Biodiversity on oceanic islands – evolutionary records of past migration events

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Abstract

Oceanic islands are mostly of volcanic origin. Most of them harbour a diverse fauna and flora, which had not been there before. All plants and animals must have reached the islands by sea or wind or through human activities. Thus, all these island taxa are witnesses of migration events in the past and are models for biogeography. In this review, fauna (especially birds) and flora of the Macaronesian islands west of Europe and North Africa in the Atlantic are discussed. The Macaronesian islands comprise 4 archipelagos with 31 main islands, including the Azores, Madeira, Canary Islands and Cape Verde Islands. These islands are of volcanic origin and between 120 and < 1 million years old. Flora and fauna mostly consist of species, that originally originated from Europe or Africa and arrived within the last 4 million years. More than 23% of the terrestrial taxa are endemic to the area. Genetic analyses have confirmed most of the morphologically defined endemic species and subspecies. In some species groups, a strong speciation signal becomes visible in that distinct genetic lineages occur on individual islands or archipelagos. This is especially apparent in *Phylloscopus canariensis*, *Regulus regulus*, *Cyanistes [caeruleus] teneriffae*, *Erithacus rubecula*, and *Fringilla coelebs*. The diversity of the Macaronesian islands offers an excellent opportunity to study adaptive radiation and speciation in organisms of differing complexity and mobility.

1 Flora and Fauna on Oceanic islands

Isolated oceanic islands, which were created by volcanic eruptions, had neither fauna nor flora at their beginning. Nevertheless, most of the oceanic islands show a species-rich biodiversity at present. Where do all the species come from? Since the islands are not connected to the mainland, all plants and animals, which now populate a volcanic island, must have migrated there or have been transported there by see, air or humans. They are records of past migration events. These events were apparently quite rare but still abundant enough that the isolated islands become populated within hundreds or thousands of years. Isolated oceanic island often have a unique flora and fauna with many endemic species. There founders usually arrived there in small numbers and started allopatric speciation. Therefore, oceanic islands can be regarded as laboratories of evolution and species formation.

1.1 How are volcanic islands populated?

Long-distance transport by sea has been assumed for plants, especially as many seeds can survive weeks and months in the sea. When they are washed ashore on an island and if they find suitable conditions, many of them start to germinate and if successfully multiply and form isolated new populations. Charles Darwin, who had explored fauna and flora of several oceanic islands, such as the Galapagos Islands, had already worked on this topic experimentally. He had tested how long seeds could survive in salt water. He found that many seeds are still viable after months in sea water. He provided detailed descriptions in his “On the Origin of species” (Darwin, 1859). Seeds can also be spread by animals, especially birds (Padilla et al. 2012). If birds have eaten fruits with seeds on the mainland, then fly to an island and leave its faces there, the seeds may germinate and start a new population (Viana et al., 2016). If raptors feed on herbivorous mammals, seeds can pass via the prey to the raptors, which can then disperse the seeds to new places via pellets. This was shown on Fuerteventura (Lopez-Darias and Nogales, 2016). Other seeds may stick to feet or feathers and may thus be transferred to an island. As humans have always been very mobile, many isolated islands have been visited by humans that explored the sea by boats. Often they carry food plants along and sometimes, some seeds may thus be accidentally brought to an island.

Animals that can fly (such as birds, bats, and some insects) can reach the newly formed islands on their regular migration routes or exceptionally if they have been drifted to the islands by storms or hurricanes from the mainland. Non-airworthy animals can float across the sea, e.g., on tree trunks or even larger vegetation rafts that have been cut off from the mainland during storms, to reach Oceanic Islands. Some of the oceanic islands harbour a diverse biodiversity of reptiles, which might have reached the islands this way. For turtles, which can survive in sea water for some time, they might even have floated in the ocean without such rafts. This seems to be likely for the large turtles, which have been found on islands such as Seychelles, Madagascar or Galapagos. Smaller animals can also be blown away by hurricanes to islands near the mainland. However, most of these shipments are likely to have remained a dead end and have not led to settlement, as most animals need at least a male and a female to start breeding.

If the number of species on oceanic islands is examined, it decreases with the distance of the islands to the mainland and their age (MacArthur & Wilson 1967). The further away an island is from the mainland and the younger it is, the lower the number of species. Conversely, large islands near the mainland and old islands show greater biodiversity. Apparently, settlement events take place regularly, so that new volcanic islands develop vegetation and fauna already after a few decades or centuries. As animals need food to survive, islands need to develop a vegetation first, before herbivores can settle which then serve as a food source for carnivores.

Often only a few individuals, possibly even only a pregnant female or a seed, represents the ancestor of an island population. As a consequence, the genetic variability of island populations is usually significantly lower due to the so-called bottleneck effect. In addition, the genetic drift is more pronounced than in large continental populations where gene flow creates genetic diversity between them. Isolated island populations are often no longer in contact with their original populations. If they survive long enough and if the living conditions on the islands differ from those on the mainland, natural selection leads to new adapted forms, which can often differ morphologically and ecologically from the original forms. This form of speciation corresponds to the classical idea of allopatric species formation (species formation by geographical separation) (Storch et al. 2013). Since these new lineages have only a very local distribution, they are regarded as endemic (leading to endemic subspecies, species, or genera). If different climatic conditions, vegetation types and/or food sources occur on an island archipelago, a fast species splitting can occur, which is called radiation. The adaptive radiation of the Darwin Finches on the Galapagos Archipelago (Grant & Weiner 1999) is famous, where 17 endemic reptile and 27 endemic bird species have been identified.

Of the 10300 bird species described today, about 18% live on islands, including 950 endemic land bird species on oceanic islands. Since the islands are often small, the habitat for endemic species is also limited and the population size low. Habitat change, persecution, the introduction of predators (rats, cats) or diseases (e.g., bird malaria in Hawaii) have already led to the extinction of some island endemics (e.g., Dodo, Moa). Therefore, many island species are currently particularly threatened (Brooks et al. 2002; Blackburn et al. 2004).

In this overview, I would like to refer to our own studies over the last 30 years on the Macaronesian Islands in the Atlantic, on which we have investigated the genetics and phylogeography of birds, especially endemic species and subspecies.

2 Origin of the Macaronesian Islands

In the western Atlantic, we know several island archipelagos with a total of 31 main islands, all of which are of volcanic origin and have never been connected to the European or African mainland by land bridges. These islands can be summarized as Macaronesian Islands. They consist of the Azores in the northwest, Madeira and the Canary Islands in the middle and the Cape Verde Islands in the southwest (Fig. 1). Cape Verde comprises 14 islands whose age varies between 125 and 2 million years. All these oceanic islands were created by volcanic eruptions. The oldest islands of the Canary Islands, Madeira and the Azores are Fuerteventura, Lanzarote, Tenerife and Porto Santo, which were formed 14 to 21 million years ago. The most recent islands include La Palma and El Hierro of the Canary Islands and Graciosa, Sao Jorge, Pico, Faial, Corvo and Flores in the Azores (Table 1), which were formed less than 2 million years ago (Illera et al., 2012, 2016; Valente et al., 2017).

3 Resettlement of the Macaronesian Islands: Endemic animal and plant species

Oceanic-subtropical climate with rich rainfall (Azores, Madeira, Canary Islands without the eastern islands) provide the framework for the development of a species-rich vegetation (mostly from Europe or Africa), which in turn forms the basis for the speciation of animals. Similar to the Mediterranean region there are warm and dry summers and rainy winters. On the Macaronesian Islands you can find for example a species-rich succulent vegetation (succulent bushes) adapted to drought with many succulent Crassulaceae and Euphorbiaceae, extensive tree heath, laurel and pine forests, lagoons, but also arid areas at altitudes (maximum altitude 3700 m) or on the eastern Canary Islands (e.g., Fuerteventura), whose

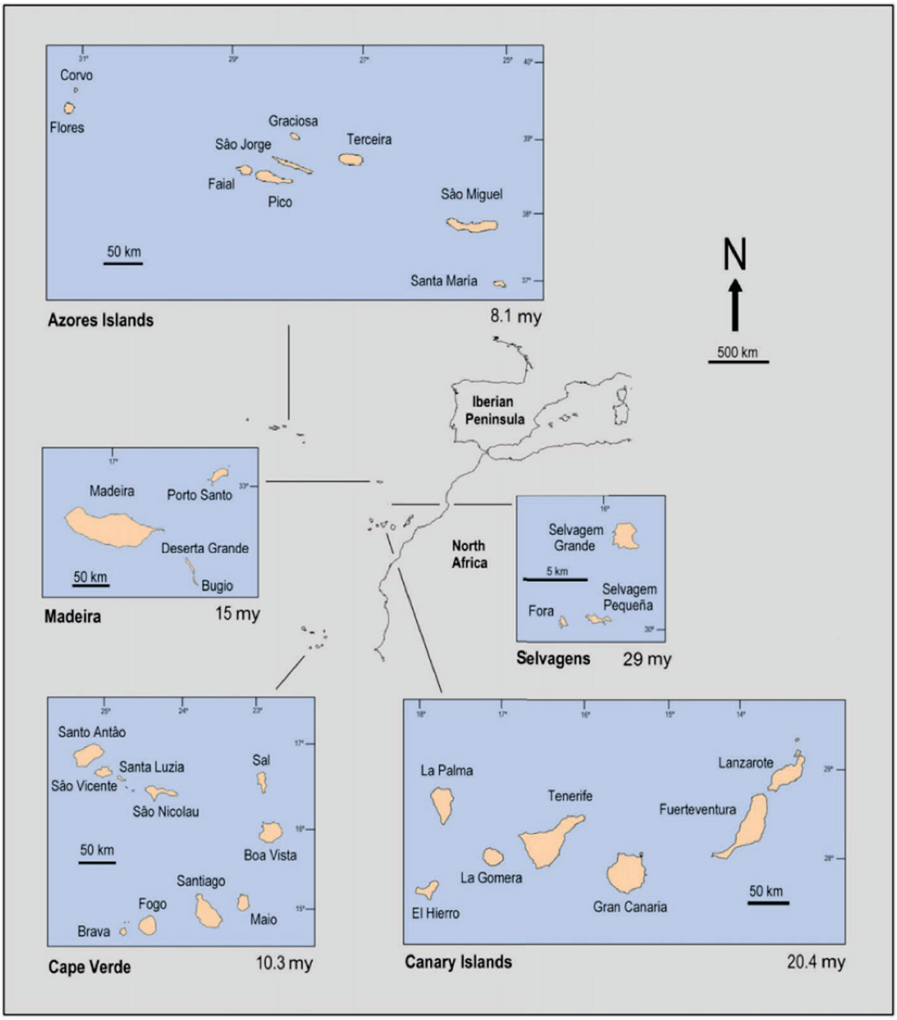

Figure 1: Location of the Macaronesian Islands (from Illera et al. 2012).

Table 1: Age of the Macaronesian Islands and their distance to the mainland.

Island	**Estimated geological age [million years]**	**Distance to mainland (km)**
Canary Islands (Spain)		
Fuerteventura	21	94
Lanzarote	15.5	131
Gran Canaria	14	188
Teneriffa	11.6	263
La Gomera	12	313
La Palma	2	375
El Hierro	1	350
Madeira (Portugal)		
Madeira	5.2	640
Porto Santo	14	625
Desertas	5.2	630
Selvagen	11	270
Azores (Portugal)		
Santa Maria	6	1 343
São Miguel	4	1 358
Terceira	3.5	1 552
Graciosa	2.5	1 625
São Jorge	0.6	1 614
Pico	0.3	1 640
Faial	0.7	1 688
Corvo	0.7	1 890
Flores	0.7	1 898
Cape Verde (República de Cabo Verde)		
14 Islands	2-125	570

dunes are reminiscent of the Sahara, or on the Cape Verde Islands (Schönfelder 2002).

About 23% of all terrestrial taxa of Macaronesia are considered endemic (Illera et al. 2012, 2016; Valente et al., 2017). Among the more than 2500 plant species of the Canary Islands, over 21%, of the 1800 fungi and 1100 lichens 5.7 and 2.7% are considered endemic. Even higher is the proportion of endemics among arthropods. Of the more than 6400 species, over 45% are endemic. Endemic taxa have also been described in vertebrates, especially reptiles and birds (approx. 7% of over 370 vertebrates; Clarke et al. 2006; Garcia-Del Rey 2011).

3.1 Birdlife of the Macaronesian Islands

Over 400 bird species have been recorded on the Macaronesian Islands (Clarke et al. 2006; Garcia-Del-Rey 2011). Most species are migrants and guests which visit the islands only on a short-term base. Only 82 species are considered as breeding birds, including 21 endemic species and 10 neozoa. In addition, more than 70 endemic subspecies have been described (Table 2). The proportion of endemic bird taxa (species, subspecies) is 17 % (Illera et al. 2012, 2014, 2016). While the bird species of the Canary Islands, Madeira and the Azores have great similarities with the bird fauna of Europe and North Africa, African species dominate on the Cape Verde Islands. Although these islands are halfway between Europe and Americas, American elements seem to be missing.

Fossil and subfossil bird taxa have also been discovered on the Canary Islands and Azores, showing that some island species have already become extinct in the last 10,000 years (overview in Sanchez Marco 2010; Illera et al. 2012; 2014; Rando et al. 2017). The more recent extinction of some species may be related to hunting (the islands were populated by *Homo sapiens* from Africa for about 2500 years), habitat loss and the introduction of exotic predators (Illera et al. 2012).

Table 2: Endemic birds of the Makaronesian Islands and their systematics (sequence as in Garcia-Del Rey 2011). BB = breeding taxon.

Species	Azores	Madeira	Canary Islands	Cape Verde Islands
Alectoris barbara			ssp. *koenigi*	
Coturnix coturnix	ssp. *conturbans*	ssp. *confisa*	ssp. *confisa*	ssp. *iopinata*

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Table 2 – continued from previous page

Species	Azores	Madeira	Canary Islands	Cape Verde Islands
Pterodroma deserta		only on Desertas		
Pterodroma feae				BB on 4 islands
Pterodroma madeira		only on Madeira		
Calonectris borealis	BB	BB	BB	
Calonectris edwardisii				BB
Puffinus baroli	ssp. *baroli*	ssp. *baroli*	ssp. *baroli*	ssp. *boydi*
Pelagodroma marina		ssp. *hypoleuca* (Salvages)	ssp. *hypoleuca*	ssp. *eadesi*
Oceanodroma monteroi	BB (Baixa, Praia)			
Fregata magnificens				ssp. *lowei*
Ardea purpurea				ssp. *bournei*
Neophron percnopterus			ssp. *majorensis*	ssp. *percnopterus*
Milvus milvus				ssp *fasciicauda* (probably extinct)
Accipiter nisus		ssp. *granti*	ssp. *granti*	
Buteo buteo	ssp. *rothschildi*	ssp. *buteo*	ssp. *insularum*	ssp. *bannermani*
Falco tinnunculus		ssp. *canariensis*,	ssp. *canariensis*, ssp. *dacotiae*	ssp. *alexandri*; ssp. *neglectus*
Falco peregrinus			ssp. *pelegrinoides*	ssp. *madens*

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Table 2 – continued from previous page

Species	**Azores**	**Madeira**	**Canary Islands**	**Cape Verde Islands**
Chlamydotis undulata			ssp. *fuerteven-turae*	
Burhinus oedicnemus			ssp. *distinctus*, ssp. *insularum*	
Cursorius cursor			ssp. *bannermani*	ssp. *exsul*
Charadrius dubius			ssp. *curonicus*	
Larus michahellis	ssp. *atlantis*	ssp. *atlantis*	ssp. *atlantis*	
Columba livia	ssp. *atlantis*	ssp. *atlantis*	ssp. *canariensis*	ssp. *atlantis*
Columba palumbus	ssp. *azorica*	ssp. *maderensis*		
Columba trocaz		BB Madeira		
Columba bollii			BB	
Columba junoniae			BB	
Tyto alba		ssp. *schmitzi*	ssp. *alba*, ssp. *gracilirostris*	ssp. *detorta*
Asio otus	ssp. *otus*		ssp. *canariensis*	
Apus alexandri				BB
Apus unicolor		BB	BB	
Apus pallidus		ssp. *brehmorum*	ssp. *brehmorum*	
Halcyon leucocephala				ssp. *acteon*
Dendrocopos major			ssp. *canariensis*; ssp. *thanneri*	
Alauda razae				Only on Raso

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Table 2 – continued from previous page

Species	**Azores**	**Madeira**	**Canary Islands**	**Cape Verde Islands**
Alauda rufescens			ssp. *rufescens*; ssp. *polatzeki*	
Anthus berthelotii		ssp. *madeirensis*	ssp. *berthelotii*	
Motacilla cinerea	ssp. *patriciae*	ssp. *schmitzi*	ssp. *canariensis*	
Erithacus rubecula	ssp. *rubecula*	ssp. *rubecula*	ssp. *rubecula*, ssp. *superbus*, ssp. *marionae*	
Saxicola dacotiae			ssp. *dacotiae*: Fuerteventura; ssp. *murielae*: Alegranza, Montana Clara (extinct);	
Turdus merula	ssp. *azorensis*	ssp. *cabrera*	ssp. *cabrera*	
Sylvia atricapilla	ssp. *gularis*	ssp. *heineken*	ssp. *heineken*	ssp. *gularis*
Sylvia melano-cephala			ssp. *leucogastra*; ssp. *melanoce-phala*	
Sylvia conspicillata		ssp. *bella*	ssp. *orbitalis*	ssp. *orbitalis*
Acrocephalus brevipennis				BB
Phylloscopus canariensis			ssp. *canariensis*, ssp. *exsul* (extinct)	
Regulus regulus	ssp. *azorica*, ssp. *sanctae-mariae*, ssp. *inermis*,		ssp. *ellenthalerae*, ssp. *teneriffae*	

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Table 2 – continued from previous page

Species	Azores	Madeira	Canary Islands	Cape Verde Islands
Regulus madeirensis		BV		
Cyanistes teneriffae			ssp. *teneriffae*, ssp. *hedwigii*, ssp. *palmensis*, ssp. *ombriosus*, ssp. *ultramarinus*	
Lanius meridonialis			ssp. *koenigi*	
Corvus corax			ssp. *tingitanus*, ssp. *jordani*	
Pyrrhocorax pyrrhocorax			ssp. *barbarus* (only on La Palma)	
Sturnus vulgaris	ssp. *granti*			
Passer iagoensis				BB
Petronia petronia		ssp. *madeirensis*	ssp. *madeirensis*	
Fringilla teydea			ssp. *teydea*, ssp. *polatzeki*	
Fringilla coelebs	ssp. *moreletti*	ssp. *maderensis*	ssp. *palmae*,ssp. *ombriosa*; ssp. *canariensis*	
Serinus canaria	BB	BB	BB	
Carduelis cannabina		ssp. *guentheri*	ssp. *harterti*, ssp. *meadewaldoi*	
Bucanetes githagineus			ssp. *amantum*	

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Table 2 – continued from previous page

Species	Azores	Madeira	Canary Islands	Cape Verde Islands
Pyrrhula murina	BB (only Sao Miguel)			

3.2 Results of DNA analyses from Canary Island bird taxa

More than 25 years ago we started to systematically catch all breeding bird species on all islands of the Canary Islands and take blood samples. With the support of local ornithologists we finally received not only material from the Canary Islands but also from other islands of Macaronesia. Our question was whether we could use DNA marker analysis to determine where the founders of the endemic taxa came from and since when they have been colonizing the islands. We also wanted to check whether the endemic taxa were also genetically differentiated. Since the individual islands are within sight of each other within an archipelago, there was also the question of whether the populations of the neighbouring islands mix, i.e. whether a gene flow exists between the islands. After our first work yielded exciting data, further research groups have joined in the following time, so that today we have a good analysis of most bird species. These papers are presented in this overview (see also Garcia-Del Rey 2011; Illera et al., 2012, 2016).

3.3 Nonpasseres

Four endemic pigeon taxa (Tab. 2) live on the Macaronesian Islands, especially in the laurel forests: *Columba bollii* and *C. junoniae* on the Canary Islands, *C. trocaz* on Madeira and *C. palumbus azorica* on the Azores. Studies of mtDNA have shown that *C. bollii* (Fig. 2a) is closely related to the European Wood Pigeon (*C. palumbus*) and separated a maximum of 5 million years ago (Gonzales et al. 2009). Presumably, wood pigeons, which settled in laurel forests, reached the Canary Islands (Tenerife, Gran Canaria, La Palma, El-Hierro) on their migrations, became settled there and differentiated themselves to an independently adapted taxon. The endemic subspecies *C. palumbus azorica*, which occurs on the Azores, cannot be distinguished from *C. palumbus* at the mtDNA sequence level (Dourado et al. 2014). This taxon must therefore still be very young, if it is independent at all. *C. trocaz* of Madeira clusters as a sister group to *C. bollii* (Dourado et al. 2014) and is therefore also a descendant from the wood pigeon. *C. junoniae* populates the laurel forests on the same islands as *C. bollii*. Phylogenetically, the species is located at the base of the genus *Columba*, so it is not clear where the original species comes from (probably Africa). The Canary Islands were settled no more than 15 million years ago (Gonzales et al., 2009). This high age has now been questioned, as all other bird lines began less than 4 million years ago on the Macaronesian Islands (Illera et al. 2012).

The Houbara bustard occurs with the subspecies *Chlamydotis undulata fuertaventurae* (Fig. 2b) on Fuerteventura, Lanzarote and Graciosa (Tab. 2). At the level of mtDNA (cyt b = cytochrome b; control region), the subspecies cannot be distinguished from the mainland form (Gaucher et al. 1996; Broders et al. 2003; Idaghdour et al. 2004; Korrida & Schweizer 2013). Microsatellite analyses also show no clear separation (Korrida et al. 2012), so that it must be assumed that *Chlamydotis undulata fuertaventurae* (Fig. 2b) is a young form that colonized the eastern islands of the Canary Islands from the African mainland rather recently, i.e. only a few thousand years ago. Whether there is still a direct exchange with the North African Houbara bustards is an open question.

Storm petrels and shearwater (Procellariiformes) are colony breeders that breed on many of the oceanic islands. Since these sea birds have very high philopatry (i.e. they return to their natal colonies every year, Warham 1990), genetically distinct and island- or archipelago-specific haplotypes can often be detected, some of which were already separated as endemic taxa (Heidrich et al. 1996, 2000; Swatscheck et al. 1994; Carneiro Da Silva & Granadeiro, 1999; Gómez-Díaz et al. 2006; Smith et al. 2007; Zino et al. 2008; Jesus et al. 2009; Delgado et al. 2013). Important representatives for Macaronesia are Madeiran Storm Petrel (*Oceanodroma castro* and various subspecies), Fea's and Zino's Petrels (*Pterodroma deserta*, *P. feae*, *P. madeira*, *P. marina*) and Cory's Shearwater (formerly only *Calonectris diomedea*, currently divided into three species: *Calonectris borealis* on the Canary Islands, Madeira and Azores, *C. edwardsii* on Cape Verde and *C. diomedea* in the Mediterranean). Originally, all small black shearwaters of the Atlantic and in the Mediterranean area were combined as Manx shearwater (*Puffinus puffinus*). DNA studies led to the early splitting of this polytypic species into several new taxa, such as Mediterranean shearwater (*P. yelkouan*; eastern Mediterranean), *P. mauretanicus* (Balearic Islands) and *P. assimilis* (Macaronesia; Heidrich et al. 2000). Two new species were separated from the Little Shearwater (*Puffinus assimilis*) due to mtDNA differences (*P. baroli*, *P. boydi*). The Storm-petrel *Hydrobates pelagicus* breeds on Atlantic islands, but also in the Mediterranean Sea. Mediterranean birds are genetically easily distinguishable from the Atlantic storm petrels and probably represent a separate taxon (M. Wink, J. Gonzales; unpublished). An exact and island-specific phylogeographic analysis of the various shearwaters and petrels is far from complete, as many colonies have not yet been analysed; in addition, nuclear marker analyses are still missing in most studies. Only when this data is available the taxonomy of the often cryptic forms can be established with some certainty.

Among the birds of prey and owls, endemic subspecies have been described for peregrine falcon, kestrel, sparrow hawk, barn owl and long-eared owl (Table 2). Most of the genetic analyses carried out so far (Groombridge et al. 2002; Hille et al. 2003; M. Wink, unpublished) showed little or no differences to the taxa of the African or European mainland. The buzzards of the genus *Buteo* are all closely related (Kruckenhauser et al. 2004). This is especially true for the buzzards of Macaronesia, where some subspecies are distinguished (Table 2). *B. b. rothschildi* and *B. b. insularum* cannot be distinguished from *B. b. buteo*. Only *B. b. bannermani* from the Cape Verde Islands is genetically distinguishable and clusters as a sister species to *B. socotrae* from Sokotra together with *B. rufinus*. *B. bannermani* is a young taxon and probably not much older than 100000 years (Clouet & Wink 2000). On Fuerteventura, less than 30 pairs of Egyptian Vulture (Fig. 2c) breed, described as the endemic subspecies *Neophron percnopterus majorensis* (Donázar et al. 2002). The species has disappeared from the other Canary Islands. The genetic autonomy could be proven by nucleotide sequences of marker genes of mtDNA (Donázar et al. 2002), which differ slightly from the mainland population, and by microsatellite analyses of nuclear DNA (Agudo et al. 2010). The microsatellite data also show an immigration of Egyptian vultures from the mainland into the island population.

The only woodpecker species that breeds on the Macaronesian Islands is the Great-spotted woodpecker (*Dendrocopos major*, Fig. 2d). Breeding occurs only in pine forests on Tenerife and Gran Canaria. Two subspecies have been described (*D. m. canariensis* and *D. m. thanneri*; Table 2), which do not differ genetically and should probably only be regarded as *D. m. canariensis* (Garcia-Del Rey 2011). *D. m. canariensis* is distinct, but only slightly different from the woodpeckers of Eurasia (*D. m. major*). The Canary Islands were probably not settled until 150000 to 50000 years ago (Garcia-Del Rey et al. 2007).

Among the swifts of the genus *Apus*, to which the Common swift (*Apus apus*) belongs, two endemic species for Macaronesia have been described: *Apus alexandri* on the Cape Verde Islands and *A. unicolor* on the Canary Islands and Madeira. Both species, which are derived from African ancestors, are also phylogenetically differentiated (Päckert et al. 2012), but closely related to *Apus apus*. Common

Swift and Pallid swift (*A. pallidus*) cannot be clearly separated by mtDNA markers (Päckert et al. 2012), so that the differentiation of the subspecies *A. pallidus brehmorum*, which should represent *A. pallidus* on Macaronesia, also seems rather questionable. Stone-curlews (*Burhinus oedicnemus*) form distinct genetic lineages on the Canary Islands (Mori et al., 2017). The genetic status of the remaining endemic non-passerine birds and subspecies of Macaronesia (*Alectoris*, *Coturnix*, *Fregata*, *Ardea*, *Cursorius*, *Charadrius*, *Columba livia*, *Halcyon*; Table 2) has not yet been studied or noticeable differences were not discovered.

a. Bolle's Pigeon (*Columba bollii*; Photo: M. Vences).

Figure 2: Photographs of some Canarian birds.

b. Houbara Bustard (*Chlamydotis undulata fuerteventurae*; Photo: D. Koch).

c. Egyptian vulture (*Neophron percnopterus*; Photo: M. Wink).

Figure 2 (continued): Photographs of some Canarian birds.

d. Great Spotted Woodpecker (*Dendrocopos major*; Photo: M. Vences).

e. Berthelot's Pipit (*Anthus berthelotii*; Photo: M. Vences).

Figure 2 (continued): Photographs of some Canarian birds.

f. Canarian Robin (*Erythacus r. superbus*; Photo: M. Vences).

g. Canarian Chiffchaff (*Phylloscopus canariensis*; Photo: M. Vences).

Figure 2 (continued): Photographs of some Canarian birds.

h. Canarian Blue Tit (*Cyanistes teneriffae*; Photo: M. Vences).

i. Grey Shrike (*Lanius meridonialis koenigi*; Photo: M. Vences).

Figure 2 (continued): Photographs of some Canarian birds.

k. Chaffinch from Tenerife (*Fringilla coelebs canariensis*; Photo: M. Vences).

l. Blue Chaffinch (*Fringilla teydea*; Photo: M. Vences).

Figure 2 (continued): Photographs of some Canarian birds.

m. Canary (*Serinus canaria*; Photo: M. Vences).

n. Bullfinch (*Pyrrhula pyrrhula*; Photo: F. Schrauth).

Figure 2 (continued): Photographs of some Canarian birds.

3.4 Passeriformes

The songbirds of Macaronesia have been studied much more extensively, as many species have noticeable morphological or bioacoustic differences, e.g., in Blackcaps, Blue Tit or Chaffinch/ Blue Chaffinch. Independent subspecies have been defined for these forms for some time already (Table 2). Phylogenetic and phylogeographic studies have often shown a corresponding genetic differentiation and in some cases have even discovered new, previously unrecognized island forms.

Berthelot's Pipit (*Anthus berthelotii*, Fig. 2e) is found on the Canary Islands (*A. b. berthelotii*) and Madeira (*A. b. madeirensis*). The Berthelot's pipit is a sister species of the Tawny pipit (*Anthus campestris*; living in Europe and North Africa) and shared a common ancestor with it about 2.5 million years ago (Arctander et al. 1996; Illera et al. 2007). While on the mtDNA level hardly any variability between the island populations is detectable, microsatellite analyses show a separation of the three island archipelagos (Madeira, Canaries, Selvage Islands; Illera et al. 2007), so that the differentiation into two subspecies appears acceptable.

With the European robin (*Erithacus rubecula*), 5 subspecies are distinguished in Europe, of which *E. r. rubecula* occurs in Central Europe and on Macaronesia. For Tenerife and Gran Canaria the subspecies *E. r. superbus* (Fig. 2f) was separated. Analyses of mtDNA showed that the robins of Tenerife differ significantly from those in Gran Canaria. Since morphometric differences also exist, the robin of Gran Canaria was described as a new subspecies *E. r. marionae* (Dietzen et al. 2003, 2015; Fig. 2f). Both subspecies colonized the Canary Islands probably 1.8 million years ago. The robin of the other Canary Islands, Madeira and Azores is much younger (Rodrigues et al. 2013) and occurred 350000 years ago. These populations correspond to the European nominate form, *E. r. rubecula.*

The Fuerteventura Stonechat (*Saxicola dacotiae*) breeds exclusively on the Canary Island Fuerteventura. The subspecies ssp. *murielae*, formerly found on Alegranza and Montana Clara, is now extinct there. Analyses of mtDNA showed early on that *S. dacotiae ssp. dacotiae* is genetically clearly differentiated and clearly related to the Common stonechat (which has now been divided into various independent species) and not to the Whinchat (Wittmann et al. 1995; Wink et al. 2002; Zink et al. 2009). Apparently, Stonechats have settled on Fuerteventura from Europe; surprisingly, none of the other island archipelagos has been colonized, although suitable habitats also exist there.

Three species of warblers breed on the Macaronesian Islands, such as the *Sylvia atricapilla*, *S. melanocephala* and *S. conspicillata*. Various endemic subspecies have been described due to plumage differences (Table 2; Berthold et al. 1997; Garcia-Del Rey 2011). Investigations of mtDNA show that the colonization of Macaronesia is young; therefore the island forms cannot be genetically differentiated (Dietzen et al. 2008) and the breakdown of warblers into endemic subspecies must be questioned. For the Spectacled Warbler, also a clear differentiation between mtDNA and population structure could not be found on the Atlantic islands (Illera et al., 2014).

Among the species-rich reed warbler (genus *Acrocephalus*) only the Cape Verde reed warbler (*A. brevipennis*) has managed a settlement on the Cape Verde Islands. *A. brevipennis* is a sister species of *A. gracilirostris* from East Africa, both belonging to the African subgenus *Calamocichla* (Leisler et al. 1997). Therefore, it is obvious that the settlement of the Cape Verde Islands took place by reed warbles, which were native to Africa.

Among the warblers (genus *Phylloscopus*) only the Chiffchaff has found its way to the Canary Islands. While in former times, on Fuerteventura the now extinct species *P. exsul* occurred, today Chiffchaffs only populate the West Islands. The Canarian Chiffchaff, now known as *Phylloscopus canariensis* (Fig. 2g) due to clear genetic differentiation (Helbig et al. 1996), also differs bioacoustically and ecologically from European Chiffchaffs. On the Canary Islands, the Canarian Chiffchaff (but also the blackcap, the Spectacled warbler, the Sardinian warbler, the Canary Blue Tit, and the Canary) has developed into a successful nectar eater, thus opening up a new food resource in tropical and subtropical flora (Valido et al. 2004; de Castro et al., 2017). Preliminary mtDNA studies show a strong differentiation of island-typical haplotypes for Canarian Chiffchaffs on Gran Canaria, Tenerife, La Palma and El Hierro (M. Wink, P. Kremer; unpublished), similar to what we found in blue tit and goldcrest and Firecrest (see below).

The Goldcrests and Firecrests, native to Europe (*Regulus regulus* and *R. ignicapillus*) have both settled on Macaronesia. Genetic investigations (Päckert et al. 2006, 2009) showed that the Firecrests on Madeira is a sister taxon to the Goldcrests and represent an independent taxon *R. madeirensis*. As Firechrests are migratory birds, one can imagine a colonisation by migratory birds that have settled; however, the absence of the species on the other islands, which also have adequate habitats, is inexplicable. Since both, Goldcrest and Firecrest, are sympatric in Europe, one would have expected something similar on the Macaronesian Islands. On the Azores and the Canary Islands, on the other hand, descendants of Firechrest colonized Macaronesia several times, presumably coming from Europe. In the Azores, island-specific haplotypes corresponding to the subspecies *R. r. sanctaemariae*, *R. r. azoricus* and *R. r. inermis* can be detected, but genetic differentiation is low (Rodrigues et al. 2014). For the Canary Islands, only a subspecies *R. r. teneriffae* had been defined so far. However, our DNA studies have shown that an independent taxon exists on La Palma and El Hierro, which is now known as the endemic subspecies *R. r. ellenthalerae* (Päckert et al. 2006; Fig. 3). The settlement of the Azores is relatively young, while the colonization of the Canary Islands probably took place 1–2 million years ago.

The blue tit complex on the Canary Islands was morphologically and bioacoustically investigated at an early stage. Within *Parus caeruleus* (today *Cyanistes teneriffae*, Fig. 2h) the subspecies *caeruleus, obscuros*, *ogilstrae*, *balearicus* and on the Canary Islands *teneriffae*, *ultramarinus*, *degener*, *ombriosus* and *palmensis* were distinguished due to striking differences in plumage characters. Studies of mtDNA clearly showed (Kvist et al. 2005; Dietzen et al. 2008; Illera et al. 2011; Päckert et al. 2013) that the blue tits of the Canary Islands originated from the blue tits in Europe and North Africa, but represent an independent monophylum (*Cyanistes teneriffae*) that probably evolved 4-6 million years ago. Surprisingly, almost every Canary Island populated by blue tits has its own haplotype, i.e. genetic lineage. This suggests that the populations have been genetically isolated for some time and are not in constant exchange. The haplotypes largely correspond to the morphologically defined subspecies. Our own investigations could identify a so far overlooked but independent lineage on Gran Canaria, which we baptized *C. teneriffae hedwigii* (Dietzen et al. 2008). Molecular data also allow a reconstruction of the settlement history, which is however extremely complex and assumes more than one immigration event (Dietzen et al. 2008; Illera et al. 2011; Päckert et al. 2013).

On Tenerife, Gran Canaria, Fuerteventura and Lanzarote lives a predator, which until now was regarded as an endemic taxon *Lanius meridionalis koenigi* (Fig. 2i). However, studies of mtDNA and nuclear DNA show that Canarian Grey shrikes are less related to the Great Grey Shrike of the Iberian Peninsula (*L. meridionalis*) than to the Central and Northern European Great Grey Shrike, *L. excubitor* (Gonzales et al. 2008; Klassert et al. 2008). The splitting of koenigi took place more than 1 million years ago. Taxonomically the separation would be conceivable either as *Lanius koenigi* or as renamed subspecies *L. excubitor koenigi*.

All islands of the Canary Islands are populated by ravens, which are considered as separate subspecies *Corvus corax tingitanus* and *C. corax jordansi*. Niethammer

(1953) had termed the Raven from Western Canaries *Corvus corax tingitanus* and those from the Eastern Islands *Corvus corax jordansi*. A study of mtDNA shows that only the ravens of the East Islands can be clearly differentiated (Rösner et al. 2014). The authors assume that *C. c. tingitanus* and *C. c. jordansi* are identical and suggest to use the name *C. c. jordansi* for the endemic subspecies for priority reasons. However, the phylogeny and phylogeography of the raven is very complex (Haring et al., 2012), so the last word has certainly not yet been spoken.

European starling (*Sturnus vulgaris*) breeds only in the Azores. Studies of mtDNA show that the endemic subspecies *S. v. granti* is also genetically differentiated (Neves et al. 2010).

Chaffinches (Fig. 2k) colonize the Canary Islands (*F. c. palmae*, *F. c. canariensis*, *F. c. ombriosa*), Madeira (*F. c. maderensis*) and the Azores (*F. c. moreletti*), while Tenerife and Gran Canaria also have the independent Blue Chaffinch (*Fringilla teydea*; Table 2). Within *F. teydea* (Fig. 2l), the subspecies *F. t. teydea* (on Tenerife) and *F. t. polatzeki* (on Gran Canaria) are distinguished, which can also be genetically differentiated (Pestano et al. 2000; Garcia-Del-Rey et al. 2013). The chaffinches of the Macaronesian Islands form archipelago- and island-specific mtDNA haplotypes (Marshall & Baker 1999), which largely correspond to the described subspecies (Table 2). Suarez et al. (2009) investigated mtDNA and microsatellites from the chaffinches of the Canary Islands and found three haplotype clusters: Cluster I: El-Hierro and La Palma (probably only 1 subspecies, *F. c. palmae*; possibly *F. c. ombriosa* is obsolete); II: La Gomera and Tenerife (*F. c. canariensis*) and III: Gran Canaria (new unnamed taxon). This is similar to the situation with the robin, where we also found an overlooked taxon on Gran Canaria (see above). On the Azores, gene flow still exists between Chaffinch populations from different islands (Rodrigues et al. 2014).

The Canary (*Serinus canaria*, Fig. 2m) populates the Canary Islands, Madeira and the Azores. Genetically Canary and European Serin (which also occurs on Tenerife and Gran Canaria) have a common ancestor. An analysis of the mtDNA of the Canary from all three archipelagos did not show a clear genetic differentiation, as we had seen in the blue tits, robins and chaffinches. It appears to be a species, whose populations have separated within the last 1 million years, but which are still mainly in gene flow (Dietzen et al. 2006; Arnaiz-Villena et al. 1999, 2007).

The Trumpeter Finch (*Bucanestes githagineus*) populates the middle and eastern Canary Islands. Microsatellite analyses (Barrientos et al., 2009) have shown that the Trumpeter Finch of the Canary Islands differs from the Trumpeter Finch in North Africa and southern Spain. Therefore, the assumption of an endemic subspecies *B. g. amantum* (Table 2) seems to be justified.

On the island of Sao Miguel in the Azores, a species of Bullfinch (Fig. 2n)lives in the laurel forest, that is closely related to the European bullfinch (*Pyrrhula pyrrhula*). This Bullfinch is genetically so different that it can be separated as a distinct species *P. murina* (Töpfer et al. 2011). The sperm morphology of both bullfinch species shows a similar variability and unusual morphology, suggesting close relationship of both taxa (Lifjeld et al. 2013).

Blackbirds (*Turdus merula*) from the Azores do not show genetic differentiation between islands, although two founder events have been assumed (Rodrigues et al., 2016).

Some songbirds of Macaronesia with endemic taxa (Tab. 2) have not yet be-en genetically studied, e.g., *Alauda razae*, Grey wagtail, Alpine Chough, Rock sparrow and Linnet.

Table 3: Taxa which are genetically supported are printed in **bold**, the other in normal type) *= no or little genetic differences; subspecies status questionable; ? = not studied so far.

Species	Azores	Madeira	Canary Islands	Cape Verde Islands
Pterodroma deserta		***deserta***		
Pterodroma feae				***feae***
Pterodroma madeira		***madeira***		
Calonectris borealis	***borealis***	***borealis***	***borealis***	
Calonectris edwardisii				***edwardisii***
Puffinus baroli	**ssp. *baroli***	**ssp. *baroli***	**ssp. *baroli***	ssp. ***boydi***
Oceanodroma monteroi	***monteroi***			
Neophron percnopterus			**ssp. *majorensis***	ssp. *percno-pterus?*
Buteo buteo	ssp. *rothschildi**	**ssp. *buteo***	ssp. *insularum**	ssp. ***bannermani***

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Table 3 – continued from previous page

Species	**Azores**	**Madeira**	**Canary Islands**	**Cape Verde Islands**
Chlamydotis undulata			ssp. *fuerteventurae**	
Columba palumbus	ssp. *azorica**	ssp. *maderensis?*		
Columba trocaz		***trocaz***		
Columba bollii			***bollii***	
Columba junoniae			***junoniae***	
Tyto alba		ssp. *schmitzi**	**ssp. *alba***, ssp. *gracilirostris**	ssp. *detorta?*
Apus alexandri				***alexandri***
Apus unicolor		***unicolor***	***unicolor***	
Apus pallidus		ssp. *brehmorum**	ssp. *brehmorum**	
Dendrocopos major			ssp. ***canariensis***	
Anthus berthelotii		ssp. *madeirensis**	ssp. *berthelotii**	
Alauda rufescens			ssp. ***rufescens***;	
Erithacus rubecula	**ssp. *rubecula***	**ssp. *rubecula***	**ssp. *rubecula***, ssp. ***superbus***, ssp. ***marionae***	
Saxicola dacotiae			ssp. ***dacotiae***	
Sylvia atricapilla	ssp. *gularis?*	ssp. *heineken**	ssp. *heineken**	ssp. *gularis?*
Sylvia melanocephala			ssp. *leucogastra**	
Sylvia conspicillata		ssp. *bella**	ssp. *orbitalis**	ssp. *orbitalis?*
Acrocephalus brevipennis				***brevipennis***

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Table 3 – continued from previous page

Species	**Azores**	**Madeira**	**Canary Islands**	**Cape Verde Islands**
Phylloscopus canariensis			**ssp. *canariensis***,	
Regulus regulus	**ssp. *azorica*, ssp. *sanctae-mariae* ssp. *inermis*,**		**ssp. *ellenthalerae*, ssp. *teneriffae***	
Regulus madeirensis		***madeirensis***		
Cyanistes teneriffae			**ssp. *teneriffae*, ssp. *hedwigii*, ssp. *palmensis*, ssp. *ombriosus*, ssp. *ultramarinus***	
Lanius [excubitor]			**ssp. *koenigi***	
Corvus corax			ssp. *tingitanus**, ssp. ***jordani***	
Sturnus vulgaris	**ssp. *granti***			
Passer iagoensis				***iagoensis***
Fringilla teydea			**ssp. *teydea*, ssp. *polatzeki***	
Fringilla coelebs	**ssp. *moreletti***	**ssp. *maderensis***	**ssp. *palmae*, ssp. *canariensis*; ssp *nov.***	
Serinus canaria	***canaria***	***canaria***	***canaria***	
Bucanetes githagineus			**ssp. *amantum***	

Continued on next page

Table 3 – continued from previous page

Species	**Azores**	**Madeira**	**Canary Islands**	**Cape Verde Islands**
Pyrrhula murina	***murina***			

4 Outlook

Genetic investigations by my research group and many other ornithologists have shown surprisingly high variability and the presence of island- or archipelago-specific genetic lineages, while most widespread Eurasian birds often show little internal differentiation. Although some of the Macaronesian islands are relatively old, most of them have only been colonised by species from Europe or Africa in the last 4-5 million years (Illera et al. 2012, 2016). The young age of settlement is apparently responsible for the fact that the endemism of the Macaronesian Islands is lower than in other oceanic archipelagos, such as on the Caribbean Islands, Galapagos or Hawaii (Illera et al. 2012, 2016).

In general, it will be worth taking a closer look at the genetic diversity of the individual Macaronesian islands by studying larger numbers of individuals per island and above all using high-resolution markers for mtDNA and nuclear DNA (e.g., SNPs = single nucleotide polymorphism). Our data to date show that these investigations remain exciting and can provide us with an insight into speciation processes. More detailed analyses could show whether the archipelago was colonised once or several times or whether a stepping stone model was used (Sanmartin et al. 2008).

Since birds are able to fly, we must assume that immigration from one neighbouring island to another takes place from time to time. Why do the local populations do not mix? Are there pre- or postzygotic reproductive barriers, such as different songs (there are already indications of this) or sperm incompatibility (Lifjeld et al. 2013)?

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References

Agudo, R.; Rico, C.; Hiraldo, F. & Donázar J.A. (2011): Evidence for connectivity between continental and differentiated insular populations in a highly mobile species. Diversity and Distributions 17: 1-12.

Arctander, P.; Folmer, O. & Fjeldsa, J. (1996): The phylogenetic relationships of Berthelot's pipit *Anthus berthelotii* illustrated by DNA sequence data, with remarks on the genetic distance between Rock and Water pipits *Anthus spinoletta*. Ibis 138: 263-272.

Arnaiz-Villena, A.; Álvarez-Tejado, M.A.; Ruiz-Del-Valle, V.; García-De-La-Torre, C.; Varela, P.; Recio, M.J.; Ferre, S. & Martínez-Laso, J. (1999): Rapid radiation of canaries (Genus *Serinus*). Mol. Biol. Evol. 16: 2-11.

Arnaiz-Villena, A.; Lowy, E.; Ruiz-Del-Valle, V.; Westerdahl, H.; Moscoso J.; Serrano-Vela, J.I.; Witzell, H. & Zamora, J. (2007): Evolution of the major histocompatibility complex class I genes in *Serinus canaria* from the Canary Islands is different from that of Asian and African continental *Serinus* species. J. Ornithol. 148: S479-S484.

Barrientos, R.; Kvist, L.; Barbosa, A.; Valera, F.; López-Iborra, G.M. & Moreno, E. (2008): Colonization patterns and genetic structure of peripherals populations of the trumpeter finch (*Bucanetes githagineus*) from Northwest Africa, the Canary Islands and the Iberian Peninsula. J. Biogr. 36: 210-219.

Berthold, P.; Mohr, G. & Querner, U. (1997) Die Schleiergrasmücke: Genetische Grundlagen, rezente Beobachtungen und historische Aspekte dieser melanistischen Form der Mönchsgrasmücke *Sylvia atricapilla*. J. Ornithol. 138: 136-170.

Blackburn, T.M.; Cassey, P.; Duncan, R.P.; Evans, K.L. & Gaston, K.L. (2004) Avian extinction and mammalian introductions on oceanic islands. Science 305: 1955-1958.

Broders, O.; Osborne, T. & Wink, M. (2003): A mtDNA phylogeny of bustards (family Otitidae) based on nucleotide sequences of the cytochrome b gene. J. Ornithol. 144: 176-185.

Brooks, T.M.; Mittermeier, R.A.; Mittermeier, C.G.; Da Fonseca, G.A.B.; Rylands, A.B.; Konstant, W.R.; Flick, P.; Pilgrim, J.; Oldfield, S.; Magin, G. & Hilton-Taylor, G. (2002). Habitat loss and extinction in the hotspots of biodiversity. Conserv. Biol. 16: 909-923.

Carneiro Da Silva, M. & Granadeiro J.P. (1999): Genetic variability and isolation of Cory's shearwater colonies in the northeast Atlantic. Condor 101: 174-179.

Clarke, T.; Orgill, C. & Disley, T. (2006): A Field Guide to the Birds of the Atlantic Islands: Canary Islands, Madeira, Azores, Cape Verde. Christopher Helm, London, 368 pp.

Clouet, M. & Wink, M. (2000): The Buzzards of Cape Verde (*Buteo (buteo) bannermani*) and Socotra (*Buteo buteo spp.*)- First results of a genetic analysis based on nucleotide sequences of the cytochrome b gene. Alauda 68: 55-58.

Darwin, C. (1859): On the Orgin of Species.

De Castro, A.G.F.; Moreno-Saiz, J.C & Fuertes-Aguiar, J. (2017): Ornithophily for the nonspecialist: Differential pollination efficiency of the Macaronesian island paleoendemic *Navaea phoenicea* (Malvaceae) by generalist passerines. American Journal of Botany 104: 1556-1568.

Delgado Castro, G.; Delgado, J. D.; Gonzalez, J. & Wink, M. (2013): Sexual size dimorphism of the in the extreme SW breeding population of the European Storm petrel *Hydrobates pelagicus* (Aves: Procellariformes). Vertebrate Zool. 63: 309-314.

Dietzen, C.; Michels, J. P. & Wink, M. (2015): Formal description of a new subspecies of the European Robin from Gran Canaria Island, Spain (Aves: Muscicapidae: *Erithacus rubecula marionae* subsp. nov.). Open Ornithology Journal, 8: 39-42.

Dietzen, C.; García-Del-Rey, E.; Delgado, G. & Wink, M. (2008): Phylogenetic differentiation of *Sylvia* species (Aves: Passeriformes) of the Atlantic islands (Macaronesia) based on mitochondrial DNA sequence data and morphometrics. Biol. J. Linn. Soc. 95: 157-174.

Dietzen, C.; Voigt, C.; Wink, M.; Gahr, M. & Leitner, S. (2006): Phylogeography of island canary (*Serinus canaria*) populations. J. Ornithol. 147: 485-494.

Dietzen, C.; Witt, H.-H; & Wink, M. (2003): The phylogeographic differentiation of the European robin, *Erithacus rubecula*, on the Canary Islands revealed by mitochondrial DNA sequence data and morphometrics: evidence for a new robin taxon on Gran Canaria? Avian Sci. 2-3: 115-131.

Donázar, J.A.; Negro, J.J.; Palacios, C.J.; Gangoso, L.; Godoy, J.A.; Ceballos, O.; Hiraldo, F. & Capote, N. (2002): Description of a new subspecies of the Egyptian vulture (Accipitridae: *Neophron percnopterus*) from the Canary Islands. Journal of Raptor Research, 36: 17–23.

Dourado, C.G.; Duarte, M.A.; Grosso, A.R.; Bastos-Silveir, A C.; Marrero, P.; Oliveira, P.; Paulo, O.S. & Dias, D. (2014): Phylogenetic origin of the endemic pigeons from Madeira (*Columba trocaz*) and Azores Islands (*Columba palumbus azorica*). J. Ornithol. 155: 71-82.

Friesen, V.L.; Smith, A.L.; Gómez-Díaz, E.; Bolton, M.; Furness, R.W.; González-Solís, J. & Monteiro, L.R. (2007): Sympatric speciation by allochrony in a seabird. Proc. Natl. Acad. Sci. U.S.A. 104: 18589-18594.

Garcia-Del Rey, E. (2011): Field Guide to the Birds of Macaronesia. Lynx, Barcelona

Garcia-Del Rey, E.; Delgado, G.; Gonzalez, J. & Wink, M. (2007): Canary Island Great spotted woodpecker (*Dendrocopos major*) has distinct mtDNA. J. Ornithol. 148: 531-536.

Garcia-Del-Rey, E.; Marthinsen, G.; Calabuig, P.; Estevez, L.; Johannessen, L.E.; Johnsen, A.; Laskemoen, T. & Lifjeld, J. T. (2013): Reduced genetic diversity and sperm motility in the endangered Gran Canaria Blue Chaffinch Fringilla teydea polatzeki. J. Ornithol. 154: 761-768.

Gaucher, P.; Paillat, P.; Chappuis, C.; Saint Jalme, M.; F. Lotfikhah, F. & Wink, M. (1996): Taxonomy of the Houbara bustard, *Chlamydotis undulata* subspecies considered on the basis of sexual display and genetic divergence. Ibis 138: 273-282.

Gómez-Díaz, E.; González-Solís, J.; Peinado, M.A. & Page, R.D.M. (2006): Phylogeography of the Calonectris shearwaters using molecular and morphometric data. Mol. Phyl. Evol. 41: 322-332.

González, J.; Delgado Castro, G.; García-Del-Rey, E.; Berger, C. & Wink, M. (2009): Use of mitochondrial and nuclear genes to infer the origin of two endemic pigeons from the Canary Islands. J. Ornithol. 150: 357-367.

Gonzalez, J.; Wink, M.; Garcia-Del-Rey, E. & Delgado, G. (2008): Evidence from DNA nucleotide sequences and ISSR profiling indicates paraphyly in Southern Grey shrike (*Lanius meridionialis*). J. Ornithol. 149: 495-506.

Grant P. R. & Weiner, J. (1999): Ecology and Evolution of Darwin's Finches. Princeton University Press.

Grant, P.R. & Grant, B.R. (2008): How and Why Species Multiply. The Radiation of Darwin's Finches. Princeton Series in Evolutionary Biology.

Groombridge, J.J.; Jones, C.G.; Bayes, M.K.; Van Zyl, A.J.; Carrillo, J.; Nichols, R.A. & Bruford, M.W. (2002): A molecular phylogeny of African kestrels with reference to divergence across the Indian Ocean. Mol. Phyl. Evol. 25: 267-277.

Haring, E.; Däubl, B.; Pinsker, W.; Kryukov, A, & Gamauf, A. (2012): Genetic divergences and intraspecific variation in corvids of the genus *Corvus* (Aves: Passeriformes: Corvidae): a first survey based on museum specimens. J Zool Syst Evol Res 50: 230–246.

Heidrich, P.; Amengual, P.; Ristow, D. & Wink, M. (2000): Phylogenetic relationships among Procellariiformes based on nucleotide sequences, with special reference of the Mediterranean and North Atlantic shearwaters. In "Monitoring and conservation of birds, mammals and sea turtles of the Mediterranean and Black Seas. (P. Yésou & J. Sultana, eds.), Birdlife, Malta, pp 159-175.

Heidrich, P.; Ristow, D. & Wink, M. (1996): Molekulare Differenzierung von Gelb- und Schwarzschnabelsturmtauchern (*Calonectris diomedea, Puffinus puffinus, P.*

yelkouan) und Großmöwen des Silbermöwenkomplexes (*Larus argentatus, L. fuscus, L. cachinnans*). J. Ornithol. 137: 281-294.

Helbig, A.J.; Martens, J.; Seibold, I.; Henning, F.; Schottler, B. & Wink, M. (1996): Phylogeny and species limits in the Palaearctic chiffchaff *Phylloscopus collybita* complex. Ibis 138: 650-666.

Hille, S.M.; Nesje, M. & Segelbacher, G. (2003): Genetic structure of kestrel populations and colonization of the Cape Verde archipelago. Mol. Ecol. 12: 2145-2151.

Idaghdour, Y.; Broderick, D.; Korrida, A. & Chbel, F. (2004): Mitochondrial control region diversity of the Houbara Bustard *Chlamydotis undulata* complex and genetic structure along the Atlantic seaboard of North Africa. Mol. Ecol. 13: 43-54.

Illera, J.C.; Rando, J.C.; Richardson, D.S. & Emerson, B.C. (2012): Age, origins and extinctions of the avifauna of Macaronesia: a synthesis of phylogenetic and fossil information. Quaternary Science Reviews 50: 14-22.

Illera, J.C.; Palmera, A.M; Laiolo, P.; Rodriguez, F.; Moreno, A.C. & Navascues, M. (2014): Genetic, morphological, and acoustic evidence reveals lack of diversification in the colonization process in an island bird. Evolution 68: 2259-2274.

Illera, J.C., Spurgin, L.G.; Rodriguez-Esposito, E.; Nogales, M. & Rando, J.C. (2016): What are we learning about speciation and extinction from Canary Islands? Ardeola 63: 15-33.

Illera, J.C.; Emerson, B.C. & Richardson, D.S. (2007): Population history of Berthelot's pipit: colonisation, gene flow and morphological divergence in Macaronesia. Mol. Ecol. 16: 4599-4612.

Illera, J.C.; Koivula, K.; Broggi, J.; Päckert, M.; Martens, J. & Kvist, L. (2011): A multi-gene approach reveals a complex evolutionary history in the *Cyanistes* species group. Mol. Ecol. 20: 4123-4139.

Illera, J.C.; Richardson, D.S.; Helm, B.; Atienza, J.C. & Emerson, B.C. (2008): Phylogenetic relationships, biogeography and speciation in the avian genus *Saxicola*. Mol. Phyl. Evol. 48: 1145-1154.

Jesus, J.; Menezes, G.; Gomes, S.; Oliveira, P.; Nogales, M. & Brehm A. (2009): Phylogenetic relationships of gadfly petrels *Pterodroma* spp. from the Northeastern Atlantic Ocean: molecular evidence for specific status of Bugio and Cape Verde petrels and implications for conservation. Bird Conserv. Internat. 19: 199-214.

Klassert, T.E.; Hernández, M.A.; Campos, F.; Infante, O.; Almeida, T.; Suárez, N.M.; Pestano, J. & Hernández M. (2008): Mitochondrial DNA points to *Lanius meridionalis* as a polyphyletic species. Mol. Phyl. Evol. 47: 1227-1231.

Korrida, A. & Schweizer, M. (2014): Diversification across the Palaearctic desert belt throughout the Pleistocene: phylogeographic history of the Houbara–Macqueen's bustard complex (Otididae: *Chlamydotis*) as revealed by mitochondrial DNA. J. Zoolog. Syst. Evol. Res. 52: 65-74.

Korrida A.; Jadallah S.; Chbel F.; Amin-Alami, A.; Ahra M. & Aggrey S. (2012): Patterns of genetic diversity and population structure of the threatened Houbara and Macqueen's bustards as revealed by microsatellite markers. Gen. Mol. Res. 11: 3207-3221.

Kruckenhauser, L.; Haring, E.; Pinsker, W.; Riesing, M. J.; Winkler, H.; Wink, M. & Gamauf, A. (2004): Genetic versus morphological differentiation of old world buzzards (genus *Buteo*; Accipitridae). Zoologica Scripta 33: 197-211.

Kvist, L.; Broggi, J.; Illera, J.C. & Koivula, K. (2005): Colonisation and diversification of the blue tits (*Parus caeruleus teneriffae*-group) in the Canary Islands. Mol. Phyl. Evol. 34: 501-511.

Leisler, B.; Heidrich, P.; Schulze-Hagen, K., & Wink, M. (1997): Taxonomy and phylogeny of reed warblers (genus *Acrocephalus*) based mtDNA sequences and morphology. J. Ornithol. 138: 469-496.

Lifjeld, J.T.; Hoenen, A.; Johannessen, L. E.; Laskemoen, T.; Lopes, R. J.; Rodrigues, P. & Rowe, M. (2013): The Azores bullfinch (*Pyrrhula murina*) has the same unusual and size-variable sperm morphology as the Eurasian bullfinch (*Pyrrhula pyrrhula*). Biol. J. Linn. Soc. 108: 677-687.

Lopez-Darias; M. & Nogales, M. (2016): Raptors as legitimate secondary dispersers of weed seeds. Ibis 158: 428-432.

MacArthur, R. H. & Wilson, E. O. (1967): The Theory of Island Biogeography. Princeton, NJ: Princeton University Press.

Marshall, H.D. & Baker, A.J. (1999): Colonization history of Atlantic island common chaffinches (*Fringilla coelebs*) revealed by mitochondrial DNA. Mol. Phyl. Evol. 11: 201-212.

Mori, A.; Giunchi, D.; Rodriguez-Godoy, F.; Grasso, R.; Baldaccini, N.E., & Baratti, M. (2017): Multilocus approach reveals an incipient differentiation process in the Stone-curlew, *Burhinus oedicnemus* around the Mediterranean basin. Conservation Genetics 18: 197-209.

Neves, V.C.; Griffiths, K.; Savory, F.R.; Furness, R.W. & Mable, B.K. (2010): Are European starlings breeding in the Azores archipelago genetically distinct from birds breeding in mainland Europe? Eur. J. Wildl. Res. 56: 95-100.

Niethammer, G. (1953): Der Kolkrabe (*Corvus corax*) von Fuerteventura, ein Beitrag zur Tiergeographie der östlichen Kanaren. Bonn. Zool. Beiträge 4: 73–78.

Olsson, U.; Alström, P.; Svensson, L.; Aliabadian, M. & Sundberg, P. (2010): *The Lanius excubitor* (Aves, Passeriformes) conundrum - taxonomic dilemma when molecular and non-molecular data tell different stories. Mol. Phyl. Evol. 55: 347e357.

Päckert, M.; Dietzen, C.; Martens, J.; Wink, M. & Kvist, L., 2006. Radiation of Atlantic goldcrests *Regulus regulus* spp.: evidence of a new taxon from the Canary Islands. J. Avian Biol. 37: 364-380.

Päckert, M.; Martens, J.; Wink, M.; Feigl, A. & Tietze, D.T. (2012) Molecular Phylogeny of Old World swifts (Aves: Apodiformes, Apodidae, *Apus* and *Tachymarptis*) based on mitochondrial and nuclear markers. Mol. Phyl. Evol. 63: 606-616.

Padilla, D.P.; Gonzalez-Castro, A. & Nogales M. (2012): Significance and extent of secondary seed dispersal by predatory birds on oceanic islands: the case of the Canary archipelago. J. Ecol. 100: 416-427.

Pestano, J.; Brown, R.P.; Rodríguez, F. & Moreno, A. (2000): Mitochondrial DNA control region diversity in the endangered blue chaffinch, *Fringilla teydea*. Mol. Ecol. 9: 1421-1425.

Rando, J.C.; Pieper, H; Olson, S.L.; Pereira, F. & Alcover, J.A. (2017): A new extinct species of large bullfinch (Aves: Fringillidae: *Pyrrhula*) from Graciosa Island (Azores, North Atlantic Ocean). Zootaxa 4282: 567-583.

Rodrigues, P.; Lopes, R.J.; Micael, J.; Resendes, R.; Ramos, J.A. & Da Cunha, R.T. (2014): Enetic and morphometric diversity of the Goldcrest (*Regulus regulus*) -populations in the Azores. Zoology 117: 383-391.

Rodrigues, P.; Lopes. R.J.; Reis, S.; Resendes, R.; Ramos, J.A. & Da Cunha, R.T. (2014): Genetic diversity and morphological variation of the Common chaffinch *Fringilla coelebs* in the Azores. J Avian Biology 45: 167-178.

Rodrigues, P.; Lopes; R.J.; Resendes, R.; Ramos, J.A. & Cunha, R.T. (2016): Genetic diversity of the Azores Blackbirds *Turdus merula* reveals multiple founder events. Acta Ornithologica 51: 221-234.

Rodrigues, P.; Lopes, R. J.; Drovetski, S.V.; Reis, S.; Ramos, J.A. & Tristao Da Cunha, R. (2013): Phylogeography and genetic diversity of the Robin (*Erithacus rubecula*) in the Azores Islands: Evidence of a recent colonisation. J. Ornithol. 154: 889-900.

Rösner, S.; Cimiotti, D.V. & Brandl, R. (2014): Two sympatric lineages of the Raven *Corvus corax jordansi* coexist on the Eastern Canary Islands. J. Ornithol. 155: 243-251.

Sancho-Marco, A. (2010): New data and an overview of the past avifaunas from the Canary islands. Ardeola 57: 13-40.

Sanmartin, I.; Van Der Mark, P. & Ronquist, F. (2008): Inferring dispersal: a Bayesian approach to phylogeny-based island biogeography, with special reference to the Canary islands. J. Biogeogr. 35: 428-449.

Schönfelder, I. & P. (2002) Kosmosatlas Mittelmeer- und Kanarenflora. Kosmos, Stuttgart.

Smith A.L.; Monteiro L.; Hasegawa, O. & Friesen V.L. (2007): Global phylogeography of the band-rumped storm-petrel (*Oceanodroma castro*; Procellariiformes: Hydrobatidae). Mol. Phyl. Evol. 43: 755–773.

Swatschek, I.; Ristow, D. & Wink, M. (1994): Mate fidelity and parentage in Cory's shearwater (*Calonectris diomedea*)- Field studies and DNA Fingerprinting. Mol. Ecol. 3: 259-262.

Töpfer, T.; Haring, E.; Birkhead, T.R.; Lopes, R.J.; Severinghaus, L.; Martens, J. & Päckert, M., 2011. A molecular phylogeny of bullfinches *Pyrrula* Brisson, 1760 (Aves: Fringillidae). Mol. Phyl. Evol. 58: 271-282.

Valente; L.; Illera, J.C.; Havenstein, K.; Pallien, T.; Etienne, R.S. & Tiedemann, R. (2017): Equilibrium bird species diversity in Atlantic Islands. Current Biology 27: 1660-1671.

Valido, A.; Dupont, Y.L. & Olesen, J.M. (2004): Bird-flower interactions in the Macaronesian islands. J. Biogeogr. 31: 1945-1953.

Viana D.S.; Gangoso L.; Bouten, W. & Figuerola, J. (2016): Overseas seed dispersal by migratory birds. Proc. Royal Society B 283, 20152406

Warham, J. (1990): The petrels: their ecology and breeding systems. New York: Academic Press.

Wink, M.; Sauer-Gürth, H. & Gwinner, E. (2002):A molecular phylogeny of stonechats and related turdids inferred from mitochondrial DNA sequences and genomic fingerprinting by ISSR-PCR. Brit. Birds 95: 349-355.

Wittmann, U.; Heidrich, P.; Wink, M. & Gwinner, E. (1995): Speciation in the stonechat (*Saxicola torquata*) inferred from nucleotide sequences of the cytochrome b gene. J. Zoo. Syst. Evol. Research 33: 116-122.

Zink, R.; Pavlova, A.; Drovetski, S.; Wink, M. & S Rohwer (2009): Taxonomic status and evolutionary history of the *Saxicola torquata* complex. Mol. Phyl. Evol. 52: 769-773.

Zino, F.; Brown, R. & Biscoito, M. (2008): The separation of *Pterodroma madeira* (Zino's Petrel) from *Pterodroma feae* (Fea's Petrel) (Aves, Procellariidae). Ibis 150: 326–334.

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