaternary climate change on Palearctic shrews. *Glob. Change Biol.* 19: 1865-1874.
79. R Core Team. 2024. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <<https://www.R-project.org/>>.
80. Raftery A.E., Dean N. 2006. Variable Selection for Model-Based Clustering. *Journal of the American Statistical Association* 101: 168-178.
81. Rambaut A., Drummond A.J., Xie D., Baele G., Suchard M.A. 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67: 901-904.

82. Ramírez O., Gómez-Díaz E., Olalde I., Illera J.C. Rando, J.C. González-Solís, J., Lalueza-Fox C. 2013. Population connectivity buffers genetic diversity loss in a seabird. *Frontiers in Zoology* 10: 28.
83. Ramirez O., Illera J.C., Rando J.C., Gonzalez-Solis J., Alcover J.A., Lalueza-Fox C. 2010. Ancient DNA of the Extinct Lava Shearwater (*Puffinus olsoni*) from the Canary Islands Reveals Incipient Differentiation within the *P. puffinus* Complex. *PLoS ONE* 5: e16072.
84. Ramos-Onsins S., Rozas J. 2002. Statistical properties of new neutrality tests against population growth. *Molecular Biology and Evolution* 19: 2092–2100.
85. Rando J.C., Alcover J.A., Olson S.L., Pieper H. 2013. A new species of extinct scops owl (Aves: Strigiformes: Strigidae: *Otus*) from São Miguel Island (archipelago of Azores, North Atlantic Ocean). *Zootaxa* 3647: 343–357.
86. Rando J., Pieper H., Olson S.L. Pereira F., Alcover J. 2017. A new extinct species of large bullfinch (Aves: Fringillidae: *Pyrrhula*) from Graciosa Island (Azores, North Atlantic Ocean). *Zootaxa* 4282: 567–583.
87. Rando J.C., Alcover J.A., Pieper H., Olson S.L., Hernández C.N., López-Jurado L.F. 2020. Unforeseen diversity of quails (Galliformes: Phasianidae: Coturnix) in oceanic islands provided by the fossil record of Macaronesia. *Zoological Journal of the Linnean Society* 188: 1296–1317.
88. Rando J.C., Pieper H., Pereira F., Torres-Roig E., Alcover J.A. 2024. Petrel extinction in Macaronesia (North-East Atlantic Ocean): the case of the genus *Pterodroma* (Aves: Procellariiformes: Procellariidae). *Zoological Journal of the Linnean Society* 202: zlae123.
89. Raup D.M. 1991. *Extinction: Bad Genes or Bad Luck?* W.W. Norton, New York.
90. Raposeiro P.M., Hernández A., Pla-Rabes S., Gonçalves V., Bao R., Sáez A. et al. 2021. Climate Change Facilitated the Early Colonization of the Azores Archipelago during Medieval Times. *Proc. Natl. Acad. Sci. U.S.A.* 118: e2108236118.
91. Raposeiro P.M., Hernández A., Pla-Rabes S., Gonçalves V., Bao R., Sáez, A. et al. 2022. Reply to Elias Et Al.: Multiproxy Evidence of Widespread Landscape Disturbance in Multiple Azorean Lakes before the Portuguese Arrival. *Proc. Natl. Acad. Sci. U.S.A.* 119: e2120107119.
92. Rawlence N.J., Verry A.J.F., Cole T.L., Shepherd L.D., Tennyson A.J.D., Williams M., Wood J.R., Mitchell K.J. 2024. Ancient mitogenomes reveal evidence for the Late Miocene dispersal of mergansers to the Southern Hemisphere. *Zoological Journal of the Linnean Society* 202: zlae040.
93. Recuerda M., Illera J.C., Blanco G., Zardoya R., Milá B. 2021. Sequential Colonization of Oceanic Archipelagos Led to a Species-Level Radiation in the Common Chaffinch Complex (Aves: *Fringilla Coelebs*). *Molecular Phylogenetics and Evolution* 164: 107291.
94. Renom P., de-Dios T., Civit S., Llovera L., Sánchez-Gracia A., Lizano E., Rando J.C., Marguès-Bonet T., Kergoat G.J., Casanovas-Vilar I., Lalueza-Fox C. 2021. Genetic data from the extinct giant rat from Tenerife (Canary Islands) points to a recent divergence from mainland relatives. *Biol. Lett.* 17: 20210533.
95. Reimer P., Austin, W., Bard E., Bayliss A., Blackwell P., Bronk Ramsey C., Butzin M., Cheng H., Edwards R., Friedrich M., Grootes P., Guilderson T., Hajdas I., Heaton T., Hogg A., Hughen K., Kromer B.,

- Manning S., Muscheler R., Palmer J., Pearson C., van der Plicht J., Reimer R., Richards D., Scott E., Southon J., Turney C., Wacker L., Adolphi F., Büntgen U., Capano M., Fahrni S., Fogtmann-Schulz A., Friedrich R., Köhler P., Kudsk S., Miyake F., Olsen J., Reinig F., Sakamoto M., Sookdeo, A., Talamo S. 2020. The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon* 62:725-757.
96. Rodrigues P., Lopes R.J., Reis S., Resendes R., Ramos J.A., Tristão da Cunha R. 2014. Genetic diversity and morphological variation of the common chaffinch *Fringilla coelebs* in the Azores. *Journal of Avian Biology* 45: 167-178.
 97. Rogers A.R. 2015. Bias in estimators of archaic admixture. *Theoretical Population Biology* 100: 63–78.
 98. Rogers H.S., Buhle E.R., HilleRisLambers J., Fricke E.C., Miller R.H., Tewksbury J.J. 2017. Effects of an invasive predator cascade to plants via mutualism disruption. *Nat. Commun.* 8: 14557.
 99. Ronquist F., Teslenko M., van der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu L., Suchard M.A., Huelsenbeck J.P. 2012. MrBayes 3.2: efficient bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542
 100. Rozas J., Ferrer-Mata A., Sánchez-DelBarrio J.C., Guirao-Rico S., Librado P., Ramos-Onsins S.E., Sánchez-Gracia, A. 2017. DnaSP 6: DNA Sequence Polymorphism Analysis of Large Datasets. *Mol. Biol. Evol.* 34: 3299-3302.
 101. Rozzi R., Lomolino M.V., Van Der Geer A.A.E., Silvestro D., Lyons S.K., Bover P. et al. 2023. Dwarfism and gigantism drive human-mediated extinctions on islands. *Science*, 379: 1054-1059.
 102. Rull V. 2023. Settlement and anthropization of the Azores Islands. *Journal of Biogeography* 50, 2008–2011.
 103. Rull V., Connor S. E. Elias R.B. 2017. Potential natural vegetation and pre-anthropogenic pollen records on the Azores Islands in a Macaronesian context. *Journal of Biogeography* 44: 2437–2440.
 104. Russel J. 2025. MicEco: Various functions for microbial community data. R package version 0.9.19, commit 91f8e6f5d67e0bfd018dc3b46da3994b1eadeb46, <<https://github.com/Russel88/MicEco>>.
 105. Sayol F., Cooke R.S., Pigot A.L., Blackburn T.M., Tobias J., Steinbauer M.J., Antonelli A., Faurby S. 2021. Loss of functional diversity through anthropogenic extinctions of island birds is not offset by biotic invasions. *Science Advances* 7: eabj5790.
 106. Sayol F., Steinbauer M.J., Blackburn T.M., Antonelli A., Faurby S. 2020. Anthropogenic extinctions conceal widespread evolution of flightlessness in birds. *Science Advances* 6: eabb6095.
 107. Sayol F., Wayman J.P., Dufour P., Martin T.E., Hume J.P., Jørgensen M.W., Martínez-Rubio, N., Sanglas A., Soares F.C., Cooke R., Mendenhall C.D., Margolis J.R., Illera J.C., Lemoine R., Benavides E., Lapiedra O., Triantis K.A., Pigot A.L., Tobias J.A., Faurby S., Matthews T.J. 2024. AVOTREX: A Global Dataset of Extinct Birds and Their Traits. *Global Ecol Biogeogr.* 33: e13927.
 108. Schluter D. 1988. Character displacement and the adaptive divergence of finches on islands and continents. *The American Naturalist* 131: 800–824.

109. Scrucca L., Fop M., Murphy T.B., Raftery A.E. 2016. Mclust 5: clustering, classification and density estimation using Gaussian finite mixture models. *The R Journal* 8: 289-317.
110. Scrucca L., Raftery, A.E. 2018. Clustvarsel: A Package Implementing Variable Selection for Gaussian Model-based Clustering in R. *Journal of Statistical Software* 84: 1-28.
111. Sendell-Price A.T., Ruegg K.C., Clegg, S.M. 2020. Rapid morphological divergence following a human-mediated introduction: the role of drift and directional selection. *Heredity* 124: 535–549.
112. Sibrant A.L.R., Marques F.O., Hildenbrand, A. 2014. Construction and destruction of a volcanic island developed inside an oceanic rift: Graciosa Island, Terceira Rift, Azores. *Journal of Volcanology and Geothermal Research* 284: 32-45.
113. Smith F.A., Smith R.E.E., Lyons S.K., Payne, J.L. 2018. Body size downgrading of mammals over the late Quaternary. *Science* 360: 310-313.
114. Souilmi Y., Wasef,S., Williams M.P. Conroy G., Bar I., et al. 2024. Ancient genomes reveal over two thousand years of dingo population structure. *Proc. Natl. Acad. Sci. U.S.A.* 121: e2407584121.
115. Steadman D.W. 2006. *Extinction & biogeography of tropical Pacific birds*. University of Chicago Press, Chicago.
116. Szabo J.K., Khwaja N., Garnett S.T., Butchart S.H.M. 2012. Global Patterns and Drivers of Avian Extinctions at the Species and Subspecies Level. *PLoS ONE* 7: e47080.
117. Tajima F. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics* 123, 585–595.
118. Tajima F. 1996. The amount of DNA polymorphism maintained in a finite population when the neutral mutation rate varies among sites. *Genetics* 143: 1457–1465.
119. Terzopoulou S., Rigal F., Whittaker R.J., Borges P.A.V., Triantis, K.A. 2015. Drivers of extinction: the case of Azorean beetles. *Biology Letters* 11: 20150273.
120. Triantis K.A., Rigal F., Whittaker R.J., Hume J.P., Sheard C., Poursanidis D., Rolland J., Sfenthourakis S., Matthews T.J., Thébaud C., Tobias J.A. 2022. Deterministic assembly and anthropogenic extinctions drive convergence of island bird communities. *Global Ecology and Biogeography* 31: 1741–1755.
121. Ujhelyi P. 1992. Identification of the Fringillidae of Europe on the basis of craniometric characteristics. *Aquila* 99: 99–110.
122. Valente L., Illera J.C., Havenstein K., Pallien T., Etienne R.S., Tiedemann R. 2017. Equilibrium Bird Species Diversity in Atlantic Islands. *Current Biology* 27: 1660-1666.
123. Valente L., Phillimore A.B., Melo M., Warre, B.H., Clegg S.M., Havenstein K., Tiedemann R., Illera J.C., Thébaud C., Aschenbach T. & Etienne R.S. 2020. A simple dynamic model explains island bird diversity worldwide. *Nature* 579: 92–96.
124. van Grouw H., Natural History Museum Genome Acquisition Lab, Darwin Tree of Life Barcoding collective et al. 2024. The genome sequence of the chaffinch, *Fringilla coelebs* Linnaeus, 1758 [version 1; peer review: 3 approved, 2 approved with reservations]. *Wellcome Open Res.* 9: 207.

125. Whittaker R. J., Fernández-Palacios, J.M., & Matthews, T.J. (2023). *Island biogeography: Geo-environmental dynamics, ecology, evolution, human impact, and conservation*. Oxford University Press.
126. Wiens, J.J., Saban, K.E. 2025. Recent extinctions of plant and animal genera are rare, localized, and decelerated. *PloS Biology* 23: e3003356.
127. Xia X. 2017. DAMBE6: new tools for microbial genetics, phylogenetics and molecular evolution. *Journal of Heredity* 108: 431–437.

Figures

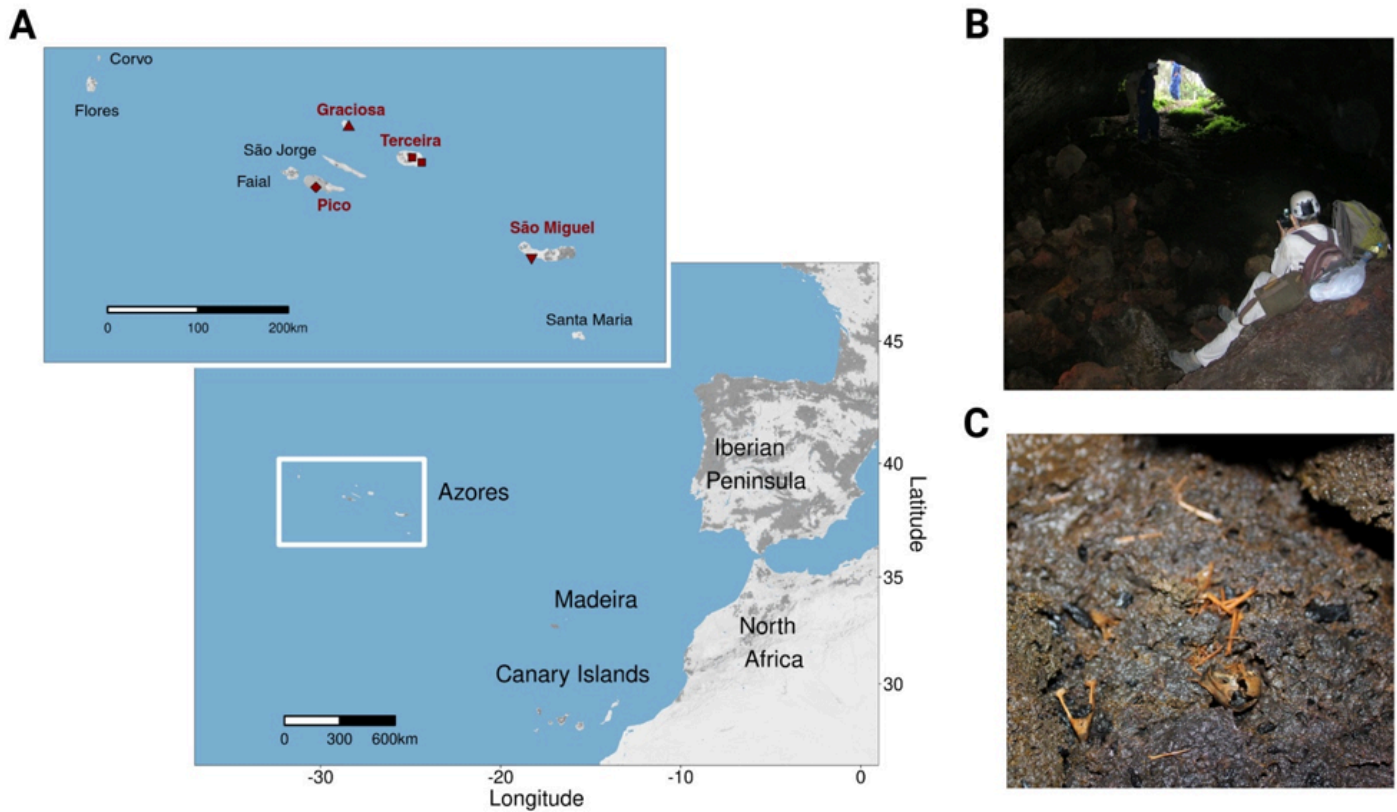


Figure 1

Map of the Azores archipelago. A) Islands (and localities) where *Fringilla* fossil remains have been recovered are highlighted in red. B) View of Furna do Calcinhas (Graciosa). C) *Fringilla* fossil remains from Furna das Cabras (Pico).

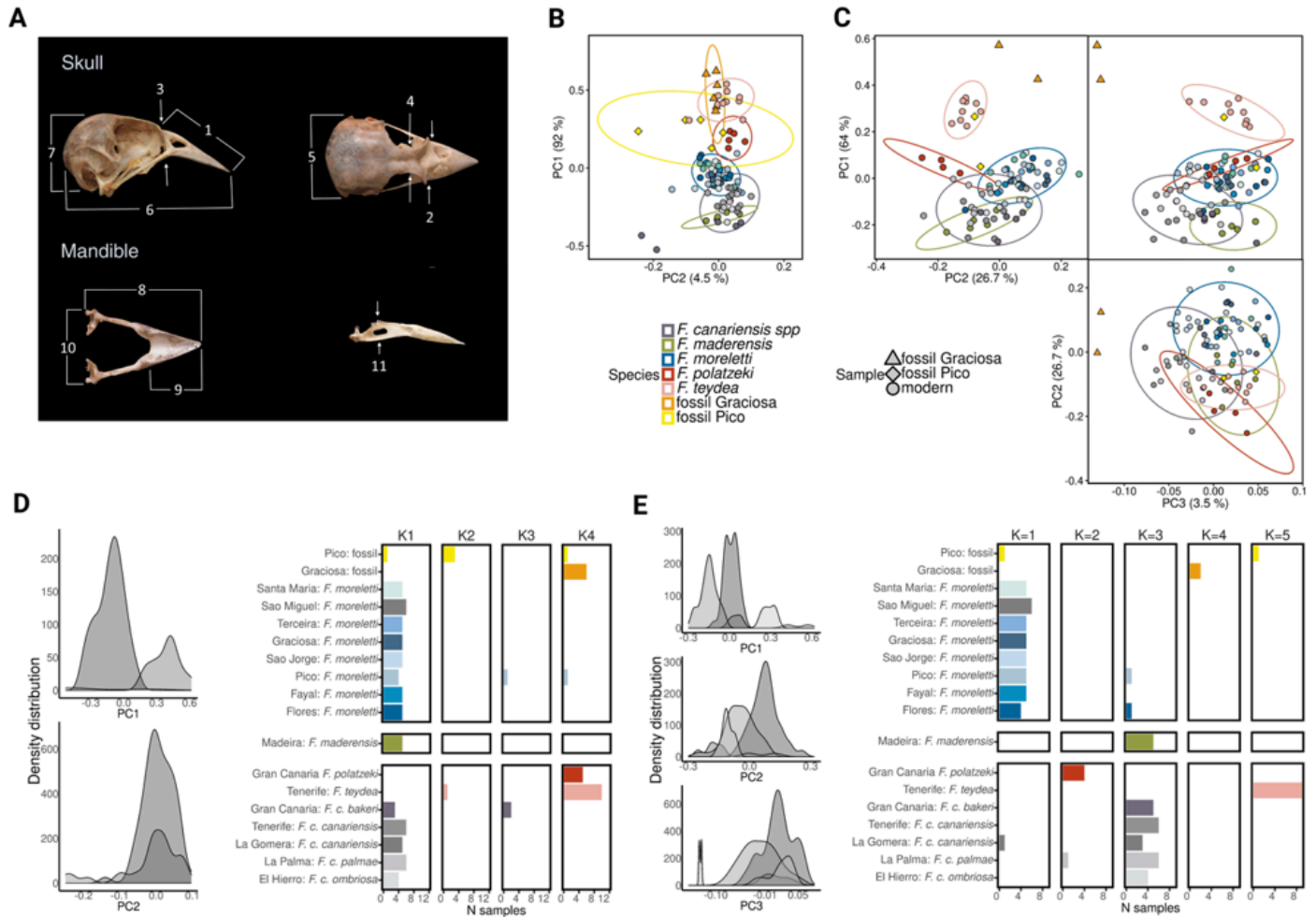


Figure 2

Morphological variation and assignment of morphological groups in *Fringilla* modern and fossil specimens from Macaronesia. **A**) Schematic illustration of measured cranial elements: (1) Maxilla length; (2) Maxilla width; (3) Maxilla height; (4) Interorbital width; (5) Cranium width; (6) Cranium length; (7) Cranium height; (8) Mandible length; (9) Symphysis length; (10) Articular end width; (11) Mandible height. **B**) PCA of mandible measurements showing PC1-PC2 (retained for NMM analysis). **C**) PCA of skull measurements showing PC1, PC2, and PC3 (retained for NMM analysis). In B and C, points represent individual specimens coloured by island of origin and sample type; symbols indicate modern specimens, diamonds indicate Pico fossils, and triangles indicate Graciosa fossils; ellipses show 95% confidence regions for each island/fossil group. **D**) NMM results for the mandible dataset. Left: probability density distributions for three morphological groups (K1-K4). Right: number of specimens from each island assigned to each morphological group. **E**) NMM results for skull dataset showing distributions and assignments for five morphological groups (K1-K5). The best-supported models

identified three distinct morphological groups for mandible measurements (BIC = 302.65) and five groups for skull measurements (BIC = 598.79).

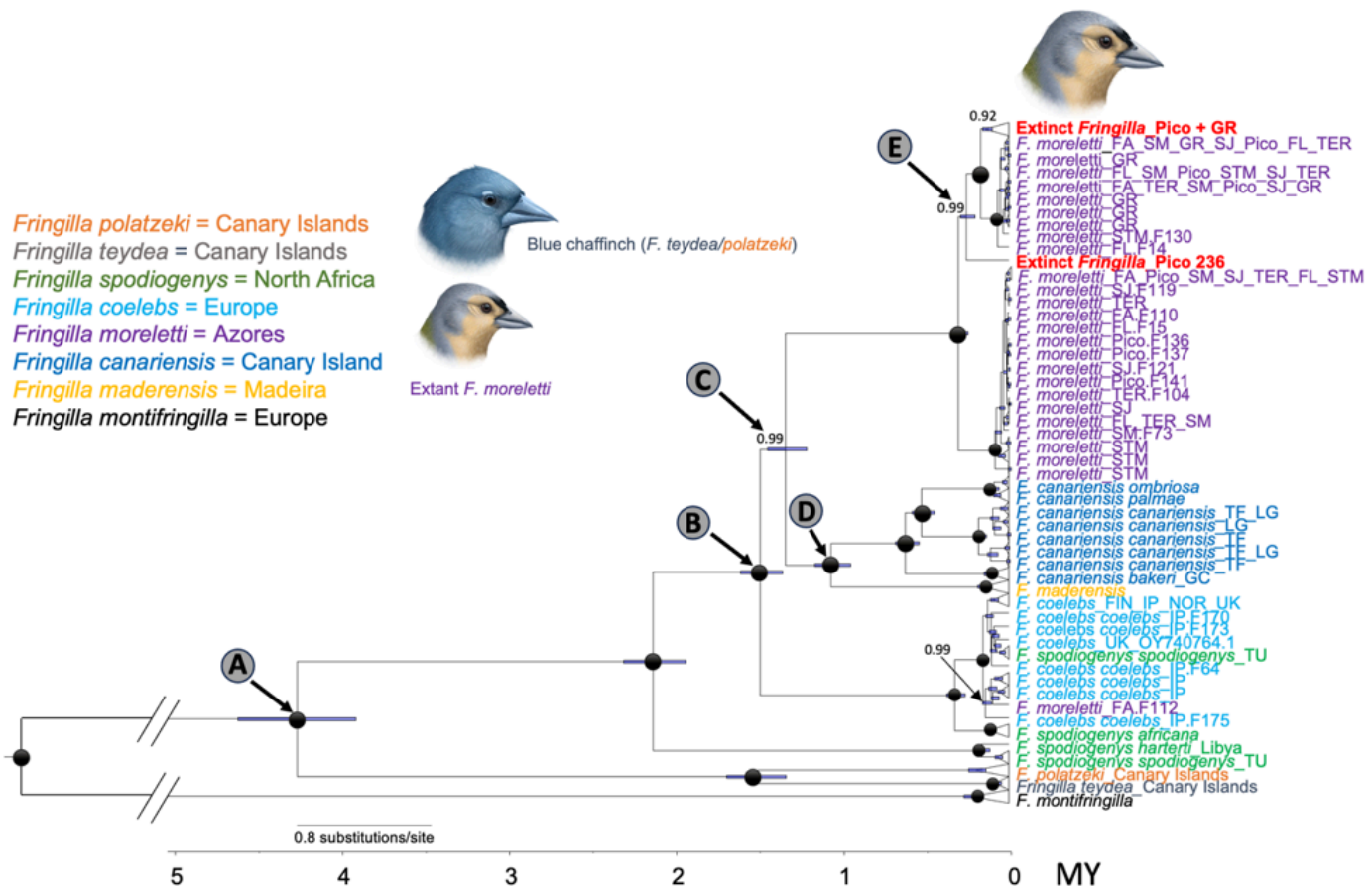


Figure 3

Dated ultrametric tree depicting the phylogenetic relationships within the genus *Fringilla*, inferred using BEAST2. All fossil individuals recovered from Pico and Graciosa (red) cluster within the *F. moreletti* clade. Filled circles (●) indicate nodes with posterior probabilities of 1.0. Concordant topologies were recovered by Bayesian (*MrBayes*) and maximum-likelihood (*IQ-TREE2*) analyses (Fig. S5). Bars represent the 95% highest posterior density (HPD) intervals for node ages. The timescale is shown in millions of years (MY). One Azorean individual (F112) clustered within the European common chaffinch clade. Letters indicate the principal nodes discussed in the text.

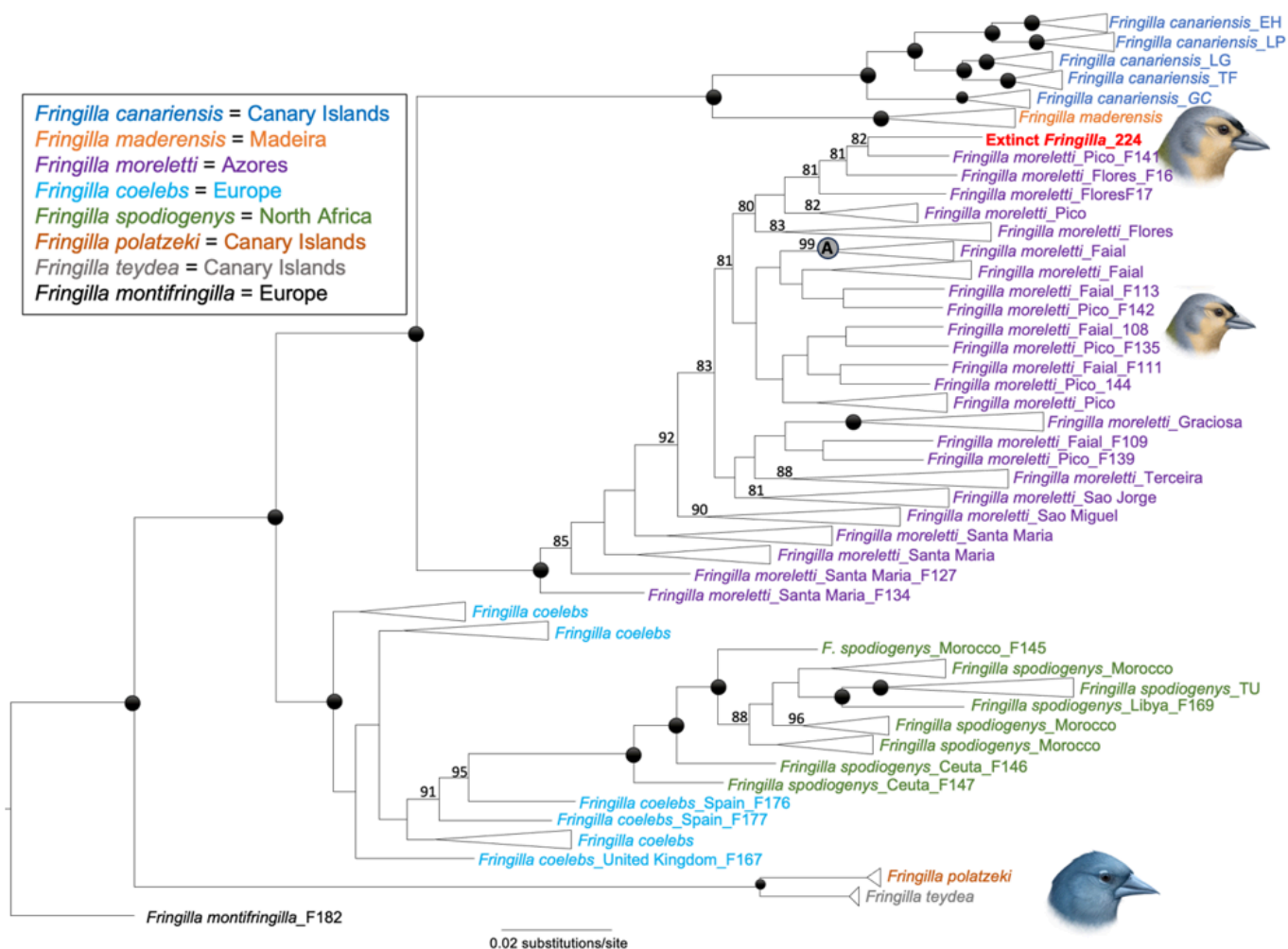


Figure 4

Maximum-likelihood (ML) phylogenetic inference based on whole nuclear genomes of modern and fossil *Fringilla*. The extinct individual 224 clustered within the *F. moreletti* clade. Filled circles (●) indicate nodes with ML bootstrap support of 100%, whereas numbers denote bootstrap values $\geq 80\%$. Node A includes individual F112 (see Fig. 3). EH: El Hierro (*Fringilla canariensis ombriosa*); LP: La Palma (*F. c. palmae*); LG: La Gomera (*F. c. canariensis*); TF: Tenerife (*F. c. canariensis*); GC: Gran Canaria (*F. c. bakeri*); TU: Tunisia. The illustrations, from top to bottom, depict the extinct giant morphotype of *F. moreletti*, the extant morphotype of *F. moreletti*, and the blue chaffinches (*F. teydea/polatzeki*).

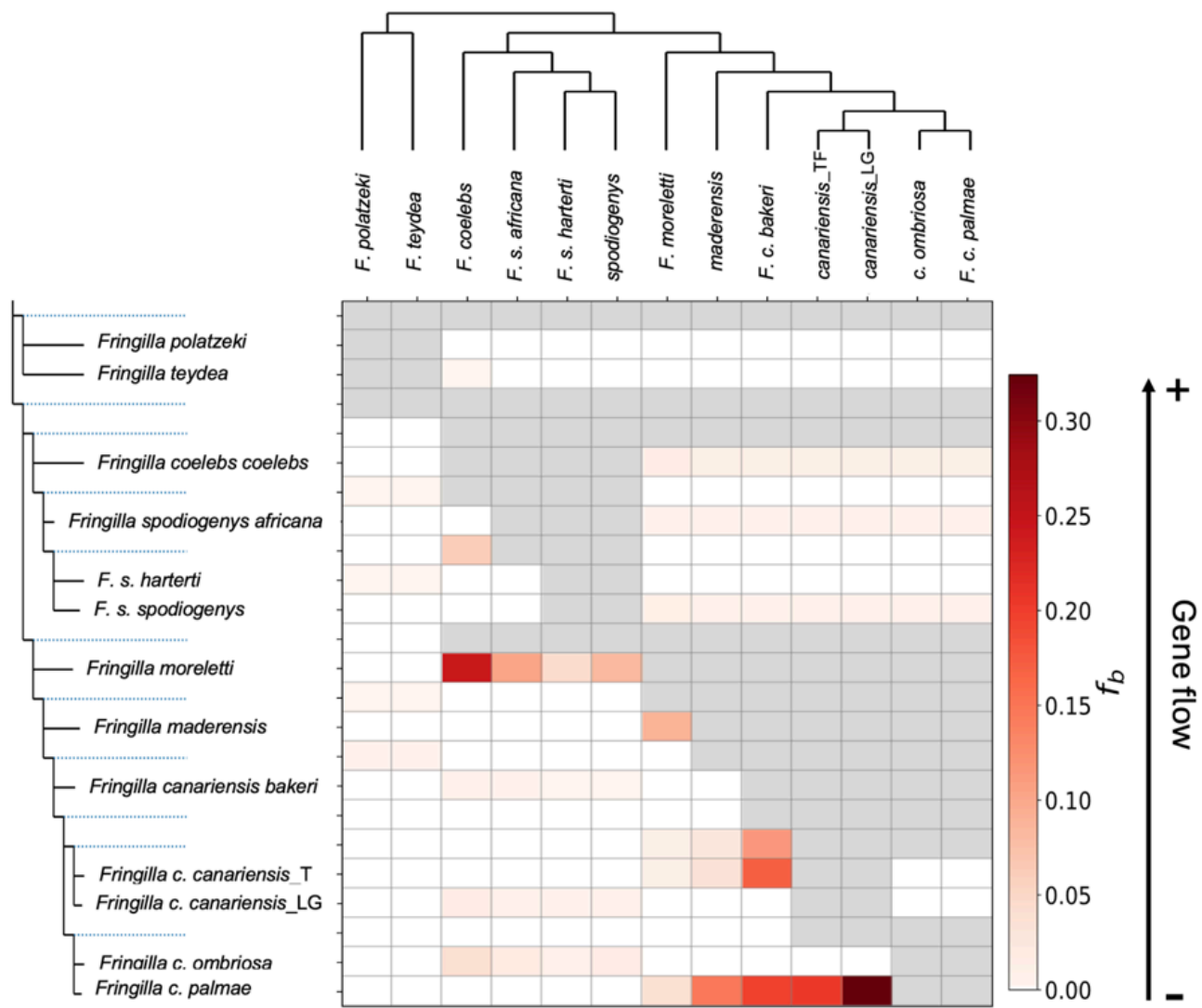


Figure 5

f -branch statistics computed based on the simplified nuclear phylogeny (Fig. 4) to assess signatures of gene flow among *Fringilla* lineages. Each cell in the matrix represents the f -branch statistic, which quantifies excess allele sharing between lineages where branches on the y axis (left) share excess alleles with species on the x axis (top) relative to their closest sister. Warm coloured cells indicate tests with significant f -branch scores where darker colours denote stronger signals. White cells indicate tests with non-significant f -branch score, whereas grey cells indicate tests that are not applicable in the given tree. Blue dashed lines denote the internal branches of the tree taken as the inferred ancestral populations predating the divergence of the descendant species or populations.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryMaterialBMCBiology.docx](#)