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

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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.

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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).