Reviews

WHAT ARE WE LEARNING ABOUT SPECIATION AND EXTINCTION FROM THE CANARY ISLANDS?

¿QUÉ ESTAMOS APRENDIENDO SOBRE ESPECIACIÓN Y EXTINCIÓN EN LAS ISLAS CANARIAS?

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Summary.—Oceanic islands are excellent systems for allowing biologists to test evolutionary hypotheses due to their relative simplicity of habitats, naturally replicated study design and high levels of endemic taxa with conspicuous variation in form, colour and behaviour. Over the last two decades the Canary Islands archipelago has proved an ideal system for evolutionary biologists who seek to unravel how biodiversity arises and disappears. In this review we have evaluated the contribution of the study of Canarian birds to our understanding of how and why species occur and change over time. We focus our attention on both extant and extinct Canarian taxa, and describe how research on these species has filled gaps in our understanding of avian speciation and extinction. In addition, we discuss the necessity of revising the current taxonomy in the Canarian avian taxa, especially the status of the endemic subspecies, some of which might be better treated as full species. An accurate classification of Canarian birds is not only necessary for testing evolutionary, biogeographic and ecological hypotheses, but also for effective decision making about conservation and environmental management. Finally we introduce future avenues of research that we feel will yield the most exciting and promising findings on island evolution in the coming years.

Key words: island diversification, island evolution, island phylogeography, island Quaternary fossil record, Macaronesia, oceanic islands.

Resumen.—Las islas oceánicas son sistemas ideales para abordar hipótesis evolutivas debido a la relativa simplicidad de sus hábitats, el adecuado número de entidades discretas donde replicar los

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resultados, y las elevadas tasas de taxones endémicos con variaciones significativas en formas, colores y comportamientos. Durante las dos últimas décadas el archipiélago canario ha sido el escenario perfecto para los biólogos evolutivos en donde entender cómo surge y desaparece la biodiversidad. En el presente artículo hemos evaluado la contribución de las aves canarias para responder a las preguntas de cómo y por qué las especies están presentes, persisten y cambian con el tiempo. Centraremos nuestra atención tanto en especies actuales y extintas, y describiremos cómo las investigaciones desarrolladas en los últimos años han facilitado nuestra compresión sobre los procesos de especiación y extinción. Además, discutiremos la necesidad de revisar la taxonomía actual de los taxones canarios, siendo ello especialmente necesario a nivel de subespecies, ya que algunas de ellas serían merecedoras de ser consideradas especies verdaderas. Una clasificación correcta de las aves canarias no sería solo determinante para abordar hipótesis evolutivas, biogeográficas y ecológicas, sino también para tomar decisiones efectivas de conservación y manejo sostenible de los taxones afectados. Finalmente, terminaremos introduciendo las líneas de investigación donde creemos que en un futuro próximo proporcionarán los hallazgos más prometedores y estimulantes sobre evolución en medios insulares.

Palabras clave: diversificación insular, evolución en islas, filogeografía, islas oceánicas, Macaronesia, registro fósil cuaternario.

Introduction

It has been 16 years since Juan *et al*. (2000) published an illuminating phylogeographic synthesis on the colonisation and diversification of different organisms in the Canary Islands. They argued that there is no common pattern or process determining species composition on islands; a conclusion they regarded as understandable since the evolutionary histories of many Canarian species are dependent on stochastic processes of colonisation and because evolutionary forces promoting speciation are likely to be distinct among the different islands, and both the islands and associated evolutionary pressures change over time. Despite these difficulties, they highlighted that the Canary Islands constitute a unique system for investigating how and why species occur and change through time (Juan *et al*., 2000). Such a review arguably resulted in the Canary Islands being placed alongside the extremely well known Galápagos and Hawaiian archipelagos as models for understanding evolutionary theory (e.g. Emerson and Kolm, 2005; Valente *et al*., 2014; Warren *et al*., 2015). The aim of this review is to provide a general

understanding about how the study of the Canarian avifauna has helped to unravel the complex evolutionary and biogeographic processes that occur on islands, emphasising its contribution in furthering understanding of how the diversity of island birds changes over time.

Over the last two decades a plethora of research has emerged about colonisation, diversification, gene flow and extinction of birds on islands. Much of this new data is genetic (from the now routine use of molecular markers in extant and extinct taxa), paleontological or based on radiocarbon dating (e.g. Kirchman and Steadman, 2007; Ricklefs and Bermingham, 2007; Ramírez *et al*., 2010, 2013; Duncan *et al*., 2013; Allentoft *et al*., 2014; Alcover *et al*, 2015). These data have undoubtedly provided insights into the ages, origins and extinctions of island birds. Yet, how species differentiation is the result of adaptive and non-adaptive processes is not clear (e.g. Carrascal *et al*., 1994; Barton, 1998; Grant, 2001; Price, 2008; Illera *et al*., 2014). In this paper we use selected examples to demonstrate how these processes have shaped the extant and extinct bird assemblages known so far in the Canary Islands.

COLONISATION, DIVERSIFICATION AND ARRIVAL DATES IN THE CANARY ISLANDS

The Canary Islands is an oceanic archipelago in the northern Atlantic and consists of seven main islands and several islets, with a maximum age of the oldest emerged rocks of 20 million years (my; fig. 1) (Carracedo and Perez-Torrado, 2013). The Canary Islands are traditionally included, together with the Azores, Madeira, Selvagens and Cape Verde archipelagos, within a wider biogeographic region named Macaronesia. It is accepted that none of the Canary Islands has ever been connected with the African mainland, although there are different hypotheses regarding their origin and volcanic evolution (see, for instance, Carracedo and Perez-Torrado, 2013). Therefore, all native taxa inhabiting the Canaries are the result of long-distance dispersal events from the European and African mainlands or neighbouring archipelagos. The geographical position, size, altitude, geological age, habitat quality and diversity and previously established taxa all influence the presence, richness and abundance of the taxa inhabiting each island (Juan *et al*., 2000; Carrascal and Palomino, 2002; Carrascal *et al*., 2008; Illera *et al*., 2006, 2012). The evolutionary history of the Canarian taxa can only be effectively tested and understood by considering related species and populations from nearby continental landmasses (Africa and Europe) and neighbouring Macaronesian archipelagos. However, geographical proximity may not be enough to disentangle the evolutionary history of taxa in situations where continental geographical distributions have repeatedly changed due to climatic events (Emerson, 2002).
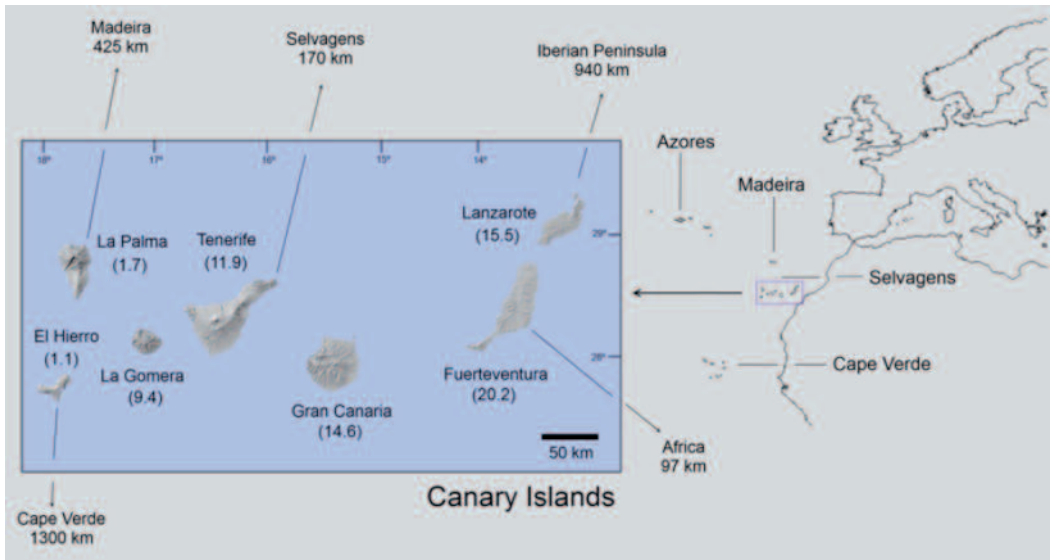

FIG. 1.—Map showing the geographical position of the Canary Islands in relation to the other Macaronesian archipelagos and neighbouring mainland areas. Oldest geological ages per island (after Coello *et al*., 1992; Carracedo and Pérez-Torrado, 2013) are shown in parentheses.
[Mapa que muestra la posición geográfica de las islas Canarias en relación con los otros archipiélagos macaronésicos y las áreas continentales más cercanas. Las edades geológicas más antiguas (según Coello et al., 1992; Carracedo y Perez-Torrado, 2013) de cada isla se muestran entre paréntesis.]

*Diversity dependent on immigration
and subsequent differentiation*

Much about the evolutionary history of Canarian birds has been inferred using sequence data from protein-coding genes. Over the last 15 years, these data have been combined with phylogenetic reconstructions obtained from extant and extinct taxa, to reveal the diversification processes of birds in the Canary Islands (see Illera *et al*., 2012, for a review). These results have provided new evidence about relatively recent colonisation and speciation events, which are younger (within the last four million years) than most of the Canary Islands (10-20 million years old). We will focus on this later.

Although we have gained insights about the origins of avian diversity in the Canary Islands, gaining a full understanding of the origin, colonisation and diversification processes of a particular group of taxa requires comprehensive sampling and extensive molecular data (Emerson, 2002). The Afrocanarian blue tit complex (*Cyanistes teneriffae*) is a clear example of why this is the case. This species shows the highest level of differentiation of all avian taxa breeding in the Canary Islands. Based on phenotypic traits, four subspecies had been described within this taxon: *Cyanistes teneriffae* [*Parus caeruleus*] *teneriffae* (Lesson, 1831) on Gran Canaria, Tenerife and La Gomera; *Cyanistes teneriffae* [*Parus caeruleus*] *palmensis* (Meade-Waldo, 1889) on La Palma; *Cyanistes teneriffae* [*Parus caeruleus*] *ombriosus* (Meade-Waldo, 1890) on El Hierro; and *Cyanistes teneriffae* [*Parus caeruleus*] *degener* (Hartert, 1901) on Fuerteventura and Lanzarote (Martín and Lorenzo, 2001). However, the first unexpected result was obtained when the first phylogenetic study, based on the control region mitochondrial gene, was published. Kvist and co-workers (2005) observed a cryptic genetic lineage on Gran Canaria, which was subsequently confirmed with another mitochondrial gene (cy-

tochrome b), and the Gran Canarian population was therefore described as a novel subspecies *Cyanistes* [*Parus*] *teneriffae hedwigae* (Dietzen *et al*., 2008). Despite subsequent efforts to disentangle the evolutionary history of this group by including more loci and populations, results were inconclusive (Illera *et al*., 2011; Päckert *et al*., 2013; Hansson *et al*., 2014, Gohli *et al*., 2015). However, a recent study using high genomic coverage and extensive sampling of all key populations has finally unravelled the evolutionary history of the Afrocanarian blue tits (Stervander *et al*., 2015). This study showed that the origin of the extant North African blue tits was undoubtedly continental; a finding contrary to the previous phylogeographic study by Illera *et al*. (2011), who suggested that North African blue tits were derived from the Canary Islands by back-colonisation. Stervander *et al*. (2015) also indicated that blue tits independently colonised the Canary Islands three times, probably triggered by changes in woodland distribution across North Africa. Remarkably, these authors revealed that the La Palma population was the result of an ancient colonisation event (*ca*. four million years ago, mya), which even precedes the splitting time between the two European taxa blue tit *C. caeruleus* and azure tit *C. cyanus*, which is estimated to have occurred *ca*. three mya. A second colonisation reached the central Canary Islands and the western island of El Hierro *ca*. two mya, while the eastern islands of Fuerteventura and Lanzarote were colonised *ca*. 100,000 years ago. Such a colonisation history suggests that either i) a classical stepping-stone pathway from the mainland never occurred, or, ii) a stepping stone colonisation did occur and the intermediate populations became extinct or outcompeted. Interestingly, this study confirms that La Palma and Libya, which represent the two most peripheral populations of the Afrocanarian blue tits, constitute relics of an ancestral and more widely geographically distributed North African population (Stervander

et al., 2015). Importantly, this study illustrates how the inference of colonisation pathways and diversification processes can be difficult to interpret in the absence of extensive taxon sampling and/or with a limited set of informative loci. Such a circumstance is, for instance, noticeable in those taxa with early Holocene founded populations (e.g. Pérez-Tris *et al*., 2004; Illera *et al*., 2014; Padilla *et al*., 2015).

DIFFERENTIATION AFTER COLONISATION:
FOUNDER EVENTS, DRIFT AND SELECTION

Island systems are ideal models for studying the processes involved in population differentiation and speciation, because each colonisation event can be viewed as an independent evolutionary episode (Clegg, 2002). Individuals colonising a new island are a subset of the mainland or neighbouring island birds. Over the last two decades a plethora of studies on divergence of phenotypic and genetic traits in Canarian birds have been published. Results obtained using neutral and non-neutral genetic markers and phenotypic traits have provided evidence for a significant role of drift (due to bottlenecks and founder effects) over selection in recently separated populations (Idaghdour *et al*., 2004; Illera *et al*., 2007; Agudo *et al*., 2011; Barrientos *et al*., 2014; Mori *et al*., 2014; Padilla *et al*., 2015; González-Quevedo *et al*., 2015).

It is widely accepted that newly founded island populations support lower genetic diversity than their mainland counterparts (Frankham, 1997) and plenty of examples from the Canary Islands exist to support this statement (e.g. Barrientos *et al*., 2014; Hansson *et al*., 2014; Stervander *et al*., 2015) (fig. 2). This lower genetic diversity is the result of increased rates of drift and inbreeding due to the reduced effective population size of island populations (Frankham, 1997). The potential negative consequences of this include decreased individual fitness due to inbreeding

depression and reduced 'evolutionary potential', compromising the ability of populations to confront future changes in the abiotic and biotic environment (Frankham, 1997; Jensen *et al*., 2007). This has been revealed to be the case in the Canarian Egyptian vulture, *Neophron percnopterus majorensis*. This raptor was widely distributed throughout the Canary Islands at the beginning of the 20th century. However, populations have since been in decline due to the generalised use of pesticides in agriculture, illegal hunting, and change in the management of animal waste (Martín and Lorenzo, 2001). A relict population (*ca* 200 individuals) remains in the Eastern Canary Islands (mainly in Fuerteventura), thanks to the intense conservation effort since the 1990s (Palacios, 2004; García-Heras *et al*., 2013). The dramatic decline in effective population size has resulted in increased rates of inbreeding in the Canarian Egyptian vulture, with negative consequences on its breeding success (Agudo *et al*., 2012).

As well as having negative consequences for individual populations, the low effective population size often found on islands can increase rates of evolution – something that has been understood for over 60 years (Mayr, 1954). Despite this, however, the role of founder effects in promoting rapid morphological and genetic divergence after the establishment of a new population is often neglected (Clegg, 2002). In a recent study of genetic and morphological differentiation in 13 island populations of an endemic Macaronesian passerine, Berthelot's pipit *Anthus berthelotii*, Spurgin and co-workers (2014) have documented a striking example of how founder effects can persist over evolutionary timescales, promoting incipient speciation among archipelagos. Using a set of 21 nuclear neutral markers (microsatellites) and seven morphological traits they compared patterns of genetic and phenotypic variation across Macaronesia to determine the evolutionary forces driving differentiation at the population level. They found a pattern of isolation by
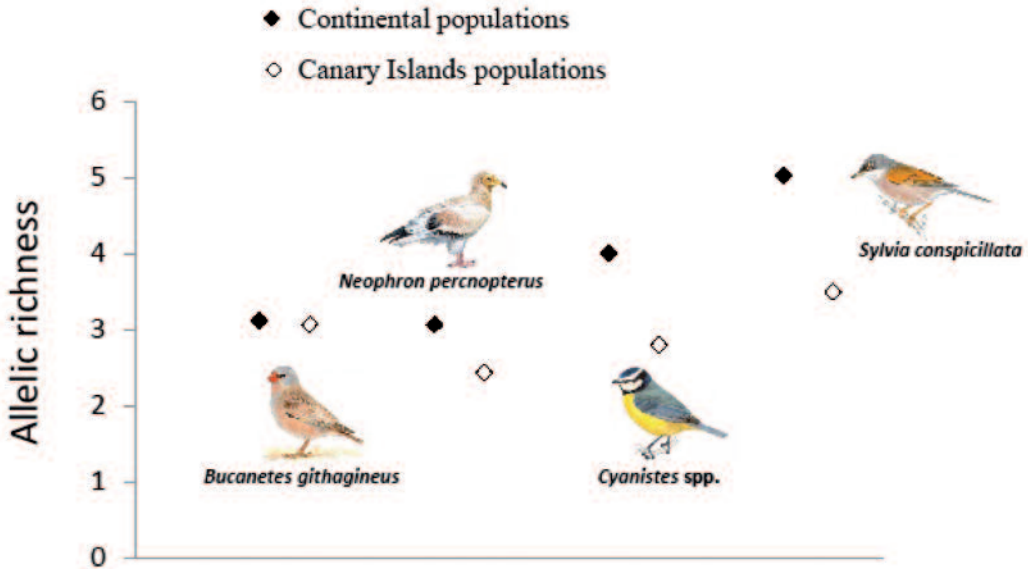
Fɪɢ. 2.—Allelic richness at microsatellite loci in four Canarian passerines, in comparison with that of related mainland populations: Trumpeter finch (*Bucanetes githagineus*, Barrientos *et al*., 2014), Egyptian vulture (*Neophron percnopterus*, Agudo *et al*., 2011), Afrocanarian blue tit (*Cyanistes* spp., Hansson *et al.,* 2014) and spectacled warbler (*Sylvia conspicillata*, Illera *et al*., 2014). Continental populations are taken from the Iberian Peninsula and North Africa (Morocco). The mean is shown where information from more than one population was available.

*[Riqueza alélica estimada en genes nucleares (microsatélites) en cuatro paseriformes canarios en relación con las poblaciones continentales de origen: camachuelo trompetero (*Bucanetes githagineus*, Barrientos* et al.*, 2014), alimoche común (*Neophron percnopterus*, Agudo* et al.*, 2011), herrerillo canario/norteafricano (*Cyanistes *spp.*, Hansson* et al.*, 2014) y curruca tomillera (*Sylvia conspicillata*, Illera* et al.*, 2014). Las poblaciones continentales proceden de la península Ibérica y norte de África (Marruecos). Cuando la información proviene de más de una población se muestra la media.]*

colonisation driving both genetic and phenotypic divergence of this passerine, with little evidence for a role of selection or gradual genetic drift (Spurgin *et al*., 2014). However, this result does not exclude the possibility that selection (natural and/or sexual) and gradual genetic drift have played a role in shaping variability in other genes and phenotypic traits (see below).

After a successful colonisation, reduced levels of genetic diversity can be recovered by immigration from other populations, or by point mutation (Hartl and Clark, 1997). In a recent study of Major Histocompatibility Complex (MHC) genes in Berthelot's pipit, Spurgin *et al*. (2011) demonstrated a novel way in which genetic polymorphisms can be introduced into recently founded and isolated populations. MHC genes are the most polymorphic known in vertebrates, and this extraordinary diversity is thought to be the result of pathogen-mediated selection (Spurgin and Richardson, 2010). Spurgin *et al*. (2011) found that a combination of natural selection and gene conversion, a process involving the 'copying' of DNA within and among duplicated loci, had rapidly regenerated allelic variation among the bottlenecked Berthelot's

pipit populations (Spurgin *et al*., 2011). Although gene conversion in MHC genes had previously been detected in other organisms, including humans (Miller and Lambert, 2004; Chen *et al*., 2007), its evolutionary role had been obscured due to the difficulty of distinguishing its effects from those produced by convergent accumulation of point mutations driven by selection (Promerová *et al*., 2013; Backström *et al*., 2013). However, the simplified nature of the colonisation history of Berthelot's pipit enabled Spurgin *et al*. (2011) to unravel the specific contribution of each evolutionary force, highlighting the benefit of island research in evolutionary study.

Finally, it is worth noting that isolation does not guarantee differentiation *per se*. For instance, Illera *et al*. (2014) studied the mechanisms driving differentiation among recently founded spectacled warbler *Sylvia conspicillata* populations in Macaronesia and found strikingly low levels of differentiation in song, morphology and genetics. Such a lack of diversification in acoustic traits was especially striking, since song is routinely invoked to be a crucial character for triggering differentiation among bird populations (Laiolo and Tella, 2007; Grant and Grant, 2010; Laiolo, 2012), usually preceding genetic and morphological changes (Seddon *et al*., 2013).

WHAT ARE WE LEARNING FROM EXTINCT SPECIES?

Extinction is a natural and widespread evolutionary process. However, it is now widely accepted that the current extinction rate is being dramatically increased by human actions (Stuart Chapin III *et al*., 2000), and the fossil record confirms that this acceleration started at the end of the Pleistocene period (Barnosky *et al*., 2004). The loss of species on islands following human colonisation has been especially dramatic (Blackburn *et al*., 2004; Steadman, 2006;

Duncan *et al*., 2013). The Pleistocene-Holocene paleontological and archaeological sites have provided essential information on the magnitude and pattern of these extinctions in the Canary Islands. In a recent review, Illera *et al*. (2012) described the fast reduction in bird diversity in Macaronesia following human colonisation, both aboriginal and European. Such a conclusion was reached after radiocarbon dating of bone collagen of selected extinct species (see Illera *et al*., 2012 for further details). This showed that almost two-thirds of endemic Canarian species and around 13% of the native avifauna has gone extinct, suggesting a negative causal effect of human colonisation (Illera *et al*., 2012). Species with particular adaptations, such as flightlessness and restricted distributions, have been associated with increased extinction rates, due to their increased susceptibility to hunting, habitat destruction and introduced alien species (Rando, 2007; Rando *et al*., 1999, 2010). Indeed, on comparing the endemic bird taxa, both extinct and extant, of the Canary Islands, it becomes clear that extinctions on this archipelago have not occurred randomly. All extinct birds (see Supplementary Electronic Material) were ground nesters (Alcover and Florit, 1987; McMinn *et al*., 1990; Walker *et al*., 1990; Jaume *et al*., 1993; Rando *et al*., 1999, 2010), and four of the five extinct land birds (*Coturnix gomerae*, *Carduelis triasi*, *C. aurelioi* and *Emberiza alcoveri*) were either flightless or weak fliers. These features fit with results obtained in Hawaii, where an analysis of the extinction patterns of land and freshwater birds indicates that higher extinction rates have occurred in birds with larger body sizes and in ground-nesting and flightless species, with nest type being the primary risk factor for extinction (Boyer, 2008).

Since the Canarian fossil record has not been completely scrutinised it seems likely that the number of extinct taxa found on the archipelago will increase in the future. It is essential, however, that future studies are carried out using standard and internationally

recognised protocols, thus making it possible to corroborate or refute any new findings. For instance, in a review published in this journal, Sánchez Marco (2010) introduced new data on extinct birds in the Canary Islands (i.e. *Sturnus* sp. and *Hieraaetus pennatus*). However, the new fossil records presented cannot be considered valid, due to three critical omissions: i) the scientific collection where specimens were stored, ii) the unique numbered reference of each specimen studied, and iii) pictures of the examined bones. Without such information it is impossible to review this material to confirm or disprove new findings.

Beyond documenting the number of species that have gone extinct following human arrival, the fossil record may shed light on the ecological interactions among species, and in reconstruction of past environments. Research on Canarian birds has helped address both of these aims. For example, the discovery of an extinct flightless bunting *Emberiza alcoveri* in Tenerife suggests that predator pressure on terrestrial woodland birds must have been limited before human arrival (Rando *et al.*, 1999). In addition, extinct endemic greenfinches found in the Canary Islands have revealed a surprising scenario of ecological interactions in sympatry with extant *Fringilla* finches. The continuous variation in beak morphology (size and shape) observed in the Canarian finch species suggests a role for character displacement driving diversification within this group (Rando *et al.*, 2010). Overall, it is clear that the extant bird assemblages breeding in the Canary Islands are now impoverished as a result of human arrival. However, there is no simple way of ascertaining how new available niches, which emerged after extinction events, have been occupied by new species. Alien species (e.g. rats and mice) may affect ecological interactions among extant species, as they can act both competitors and predators (Schluter, 1988; Rando *et al.*, 2010). Disentangling the eco-

logical interactions among birds and introduced mammals is likely to be an interesting challenge for future studies.

Vertebrates, and birds in particular, are important components of the antagonistic (herbivory) and mutualistic (pollination and seed dispersal) ecological processes through which ecosystems are self-regulated. Antagonistic and mutualistic interactions are critical in the maintenance of the demographic balance of populations, species and communities (see, for instance, Traveset *et al.*, 2014). When a species becomes extinct its interactions in the ecosystem also disappear (Valiente-Banuet *et al.*, 2015). In the case of Canarian birds, while we do not understand how extinction has affected many ecological interactions among species, a number of interesting findings have been documented. For example, it is clear that the versatility of seed-eaters has been significantly diminished following the extinction of the greenfinches, and that variation in beak morphology in Canarian finches suggests a role for resource competition resulting in ecological niche divergence (Rando *et al.*, 2010; see also above). However, patterns of beak morphology suggest that extant finches have not able to fill the empty niches left after the extinction of greenfinches (fig. 3). Such a result suggests that plant species with large seeds (i.e. bigger than the beak of the common chaffinch) are not being consumed by any avian species in the Canarian woodlands, except in the pine forests of Tenerife and Gran Canaria where the blue chaffinches *Fringilla teydea* and *F. polatzeki*, respectively, do so). It is still possible, however, that other species (e.g. introduced mammals) are occupying these vacated niches. Attempting to disentangle the ecological and evolutionary significance of lost interactions on islands will be undoubtedly a promising and challenging line of research in the future.

According to molecular studies published so far, most extant bird species on the Canary Islands are recent colonisers, which contrasts

with the older colonisation events proposed for many plant species (e.g. Kim *et al*., 2008; Vitales *et al*., 2014). However, such recent arrival times do not necessarily mean that birds have had a limited historical and evolutionary role in plant-animal interactions. Indeed, looking at the Upper Pleistocene-Holocene fossil record in the Canary Islands (which is incomplete), we can find extinct specimens, probably of new species, of the genera *Turdus* and *Erithacus* (J. C. Rando, unpublished data), two taxa that presumably participated in seed dispersal of Canarian plants (see for instance González-Castro *et al*., 2015 for extant ecological interactions). These findings suggest that multiple colonisation events by birds to the Canary Islands may have acted as a buffer against losses of mutualistic interaction due to extinction. Importantly, this pattern has also been identified in Madeira and Azores (J. C. Alcover and J. C. Rando, unpublished data). Overall, these results highlight the importance of using the fossil record to understand evolutionary processes on oceanic islands.
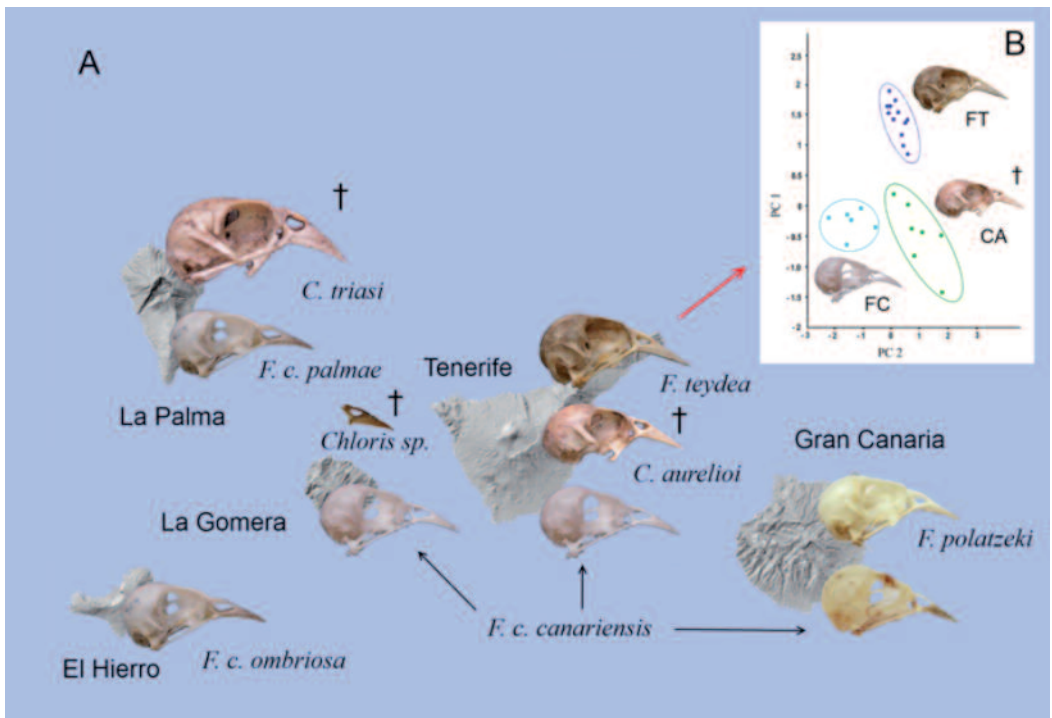

FIG. 3.—(A) Comparison of beak size among extinct (†) and extant finches (genera *Fringilla* and *Chloris*) from the Canary Islands. Skulls and beaks are depicted on the same scale. (B) Principal Component Analysis (PCA) plot for the two principal components obtained from measurements of cranial and beak traits of *F. teydea* (FT), *F. coelebs* (FC) and *C. aurelioi* (CA) on Tenerife after Rando *et al*. (2010). *[(A) Comparación del tamaño del pico entre fringílidos (géneros* Fringilla *y* Chloris*) extintos (†) y actuales de las islas Canarias. Cráneos y picos están representados en la misma escala. (B) Representación gráfica de los dos componentes principales obtenidos en un análisis de componentes principales (ACP) de las características del cráneo y pico de* F. teydea *(FT),* F. coelebs *(FC) y* C. aurelioi *(CA) en Tenerife (según Rando* et al., *2010).]*

WHY IS IT IMPORTANT TO KNOW HOW MANY SPECIES THERE ARE?

The final step in the population divergence process is the formation of new species. Yet, despite the relevance of this evolutionary process, what constitutes a species remains a disputed matter (Coyne and Orr, 2004) and there are numerous attempts to achieve an agreed definition (Hausdorf, 2011). Although there are many schools of thought with different approaches in constructing biological classifications, two definitions of 'species' have traditionally dominated the discussion: the biological species concept and the phylogenetic species concept (de Queiroz, 2005). The phylogenetic species concept (Cracraft, 1989) is based on genetic divergence among groups, where a species would be characterised as the smallest set of individuals that share an ancestor and can be distinguished from other groups. The biological species concept, meanwhile, emphasises the evolution of reproductive isolation among groups of individuals (Mayr, 1942). Nowadays the biological species concept is probably the most widely accepted of all the species definitions (Coyne and Orr, 2004). However, in a recent review, Sangster (2014) has demonstrated that although this concept has dominated avian taxonomy, a detailed analysis of taxonomic studies published during last 60 years does not support this definition of the species. In fact, diagnosability (i.e. the phylogenetic species concept) has been the most widely used criterion for defining species (Sangster, 2014). However, many currently well-established species do not meet this definition in a strict sense. For instance, although over 15 well-established species of Darwin's finches exist (but see McKay and Zink, 2014, for a challenging view), genetic differences between them are extremely low due to extensive interspecies gene flow events (Lamichhaney et al., 2015). Such a scenario is likely to be a normal process during the initial stages of speciation

(Grant and Grant, 2008) but it makes it difficult to find an unambiguous definition of 'species' (Padial et al., 2010). Other recognised ranks of classification below the species level, such as subspecies and evolutionary significant units (ESUs), generate less discussion and are more easily accepted (Crandall et al., 2000). However, the absence of clear criteria to delimit when these populations are diagnostically distinct can result in the inclusion of massive groups of vaguely differentiated taxa within this category (Zink, 2004). Independently of what criterion is applied, it is clear that having a definition of 'species' provides a basis for understanding biodiversity and, undoubtedly, plays a central role in conservation and environmental management (Mace, 2004; Zink, 2004; Phillimore and Owens, 2006; Seoane et al., 2011; Frankham et al., 2012).

The Canary Islands, due to their high number of endemic species, comprise an ideal system for unravelling how biodiversity arises and disappears, but also for understanding how biodiversity responds in the face of environmental changes. Nonetheless, before beginning to answer such questions it is necessary to know how many species there are. In addition, we know that extant native avian assemblages on the Canary Islands are actually subsets of former and richer bird communities, which were dramatically extirpated by historic and prehistoric human activities (see above). Therefore, biogeographical, ecological and evolutionary approaches using incomplete lists of extant or recently extinct taxa may obscure our general understanding of the mechanisms that generate diversity patterns in island systems (Gray and Cavers, 2014).

Although there are plenty of methods for species delineation (e.g. Hausdorf, 2011; Fujita et al., 2012; Solís-Lemus et al., 2015), an ideal method does not exist, due to the intrinsically fuzzy nature of species boundaries (Padial et al., 2010). However, the best strate-

gy could be to use a wide spectrum of data types; for instance, genetic, morphological and acoustic information, to reach a consensus on the extent of lineage differentiation (Padial *et al*., 2010; Solís-Lemus *et al*., 2015). Using this consensus method, also named "integrative taxonomy", it becomes clear that Canarian avian taxonomy should be reshuffled. Most of Canarian avian taxa were described at the end of the 19th and early 20th centuries (Martín and Lorenzo, 2001), when species and subspecies were defined on the basis of visual inspection of phenotypic characteristics, without any statistical analyses for assessing diagnosability. At present, only five extant endemic species are recognized (Illera *et al*., 2012) and they are strongly supported by genetic, morphological, acoustic and behavioural data (Martín and Lorenzo, 2001). We suggest that the number of endemic Canarian species is underestimated and that a number of known endemic subspecies could be raised to full species status (e.g. Pratt, 2010; Sangster *et al*., 2016). There are currently more than 30 endemic subspecies described from the Canary Islands (Supplementary Electronic Material), some of which have been intensively studied since the 1990s (Martín and Lorenzo, 2001; Illera *et al*., 2012). Thus, there is now much information on many endemic Canarian birds. We focus below on the two taxa that are characterised by an especially high degree of differentiation in Macaronesia: the Afrocanarian blue tit *Cyanistes teneriffae* and the common chaffinch *Fringilla coelebs*.

The Afrocanarian blue tit shows the deepest levels of differentiation in the Canary Islands studied to date, with five endemic subspecies described (see above). Two more subspecies inhabit North Africa: *C. t. ultramarinus*, which occurs throughout Morocco, Algeria and Tunisia, and the isolated Libyan population *C. t. cyrenaicae*. As explained above, the evolutionary history of the Afrocanarian blue tit was recently resolved by combining complete taxon sampling and high genomic coverage (Stervander *et al*., 2015). According to the long-term isolation found among subspecies, and also considering the significant differences found in morphology (Grant, 1979a; Martin, 1991), acoustic traits (Schottler, 1993, 1995) and plumage coloration (Cramp and Perrins, 1993), it seems warranted to consider each of the Afrocanarian subspecies as full species (Sangster, 2006). Thus, we suggest that the number of endemic Canarian blue tit species should be five, which must be named (from east to west): *Cyanistes degener* (Hartert, 1901), on Fuerteventura and Lanzarote; *Cyanistes hedwigae* (Dietzen, García-del-Rey, Castro, and Wink, 2008), on Gran Canaria; *Cyanistes teneriffae* (Lesson, 1831), on Tenerife and La Gomera; *Cyanistes palmensis* (Meade-Waldo, 1889), on La Palma, and *Cyanistes ombriosus* (Meade-Waldo, 1890), on El Hierro. In addition, the other two African blue tit taxa should be: *Cyanistes ultramarinus* (Bonaparte, 1841) in Northwestern Africa and *C. cyrenaicae* (Hartert, 1922) in Libya. We avoid splitting any subspecies within *C. degener* and *C. teneriffae* because further specific studies on acoustic and morphology are now needed to evaluate whether this is justified.

The common chaffinch *Fringilla coelebs*, with five subspecies described, provides the best example of diversification of extant land birds in Macaronesia (Cramp and Perrins, 1994). There is one endemic subspecies per archipelago, except in the Canary Islands where three subspecies are recognised (Martín and Lorenzo, 2001). The evolutionary biology of this passerine has been repeatedly studied using a range of different traits (Grant, 1979b; Dennison and Baker, 1991; Marshall and Baker, 1999; Suárez *et al*., 2009; Rando *et al*., 2010; Samarasin-Dissanayake, 2010; Rodrigues *et al*., 2014). Genetic data have provided strong evidence for long-term isolation between individuals from the three archipelagos and the continental areas, with indi-

viduals from each archipelago consistently grouping together (Marshall and Baker, 1999; Rando *et al*., 2010). In addition, within the Canary Islands a new cryptic lineage based on genetic data has recently been revealed on Gran Canaria (Suárez *et al*., 2009). Morphological divergence among archipelagos was also showed by Grant (1979b) and Dennison and Baker (1991). In addition to the genetic and morphological divergence, Lynch and Baker (1994) and Lachlan *et al*. (2013) found significant differences in chaffinch vocalisations among archipelagos. Overall, the information suggests that the Macaronesian chaffinch populations are distinct lineages, with diagnosable morphological and bioacoustical characteristics, and with no evidence of interbreeding. In conclusion, the birds on each archipelago may be better treated as full species following the rationale of both the biological (based on their geographic isolation and absence of gene flow) and phylogenetic species concepts. Thus, the Macaronesian chaffinches should be named as follows: *Fringilla moreletti* (Pucheran, 1859) on the Azores, *Fringilla maderensis* (Sharpe, 1888) on Madeira and *Fringilla canariensis* (Vieillot, 1917) on the Canary Islands. In addition, an extensive taxonomic re-evaluation is also needed within the Canary Islands, where the taxonomic description of the new lineage found on Gran Canaria should be a priority (Supplementary Electronic Material).

These two examples clearly highlight the necessity to perform a re-evaluation of the taxonomic status of all endemic subspecies recognised on the Canary Islands. Indeed, such an exercise should be routinely performed with all oceanic bird taxa, since they show much more restricted distributions and are often the subject of greater conservation concern than their continental counterparts (Stattersfield *et al*., 1998). Using an integrative taxonomic approach a range of characters (e.g. morphological, functional, acoustic, ge-

netic and behavioural) can be used to establish the most suitable taxonomic level for each taxon, and where incongruity among characters can be resolved by trying to establish the most plausible evolutionary explanations for such discrepancies. We suggest that such a methodology should be used routinely to reassess avian taxonomy on oceanic islands.

CONCLUSIONS AND OPEN QUESTIONS FOR FUTURE RESEARCH

Using selected examples we have demonstrated that the Canary Islands have significantly contributed to our understanding of how and why species occur and change through time. Extant species have informed us about how species diverge over time, suggesting that continued waves of colonisation with subsequent long-term isolation, along with stochastic divergence due to founder effects and associated genetic drift, are key processes operating on Canarian birds. Importantly, extinct species confirm the significance of colonisation and isolation in the past. We have also discussed the importance of using extensive genetic data for studying the evolutionary history of species.

We predict that new genomic techniques will be extremely useful in the near future for understanding not only the evolutionary history of Canarian birds, but also the specific genetic mechanisms driving diversification and, ultimately, speciation. Furthermore, we think that an important challenge in the coming years will be in applying next-generation sequencing techniques to extinct taxa. Despite the difficulties associated with working on fragmented DNA (e.g. Ramírez *et al*., 2010, 2013; Allentoft *et al*., 2014), the information extinct species can provide will be vital for disentangling ancient ecological relationships among extinct and extant species, as well as for understanding how specific morphological traits have evolved in

response to environmental changes. Moreover, although our knowledge of extinct taxa has very much improved, further paleontological efforts are still needed to get a representative picture of the extinct bird assemblages that recently inhabited the Canary Islands. Such information, in combination with a deep taxonomic re-evaluation of the extant avi-fauna, will enable us to better understand the mechanisms that generate avian diversity. Finally, future study on Canarian birds will shed new light on co-evolutionary, as well as evolutionary, processes. For example, host-parasite relationships studies carried out in the Canary Islands have provided new insight into the prevalence and diversity of parasites, as well as host-parasite specificity, host survival and pathogen-mediated selection (e.g. Carrete *et al*., 2009; Illera *et al*., 2008, 2015; Spurgin *et al*., 2012; Pérez-Rodríguez *et al*., 2013; González-Quevedo *et al*., 2014). Further investigation into parasite-host relationships, again using emerging genomic technologies, will be a promising line of research in the near future.

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SUPPLEMMENTARY ELECTRONIC MATERIAL

Additional supporting information may be found in the on-line version of this article. See volume 63(1) on www.ardeola.org

Table S1: Native breeding bird taxa (extant and extinct) in the Canary Islands.

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