Age, origins and extinctions of the avifauna of Macaronesia: a synthesis of phylogenetic and fossil information

Juan Carlos Illera [a,b,*], Juan Carlos Rando [c], David S. Richardson [d], Brent C. Emerson [b,d]

[a] Research Unit of Biodiversity (UO-CSIC-PA), Oviedo University, Campus of Mieres, Research Building, 5th Floor, C/Gonzalo Gutiérrez Quirós s/n, 33600 Mieres, Asturias, Spain
[b] Island Ecology and Evolution Research Group, IPNA, CSIC, 38206 La Laguna, Tenerife, Canary Islands, Spain
[c] Department of Animal Biology (Zoology), University of La Laguna, 38206 La Laguna, Tenerife, Canary Islands, Spain
[d] Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich Research Park, Norwich NR4 7TJ, UK

ARTICLE INFO

ABSTRACT

Understanding the age, origins and extinction of oceanic island biota has captivated the interest of evolutionary biologists since Darwin and Wallace. Because oceanic islands are discrete entities of small geographical size but with considerable habitat diversity, they provide ideal templates within which to study evolutionary processes. The peripheral North Atlantic islands, collectively referred to as Macaronesia, are considered a hot spot of biodiversity due to the fact that they contain a large proportion of endemic taxa (ca 25%). Recent molecular studies are providing insight into the patterns of colonization and radiation within the extant avifauna, while paleontological studies have described many extinct avian species, sometimes identifying the causes and chronology of extinction. The aim of this review is to develop an understanding of the evolutionary and biogeographic history of the macaronesian avifauna, combining information from phylogenetic and paleontological studies. We then compare patterns for Macaronesia with those of other oceanic archipelagos to evaluate to what extent patterns may be generalised across regions. Phylogenetic analyses have confirmed the close relationships between endemic macaronesian avifauna and the closest mainland areas (Europe and Africa), however, in contrast to other archipelagos of a similar age, we show that most extant birds appear to have colonized macaronesian archipelagos relatively recently, within the last four million years, despite some islands being approximately 30 million years old. Fossil records support the idea that higher species richness previously existed, with recent dating on bone collagen of selected extinct species suggesting that their extinction coincided with the arrival of aboriginal people ca 2500 years ago in the Canary Islands, or the arrival of Europeans across all the macaronesian islands in the 14th century. It is plausible that these human mediated extinctions may have selectively acted upon older lineages, but there is little evidence available to evaluate this.

1. Introduction

Investigating the origin and diversification of oceanic island biotas has been a key focus of biogeography, evolutionary biology and conservation biology (MacArthur and Wilson, 1967; Emerson and Kolm, 2005; Filardi and Moyle, 2005; Savolainen et al., 2006; Steadman, 2006; Grant and Grant, 2008; Ricklefs, 2010a). During the last two decades, the use of molecular markers has provided new insights into the evolutionary histories of a great many taxa, and the resulting conclusions have often challenged biogeographic and evolutionary ideas based on classical taxonomy (e.g. Raxworthy et al., 2002; Jordal et al., 2004; Glor et al., 2005; Macias-Hernandez et al., 2008). Phylogeographic syntheses may provide a framework for a general understanding of colonization and diversification within the biotas of archipelagos with different physical and ecological conditions such as age, latitude, altitude and distance to mainland (Ricklefs, 2010a,b). The reconstruction of ancestral distributions and hypotheses about the diversification of taxa have typically used data from extant species, as comprehensive paleontological information on a regional scale is often unavailable. However such analyses may result in biased interpretations if now extinct species are a non-random subset of species, and/or are informative with regard to complex ecological interactions and diversification within a community.

* Corresponding author. Research Unit of Biodiversity (UO-CSIC-PA), Oviedo University, Campus of Mieres, Research Building, Fifth Floor, C/Gonzalo Gutiérrez Quirós s/n, 33600 Mieres, Asturias, Spain. Tel.: +34 985458132.
E-mail address: illerajuan@uniovi.es (J.C. Illera).

Multidisciplinary approaches incorporating information from geology, archaeology, palaeontology and genetics could minimize these limitations and potential biases (Crisci et al., 2003).

Recently, taxa of the North Atlantic Macaronesian islands have become a focus for molecular studies of colonization and diversification of oceanic biotas. Many of these studies have focused on groups of organisms with high rates of diversification such as plants, invertebrates and reptiles (Juan et al., 2000; Emerson, 2002, 2003; Kim et al., 2008). Macaronesian birds exhibit a significant number of endemic species and subspecies (Stattersfield et al., 1998; Martín and Lorenzo, 2001), but have only more recently become the subject of phylogeographic study. These studies have revealed diverse evolutionary histories within species, or species complexes, including strong genetic differentiation between islands (Pestano et al., 2000; Dietzen et al., 2003; Kvist et al., 2005; Päckert et al., 2006), incipient differentiation and contemporary gene flow (Hille et al., 2003; Illera et al., 2007; Barrientos et al., 2008; Spurgin et al., 2011) and reverse colonization (Illera et al., 2011). However, the extent to which the overall macaronesian avifauna is the result of ancient or recent colonization and diversification events has not yet been addressed. In light of recent phylogenetic analyses of macaronesian terrestrial taxa such as insects and plants, we may expect to find both old and young evolutionary lineages (e.g. Emerson, 2008; Aigoin et al., 2009). Even though the avian radiation in the region is less spectacular than in other archipelagos such as those of the Pacific and Indian Oceans that does not necessarily mean that extant lineages are themselves young. In addition to molecular phylogenetic and phylogeographic data, fossil data may provide complementary insight into the evolutionary history and community composition of the avifauna of a region. Recent radiocarbon dating on bone collagen of extinct taxa is generating more rigorous approximations of species extinction dates and thus allowing us to better infer the causes of such extinctions. Fossil data can also contribute to a broader understanding of historical faunas and community composition, providing indirect inferences about past environments and ecological interactions.

The aim of this review is to develop a general understanding of the evolutionary and biogeographic history of the macaronesian avifauna by synthesising information from phylogenetic, phylogeographic and paleontological studies that yield information on colonization, diversification and extinction within this group. We then compare patterns for Macaronesia with those of other oceanic archipelagos to evaluate to what extent patterns may be generalised across regions, but also to identify knowledge gaps that should be the focus of future research.

2. Macaronesia

The macaronesian region consists at 31 principal volcanic islands in the north eastern Atlantic Ocean with floral and faunal affinities to the African and European mainland (Juan et al., 2000; Gillespie and Clague, 2009). The islands are grouped into five archipelagos (Azores, Madeira, Selvagens, Canary Islands and Cape Verde) situated between 39°N 31°W and 15°N 23°W (Fig. 1). The broad range of distances between archipelagos and the mainland (<100 km for the Canary Islands and 1365 km for Azores), latitude, variation of geological ages (0.25—29 million years) and altitudes (130—3700 m, above sea level) on each island (Hazevoet, 1995; Geldmacher et al., 2001; Azevedo and Ferreira, 2006) result in a broad array of ecological conditions. The region is characterised by high habitat diversity with xerophytic shrublands, pine and laurel forests, lagoons and alpine habitats (Gillespie and Clague, 2009). This habitat diversity is considered to have contributed to the evolution of a rich endemic biota, with 23% of terrestrial taxa being endemic to the region (Izquierdo et al., 2004; Arechavaleta et al., 2005; Borges et al., 2008, 2010).

The degree of geographic isolation of each archipelago and the differing levels of vagility would seem to explain the geographical distribution of vertebrates across Macaronesia. Native bats and birds are distributed throughout the region. However, the colonization history of relatively poor dispersers, such as reptiles and non-volant mammals, appears to be determined by the isolation of each archipelago or island. For example, native reptiles are absent from Azores, the most isolated archipelago, while non-volant mammals have colonized only the eastern and central Canary Islands, closest to mainland Africa.

3. Species origin: radiation *versus* multiple colonization

3.1. Geographic origins

The taxonomic affinities of native bird species suggest that the origin of the extant terrestrial macaronesian avifauna is largely from the closest Palaearctic mainland areas, although the Cape Verde archipelago, due to its much lower latitude and proximity to Africa, contains species related to the semi-arid African mainland region (Hazevoet, 1995; Martín and Lorenzo, 2001; Clarke et al., 2006). Recent phylogenetic analyses have confirmed the close relationships between endemic macaronesian avifauna and Palaearctic taxa (S-Table 1). Although these affinities are similar for other terrestrial vertebrate groups such as reptiles and mammals (Carranza et al., 2002, 2008; Juste et al., 2004; Dubey et al., 2008; Cox et al., 2010), they contrast with, for example, one Azorean native damselfly (*Ischnura hastata*), known only from North America and Caribbean Islands (Belle and van Tol, 1990; Cordero Rivera et al., 2005), and some elements of the macaronesian flora that exhibits some rare affinities with East Africa, India, South America and Australia (see Juan et al., 2000 for a review). Given the geographic proximity and similar environments of the macaronesian islands to Europe and Africa, it is perhaps not surprising that the macaronesian avifauna is largely derived from the western Palaearctic. Other factors such as wind-mediated dispersal have been invoked to explain the colonization origins (Juan et al., 2000). Prevailing northeastern or northwestern trade winds may explain observed north to south colonization patterns, while easterly winds from the Sahara, more common in the closest islands to the African continent, would facilitate colonisations from east to west and from south to north (Illera et al., 2007). Thus it seems that proximity to Europe and Africa, environmental similarity and wind patterns seem to be the most likely factors explaining the Palaearctic origin of the macaronesian land birds. However, the absence of elements from other regions is striking since every year the macaronesian archipelagos receive many North American, Asian and Sub-Saharan African migrants (Martín and Lorenzo, 2001; Clarke et al., 2006). It is possible that the number of migrants arriving from more remote landmasses is too low to establish successful populations, or maybe they are competitively inferior with the native species. Future research on the number and size of migrant flocks, and the niche breadth of migrant species, may shed light on this issue.

While it is clear that much of the macaronesian terrestrial avifauna has a Palaearctic origin (S-Table 1), deducing the specific origins of species within the Palaearctic region is not easy. Such deductions are complicated by the often broad Palaearctic distributions that many of the species related to macaronesian taxa have, and the complex colonisation pathways, involving more than one colonization event, reverse colonization, speciation and extinction, that may occur (Emerson, 2002).
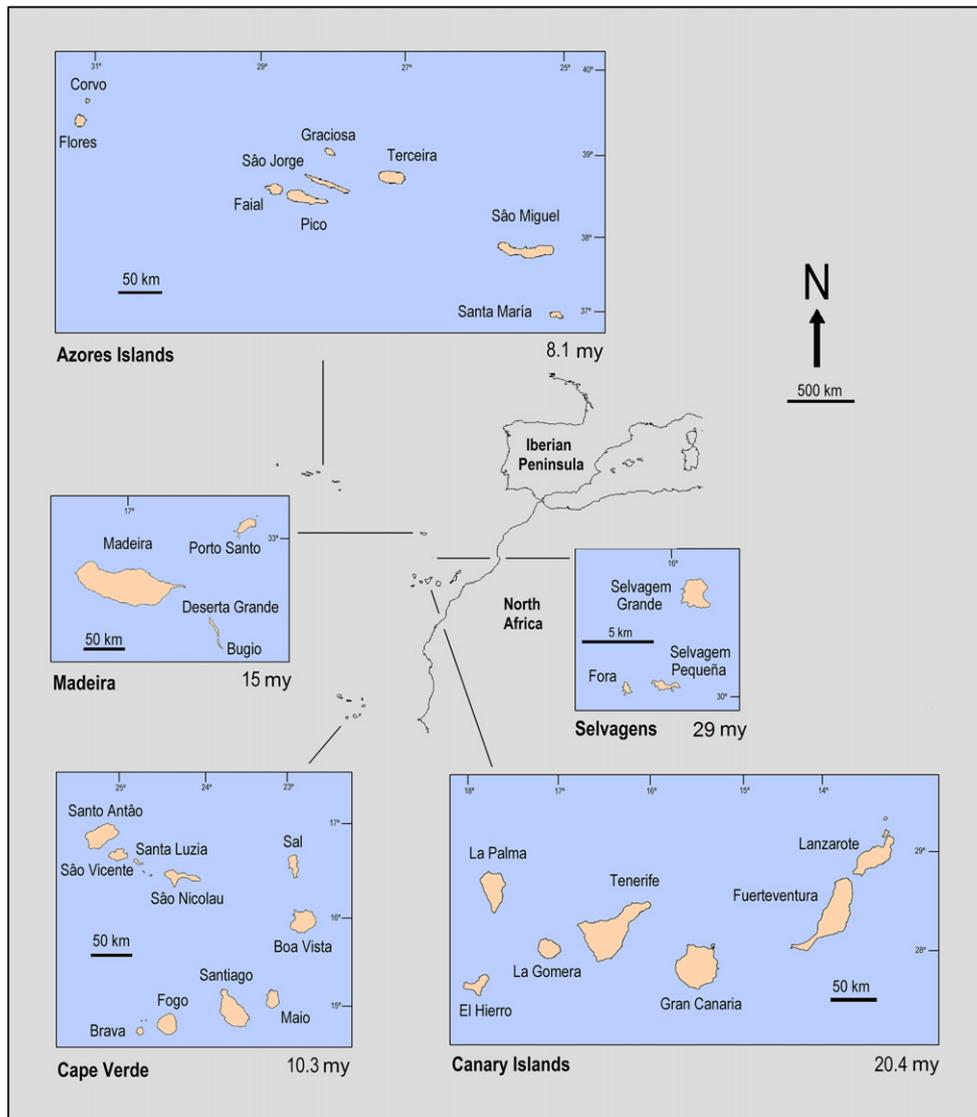
Fig. 1. Map of Macaronesia with archipelagos in boxes. The maximum geological age estimated per archipelago is presented below each box.

3.2. Evolutionary history: isolation and gene flow

During the last two decades a plethora of molecular studies including macaronesian avifauna has been published. Such studies have proven very useful for characterising the evolutionary history and, in some cases, deducing arrival dates, of macaronesian taxa (e.g. Helbig et al., 1996; Marshall and Baker, 1998; Arnaiz-Villena et al., 1999; Voelker, 1999; Groombridge et al., 2002; Gómez-Díaz et al., 2006; Illera et al., 2008a; Olsson et al., 2010). Phylogeographic approaches have tackled regional questions such as geographic origins, colonization pathways, times of colonization, gene flow between islands, and diversification in Macaronesia (e.g. Marshall and Baker, 1999; Idaghdour et al., 2004; Päckert et al., 2006; Friesen et al., 2007; Illera et al., 2007, 2011). Intriguingly, results have, at times, been counter-intuitive, with cases involving complex colonisation histories. For example populations of both *Regulus* spp. and *Erithacus rubecula* appear to represent multiple independent colonization events from the continent, rather than a single origin with subsequent colonisation of neighbouring islands (Dietzen et al., 2003; Päckert et al., 2006). There is little in the way of commonality across different bird species, with

heterogeneous results including strong genetic differentiation among islands and archipelagos, but also species exhibiting more recent colonization events and/or high rates of contemporary gene flow. The role of macaronesian palaeo-islands as stepping-stones and repositories of extant biotas has been evaluated recently (Fernández-Palacios et al., 2011), however, in contrast to taxa such as the planktonic gastropod *Tectarius striatus* (van den Broeck et al., 2008) and the endemic terrestrial moss *Hedenasiastrum percurrens* (Aigoin et al., 2009) all avian lineages studied hitherto are very much younger than the geologically oldest extant islands (Table 1 and S-Table 2, see below).

The radiation of a single ancestral species into multiple descendant species is a complex process influenced by factors such as ecology, geology, genetics, and historical contingency (Sol et al., 2005; Ricklefs and Bermingham, 2007; Blount et al., 2008; Gavrilets and Losos, 2009). Despite their relative isolation and range of ages and habitats, the macaronesian archipelagos harbour relatively few endemic birds (17% of species are endemic, and there is no endemic genus) (Stattersfield et al., 1998; Clarke et al., 2006). This contrasts with the higher levels of endemism observed in other oceanic archipelagos, such as the Lesser Antilles (43% and 27%, endemic

Table 1

Characteristics of the five macaronesian and five other oceanic archipelagos. Number of genera and species (extant native and endemic, extinct native and endemic) per archipelago (and overall in Macaronesia) is shown, including only upper Pleistocene-Holocene and historical extinct birds. Age is the maximum oldest radiometric ages in millions of years (youngest-oldest islands). A: Africa; E: Europe; SA: South America; AU: Australia; NA: North America. G. Guinea: islands of the Gulf of Guinea (except Bioko). Geological data was obtained from Lee et al. (1994), Geldmacher et al. (2001). Carracedo and Day (2002), Azevedo and Ferreira (2006), Ricklefs and Bermingham (2007) and Dyhr and Holm (2010). Physical features obtained from Stattersfield et al. (1998), Ricklefs and Bermingham (2007), Borges et al. (2008), Gillespie and Clague (2009). Bird information obtained from Pieper (1985), Olson and den Hartog (1990), Boessneck and Kinzelbach (1993), Martín and Lorenzo (2001), Arechavaleta et al. (2005), Jones and Tye (2006), Steadman (2006), Ricklefs and Bermingham (2007), Borges et al. (2008, 2010), Boyer (2008), Tyrberg (2009), and Iwanuit et al. (2009).

Characteristics	Azores	Madeira	Selvagens	Canary Islands	Cape Verde	Macaronesia	Lesser Antilles	Vanuatu	Galápagos	Hawaii	G. Guinea
N° Islands	9	2[a]	2	8[a]	10	31	21	65[a]	13	8	3
Area (km²)	2387	785	2.73	7447	4020	14,586	6300	12,200	8000	16,300	1013
Age (my)	0.25–8.12	0.7–14	24.2–29.5	1.2–22	1–22	0.25–29.5	20	20	3.3	5.1	31
Maximum altitude (m)	2381	1810	0.153	3718	2829	3718	1500	1879	1700	4200	2024
Minimum dist. (km) continent	1365 (E)	633 (A)	373 (A)	96 (A)	568 (A)	96 (A)	150 (SA)	1150 (AU)	850 (SA)	3800 (NA)	220 (A)
N° of extant genera (endemic)	29 (0)	30 (0)	8 (0)	60 (0)	33 (0)	75 (0)	30 (8)	18 (1)	8 (4)	16 (14)	55 (5)
N° of extinct genera (endemic)	0	7 (0)	0	10 (0)	3 (0)	13 (0)	9 (0)	4 (0)	0	25 (18)	0
N° of extant species (endemic)	36 (2)	37 (4)	9 (0)	77 (5)	37 (6)	109 (19)	37 (16)	24 (4)	21 (19)	41 (41)	78 (28)
N° of extinct species (endemic)	0	10 (8)	0	12 (7)	3 (0)	21 (14)	15 (13)	5 (4)	0	57 (56)	0

[a] With human settlements.

species and genus respectively), islands of the Gulf of Guinea (36% and 9%), Galápagos (90% and 50%) and Hawaii (100% and 87%) (Table 1). The extant macaronesian avifauna shows both a lower number of endemic species and lower radiation within lineages. This is despite the fact that some genera inhabiting Macaronesia, such as *Anthus*, *Saxicola* and *Turdus*, have diversified extensively outside of the region (Voelker, 1999; Nylander et al., 2008; Illera et al., 2008a). A plausible explanation is that macaronesian species are the products of geologically recent colonisation events, or high rates of gene flow after colonization from continental or nearby islands have precluded diversification in allopatry (Price, 2008). Alternatively, the rate of extinction of species or lineages across Macaronesia may have been higher than that of other oceanic archipelagos. If so, it would be predicted that there would be more extinct genera and species in the fossil record of Macaronesia than that seen in other archipelagos (see below).

3.3. Arrival dates

Island age limits the maximum time that a taxon can have inhabited an area. The range of geological ages of the macaronesian islands is considerable (0.25–29 my) and so therefore is the range of possible colonization dates for the avifauna. However, recent studies estimating genetic divergence between island and continental lineages suggest a mainly a Pleistocene (0.01–2.6 my) colonization of Macaronesia (Voelker, 1999; Idaghdour et al., 2004; Päckert et al., 2006; Illera et al., 2008a; Töpfer et al., 2011), but with some Pliocene (3–4 my) (Dietzen et al., 2006; Illera et al., 2011) and Holocene (<0.01 my; Pérez-Tris et al., 2004; Dietzen et al., 2008) elements (Fig. 2; S-Table 2). These results contrast with the early to mid Miocene colonization dates (17–20 my) estimated for lizards (Cox et al., 2010), and skinks (Carranza et al., 2008), geckos (Carranza et al., 2002) and invertebrates (e.g. Emerson and Oromí, 2005; Contreras-Díaz et al., 2007) respectively. A notable exception are the two endemic pigeons in the Canary Islands: González et al. (2009) estimated that the laurel pigeon (*C. junoniae*) colonised during early Miocene (20.8 ± 2.2 my), while Bolle's pigeon (*Columba bollii*) colonized during the late Miocene or early Pliocene (5.2 ± 1 my). However, lineage extinction and incomplete sampling of extant taxa are important when estimating colonization times from phylogenetic relationships, as their exclusion from analyses may bias the estimation of colonization and diversification events (see Emerson et al., 2000 for further details on this issue). Consequently, the colonization time estimates of González et al. (2009) may be overestimated, as they did not include all macaronesian and neighbouring continental species. Additionally, the

fossil record does not support a Miocene colonization of the genus *Columba*, as the oldest western Palaearctic records date from the early Pliocene (Mlíkovský, 2002; Mayr, 2005).

The estimated recent arrival of birds to Macaronesia compared to reptiles (about 15 million years later) is surprising for such a vagile group. It is also perplexing given that the radiation of most bird lineages occurred during the Palaeogene in Gondwana (Cracraft, 2001; Brown et al., 2008), and that other, now submerged macaronesian landmasses were emergent some 60 my (Fernández-Palacios et al., 2011) providing a wide interval of time for the colonisation of the region. The typically young age of the macaronesian avifauna raises the general question of whether this is representative of colonization times within the avifaunas of other archipelagos. Time of colonization is constrained by island age, thus to evaluate this question comparisons must be performed with volcanic islands or archipelagos of similar age. For instance, colonization of the Galápagos archipelago is necessarily constrained to four or five million years because that is the estimated age of the oldest islands (Cox, 1983). A candidate group of islands for such a comparison is the Lesser Antilles, where the oldest parts show similar ages (≈20 my) to the oldest macaronesian islands and the nearest mainland (South America) is a similar distance away (150 km, Ricklefs and Bermingham, 2007). The last two decades have seen a phylogenetic focus on the avifauna of the Lesser Antilles (Ricklefs and Bermingham, 2002; Cadena et al., 2005; Ricklefs, 2010b) with studies showing some similarities, but also significant differences, compared to the patterns seen in the macaronesian avifauna. In the Lesser Antilles 38 avian lineages have
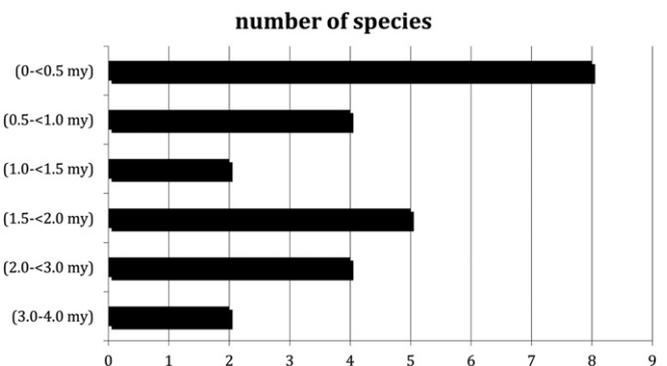

Fig. 2. Accumulation of species through time (millions of years) in Macaronesia. Species were grouped into six age categories: 3–4 my; 2–<3 my; 1.5–<2.0 my; 1.0–<1.5 my; 0.5–<1.0 my; 0–<0.5 my.

been analysed, with the most ancient of these being the Lesser Antillean tanager *Tangara cucullata* with a divergence time from its continental relative estimated to be between 9 and 12 my. Twenty lineages are estimated to have colonised the Lesser Antilles between 0.75 and 10 my, and the remaining 17 lineages are estimated to have colonized more recently during the mid-Pleistocene (0.55−0.75 my) (Ricklefs and Bermingham, 1999, 2002). The similarity between macaronesian islands and the Lesser Antilles lies in the accumulation of colonists during the Pleistocene epoch. This may have been facilitated by climate oscillations and the changing mosaic of continental species distributions associated with them (Hewitt, 2000). The main difference is the absence of avian lineages older than 3.8 my in Macaronesia. This absence could reflect a mass extinction event in the region, but there is no evidence for such a catastrophe in other animal or plant groups, so the explanation remains unknown (see below).

4. Species extinction

4.1. Patterns and processes

Recent paleontological studies in Madeira and the Canary Islands are now changing perceptions about the diversification, distribution, and composition of terrestrial avian communities on these islands (S-Table 3). Upper Pleistocene-Holocene fossil records reveal endemic species extinctions among bird families such as Procellariidae (shearwaters), Phasianidae (quails), Rallidae (rails), Strigidae (owls), Turdidae (thrushes) and Fringillidae (finches and buntings) (Pieper, 1985; Alcover and Florit, 1987; McMinn et al., 1990; Walker et al., 1990; Jaume et al., 1993; Rando et al., 1999, 2008, 2012a; Rando and Alcover, 2010). Recent ^{14}C accelerator mass spectrometry dating of bone collagen of certain species has made it possible to establish an approximate date for their extinction (Table 2), shedding light on the possible causes of their extinctions. Radiocarbon dates show a correlation between the last occurrence for these extinct species and the colonisation of the regions they inhabited by humans (Fig. 3), suggesting a negative causal effect of human arrival (Rando and Alcover, 2008, 2010). In addition to the radiocarbon dates the extinct quail *Coturnix gomerae* has been found in archaeologist sites, plus other two species being extinct during the last century (Fig. 3). Similar conclusions have been reached concerning extinct endemic mammals and native plant species in the Canaries (Criado and Atoche, 2003; Rando et al., 2008, 2012b; de Nascimento et al., 2009). Hunting pressure, habitat loss, introduction of exotic mammals, parasites and diseases introduced as a result of the arrival of humans are thought to have caused biodiversity loss on various oceanic archipelagos (Brooks et al., 2002; Blackburn et al., 2004; Steadman, 2006; Wyatt et al., 2008). In the Canaries, these effects appear to have caused the extinction of some endemic and native species and resulted in the
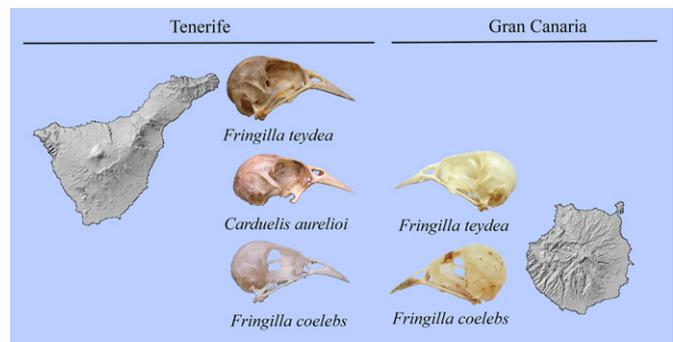

Fig. 3. A beak size comparison among the blue chaffinch (*F. teydea*), the common chaffinch (*F. coelebs*) and the extinct slender-billed greenfinch (*C. aurelioi*) is showed. Character displacement due to resource competition among chaffinches co-occurring in sympatry has been invoked to explain beak size variation in Macaronesia (Rando et al., 2010).

contraction of the once wider distributions of others (Rando, 1995a,b, 2002, 2007).

4.2. The ghost of ancient ecological interactions

In addition to documenting and quantifying the number of extinct species, palaeozoological data can also provide evidence for changes in biogeographic ranges, morphological traits, genetic variability and ecological interactions between extinct and extant species (Lyman, 2012). Although competition between extinct and extant species is difficult to study, multidisciplinary approaches can shed light on this phenomenon. To date the only study integrating phylogenetic and fossil information comes from the macaronesian finches. The family Fringillidae is the classic group used by evolutionary biologists to explain bird adaptive radiation on islands (Price, 2008), with Darwin's finches in Galápagos and the Hawaiian honeycreepers being regarded as among the best examples (Prat, 2005; Grant and Grant, 2008). In contrast the Macaronesia avifauna reveals much less diversification within this family, with only three endemic species: the blue chaffinch (*Fringilla teydea*) in Tenerife and Gran Canaria (Canary Islands), the Azores bullfinch (*Pyrrhula murina*) in São Miguel (Azores), and the wild canary (*Serinus canarius*) in the Azores, Madeira and Canary Islands. The chaffinch (*Fringilla coelebs*) is, perhaps, a notable exception. Five endemic subspecies have been described in Macaronesia: *F. c. moreletti* in Azores, *F. c. maderensis* in Madeira, and three other subspecies in the Canary Islands, *F. c. palmae* in La Palma, *F. c. ombriosa* in El Hierro and *F. c. canariensis* in Tenerife, La Gomera and Gran Canaria (Martín and Lorenzo, 2001). Phylogeographic analyses of mitochondrial and nuclear genes have provided support for monophyly within the Atlantic island common chaffinch populations, suggesting they are the result of a single colonization event from the Iberian Peninsula (Marshall and Baker, 1999; Samarasin-Dissanayake, 2010). Interestingly, the picture of low diversification within Macaronesian finches changes when extinct species are taken into account. These extinct species include the long-legged bunting (*Emberiza alcoveri*), a minimum of two *Carduelis* finches, which inhabited the woodlands of the Canary Islands and another undescribed thick-billed finch species on Madeira (S-Table 3). Furthermore, the coexistence of the blue and common chaffinches on two islands (Tenerife and Gran Canaria), and the variation in beak morphology within extant chaffinches − the common chaffinches on the Azores have deeper and wider beaks than in Madeira and the Canary Islands − has intrigued evolutionary biologists for many years (Grant, 1979; Dennison and Baker, 1991). This issue has recently been addressed by combining the study of: (1) the morphology of the extinct greenfinch *Carduelis*
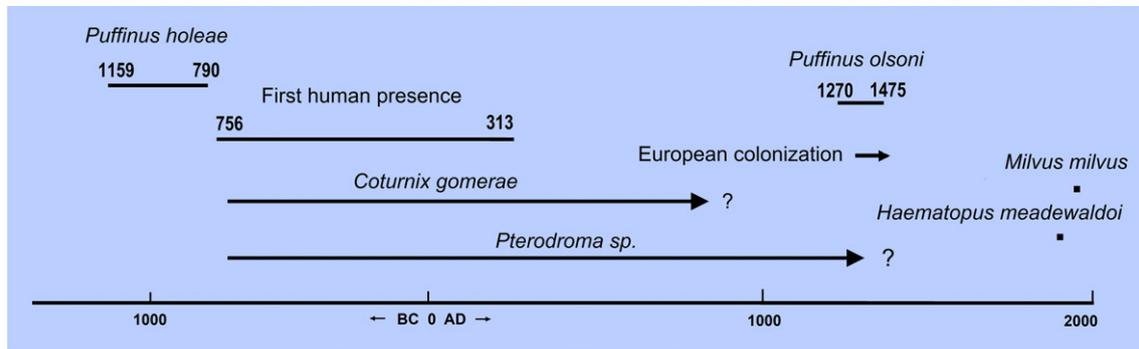
Table 2
Radiocarbon age (years before present) and 2σ calibration intervals (calibrated years Annus domini) from endemic extinct bird bones of the Canary Islands. The 2σ calibration intervals were obtained using the program OxCal. V4.0, the marine 04.14C calibration curve and ΔR = 275 ± 67, for marine (*) bird bones, and intcal04.14C calibration curve, for the land species (see Rando and Alcover, 2008, 2010; Rando et al., 2010, for further details). The lower value of each interval must be considered a minimum age estimate of extinction. AD: *Annus Domini*. BP: Before Present. BC: Before Christ.

Laboratory number	Species	Radiocarbon age (yrs. BP)	2σ calibration intervals
KIA-29159	*Puffinus olsoni**	1265 ± 25	1270−1475 cal. yrs. AD
KIA-36249	*Puffinus holeae**	3395 ± 30	1159−790 cal. yrs. BC
KIA-30992	*Carduelis aurelioi*	11,460 ± 60	11,478−11,258 cal. yrs. BC

Fig. 4. Extinction dates of macaronesian birds estimated with radiocarbon and historical records plotted in relation with human occupation of the archipelagos.

spp., and the extant chaffinches, (2) molecular estimation of the colonization times of the extant finch species, and (3) the use of radiocarbon techniques to estimate the extinction date of the greenfinches (Rando et al., 2010). Results point to an ecological interaction between extinct and extant finches, as radiocarbon dating and colonization times reveal that the three forest finch species occurred in sympatry on Tenerife for approximately 1 million years. The differing bill size of the three species (Fig. 4) is thus most compellingly explained by resource competition between the extinct and extant sympatric species (Rando et al., 2010), suggesting a role for character displacement within the diversification of this group in Macaronesia.

4.3. Turnover in bird assemblages

Paleontological data are a useful complement to phylogenetic data to aid the quantification of speciation and extinction events within a region. Because of the volcanic origin of Macaronesia, there are few ancient paleontological sites, and fossils have been mainly collected in the absence of chronologies. The most detailed information so far comes from sites within the Canary Islands (S-Table 3). The oldest bird fossil recorded in Macaronesia corresponds to eggshells found in calcarenite rocks on Lanzarote, with an age estimate of between five and 12 million years ago (Sauer and Rothe, 1972). Based on egg morphology and pore structure Sauer and Rothe (1972) suggested affinities with ostriches (genus *Struthio*) and an extinct aepyornithoid (genus *Aepyornis*). Because all extant ratite birds are flightless, and the Canary Islands have never been connected with the mainland, the presence of these eggshells remain intriguing, and being object of different interpretations (García-Talavera, 1990). However, despite the uncertainty of the dating of the eggshell it is clear that it predated the arrival of any currently extant species.

The most complete fossil information comes from Upper Pleistocene–Holocene paleontological and archaeological sites. The data show very different bird assemblages with the highest species richness present before the arrival of humans. Within these sites various species of now extinct birds have been identified. In addition, there have been historic documented extinctions of the endemic Canary Island Oystercatcher (*Haematopus meadewaldoi*) and the red kite (*Milvus milvus*) during the last century. Among these extinct taxa seven (58%) were endemic. With only five extant endemic species left this means that the Canary Islands have lost more than half of their endemic richness and approximately 13% of the native avifauna. The emerging picture of extinction of species places the Canary Islands with values above Galápagos and islands of the Gulf of Guinea, but at a lower level to other oceanic archipelagos, such as Hawaii and the Lesser Antilles (Table 1). In Hawaii approximately 58% of original avifauna went extinct after the arrival of Polynesians ca 1600 yrs ago. In contrast,

despite the fact that at least 14 separate bird populations have gone extinct in Galápagos during the last 150–300 yrs, no overall avian species extinctions have been recorded so far (James and Olson, 1991; Olson and James, 1991; Steadman, 1991; James, 1995; Boyer, 2008). In a similar way, no species in the islands of the Gulf of Guinea have gone extinct and there is no evidence for any bird species within the fossil record (Jones and Tye, 2006). In the Lesser Antilles, around 29% of the original avifauna has gone extinct (Table 1), although the impact on the small land birds does not appear to have been dramatic (Ricklefs and Bermingham, 2007).

Given that many of the current Neornithine lineages are estimated to be Late Cretaceous (Cracraft, 2001) and considering the Miocene age of macaronesian islands there is little doubt that older lineages were, at some time, well distributed throughout the region. Because the extinct macaronesian taxa have provided evidence that higher avian diversity existed before human arrival, a plausible explanation for the lack of older avian lineages is that these lineages have gone extinct. The taxon cycle theory predicts older lineages to have higher extinction probabilities due to evolutionary and ecological interactions among colonizing and native species (Wilson, 1961; Ricklefs and Bermingham, 2002). The absence of geochronologies at the paleontological sites limits inferences regarding colonization and diversification. Approaches for the sequencing of ancient DNA provide an opportunity address this issue (Bunce et al., 2005; Gilbert et al., 2005). However, the only species where this has been achieved to date is the extinct lava shearwater (*Puffinus olsoni*). Phylogenetic analyses performed on the genus *Puffinus* revealed low genetic differentiation between the lava shearwater and its extant sister species, the Manx shearwater (*P. puffinus*), suggesting incipient differentiation within the last million years, with incomplete linage sorting between both taxa (Ramírez et al., 2010). This result suggests that extinct taxa are not necessarily older than extant lineages, but further studies are needed to shed light on this topic.

5. Conclusions

This review indicates that, despite the relatively old (Miocene: ca 5–29 my) age of the majority of the macaronesian islands, the extant avian lineages on these islands appear to have colonized the region relatively recently (less than four my). Fossil records suggest that greater species richness existed in the past, and that the arrival of aboriginal people from North Africa ($\approx$ 2500 yrs), and then the later colonisation of the islands by Europeans both caused significant extinctions. Nevertheless, it is striking that the extinction process has extirpated all ancient lineages from the current bird assemblages. Because there is not evidence for catastrophic volcanic events to have produced such result, other hypotheses need to be considered.

Introduction of small mammals to islands is known to produce terrible effects on native birds due to the lack of effective anti-predator behaviour and their reduced fecundity (Steadman, 2006; Boyer, 2008). The presence of mice and rats has been documented to occur with the human arrival in the Canary Islands (Alcover et al., 2009; Rando et al., 2012b), and the introduction of these species had negative effects on the native birds (Martín and Lorenzo, 2001). This arrival, however, was not the first one. In the Canary Islands there is an endemic extant shrew (Crocidura canariensis) and three endemic extinct rodents (Malpaisomys insularis, Canariomys bravoi and C. tamarani) (Rando et al., 2012b). The two first ones are endemic to the eastern islands (Fuerteventura and Lanzarote) and Canariomys spp. was endemic to the central islands (Gran Canaria and Tenerife). The colonization of the former is estimated to have been approximately 2.14 my (Dubey et al., 2008), whereas the arrival of M. insularis is estimated to have been approximately 6 my (Pagès et al., 2012), there is no information regarding the estimated arrival date of Canariomys. The arrival time of the first land mammals predates the time of colonization of all extant bird lineages (Fig. 2). Therefore, we can speculate that shrews and rodents may have produced a limited negative effect on bird species that can be considered recent colonists, while there may have been more dramatic consequences for the ancient endemic avifauna that had evolved in the absence of these mammals in the Canary Islands. However, this hypothesis cannot be invoked in archipelagos or islands that were never naturally colonized by land mammals and, consequently, other hypotheses are necessary. An additional, and not mutually exclusive, potential explanation for the observed pattern of young lineages is the possible negative consequences of novel avian pathogens arriving with more recent colonists. Avian malaria has been implicated in the decline and extinction of many endemic species in Hawaii (van Riper et al., 1986, 2002), and it is known that avian malaria and avian pox are pathogens present in Macaronesia, but apparently do not limit the distributions or population sizes of their avian hosts (Illera et al., 2008b; Carrete et al., 2009; Spurgin et al., 2012). However, it is plausible that colonists accumulated recently after the major Pleistocene climate oscillations could have introduced novel pathogen strains to which older established lineages of birds were naïve, which can potentially produce a fast and dramatic effect on their survival (Ricklefs and Bermingham, 2002, 2007). If the first arrival of mammals was the major driver of extirpation of older lineages in those islands colonized by ancient mammals lineages, only continued efforts to obtain more fossils in combination with further geochronologies and dating of bone of each new fossil found could shed light on this hypothesis. If so, we expect to find bird fossils in dated layers older than the estimated colonization times for these mammals, which might suggest a cause-effect relationship between both events. Interestingly, the oldest bird eggshells found in the Canary Islands (see above) are contained in rock layers dated within the range of mammal arrival to Lanzarote. In contrast, if the extinction of ancient lineages were due to more recent processes such as the arrival of young bird lineages (with their parasites) with stronger competitive abilities than ancient ones (Rando et al., 2010), a multidisciplinary approach would seem to be the best way forward to investigate this issue further. DNA amplification has been achieved in bones more than 50,000 years old (e.g. Shapiro et al., 2004; Willerslev and Cooper, 2005), and most bird extinctions in the Canaries have been dated at less than 15,000 years ago (Table 2). Consequently the successful extraction and analysis of ancient DNA from Canary Island avian fossils is theoretically within reach (De Bruyn et al., 2011). Results obtained from ancient DNA may provide insights on phylogenetic relationships and understanding on dates of divergence for the most recent common ancestors, which can in turn be used to infer the time of colonization. In combination with morphological data (of both extinct and extant taxa) and palaeological data, this may help to improve our understanding of the adaptive and non-adaptive events that occurred among related species, facilitating inferences about the ecological processes that may have caused them and, ultimately, provide insights about the extinction process.

Acknowledgements

Appendix A. Supplementary material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.quascirev.2012.07.013.

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