Bird–flower interactions in the Macaronesian islands

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ABSTRACT

Aims Several bird-pollinated or ornithophilous flowers are present on the Macaronesian archipelagos, the Canary Islands and Madeira, but absent from nearby NW Africa and Europe. In Macaronesia, no specialist nectar-feeding birds are found, but several generalist passerine bird species visit flowers for nectar. Two hypotheses attempt to explain the origin and evolution of ornithophily in the Macaronesian flora. According to ‘the island de novo hypothesis’, bird-flowers evolved from mainland insect-pollinated ancestors after island colonization. Alternatively, ancestors of the ornithophilous Macaronesian plant species evolved bird-flowers before reaching the islands (‘the relict hypothesis’). In this study we first compile information of Macaronesian bird–flower interactions from the literature and our own field observations. Secondly, we discuss the two hypotheses of origin of ornithophily in the light of evidence from recent molecular plant phylogenies, palaeontology, historical biogeography of the African avifauna and flora, and present-day ecological patterns.

Location Madeira and Canary Islands.

Results At least eleven endemic Macaronesian plant species from six genera have typical ornithophilous floral traits. These genera are: Canarina and Musschia (Campanulaceae), Isoplexis (Scrophulariaceae), Echium (Boraginaceae), Lotus (Fabaceae) and Lavatera (Malvaceae). These lineages have clear affinities to the Mediterranean region, except for Canarina whose closest relatives grow in East African mountains. Six generalist passerine bird species of Sylvia, Phylloscopus (Sylviidae), Serinus (Fringillidae) and Parus (Paridae) visit this flora for nectar.

Main conclusion We suggest that the origin and evolution of ornithophilous traits in these plant species took place mostly in mainland areas prior to island colonization. In Canarina and Lavatera, it is well supported that ornithophily is a relict condition, which originated in mainland areas possibly in association with specialist nectar-feeding birds. For the remaining plant species except Echium wildpretii bird floral traits probably also are a relict condition. These species may be derived from ancestors, which were visited by specialist nectar-feeding birds during geological periods when the Mediterranean and the Ethiopian vegetation were intermingled in mainland Africa. Probably, these mainland ancestors went extinct due to severe climatic fluctuations, while their Macaronesian descendants survived in ‘refuge’ on the islands. Finally, the island de novo hypothesis may explain the evolution of a mixed bird/insect-pollination system in the neo-endemic red-flowered Echium wildpretii.

Keywords Ornithophily, Canary Islands, Madeira, island evolution, generalist nectar-feeding passerine birds, Isoplexis, Lotus, Lavatera, Canarina, Echium, bird pollination syndrome, oceanic islands.
RESUMEN

Objetivo En el presente estudio se aportan nuevos datos acerca de las interacciones entre aves y flores en los archipiélagos de Macaronesia (Islas Canarias y Madeira) con el fin de explicar el origen y la evolución de los caracteres ornitófilos presentes en algunas plantas endémicas de estas islas. Tanto la ausencia de este tipo de flora ornitófila en las áreas continentales cercanas, como la no existencia de aves nectarívoras especializadas en estas islas (inclusive en el pasado), hace que este fenómeno se haya considerado como un enigma biológico, aún sin resolver. Dos hipótesis principales han sido propuestas para explicar estos casos. Primero, que los caracteres florales evolucionaron recientemente en las islas a partir de ancestros que eran polinizados por insectos en el continente (hipótesis de novo). Alternativamente, que los ancestros que colonizaron estas islas ya presentaban caracteres ornitófilos previo a la colonización insular (hipótesis relictual). En el presente estudio, se discute ambas hipótesis utilizando información reciente acerca de las relaciones filogenéticas de estas plantas, así como datos paleontológicos, de la historia biogeográfica de la flora y avifauna de Africa, y de los patrones ecológicos actuales.

Localización Madeira y Canarias.

Resultados Los datos obtenidos muestran que al menos once plantas endémicas procedentes de seis líneas evolutivas independientes: especies de Canarina y Musschia (Campanulaceae), Isoplexis (Scrophulariaceae), Echium (Boraginaceae), Lotus (Fabaceae), y Lavatera (Malvaceae) presentan caracteres florales típicamente ornitófilos. Seis paseriformes generalistas: especies de Sylvia y Phylloscopus (Sylviidae), Serinus (Fringilliidae) y Parus (Paridae), son asiduos visitantes de estas flores para libar su néctar. Si excluimos a Canarina, la cual presenta sus relativos más cercanos en plantas de la flora etiópica, el resto de los taxones presentan clara afinidad con la flora del área mediterránea (donde actualmente no se encuentran ninguna especie de planta que podamos considerar como ornitófila, ni aves nectarívoras especializadas).

Conclusión Acorde a las evidencias presentadas, la principal conclusión obtenida en el presente estudio es que el origen y la evolución de los caracteres florales ornitófilos parece que tuvo lugar en el continente previo a la colonización insular. Para Canarina y Lavatera, parece evidente que la ornitofilia es una condición relictual que posiblemente se originó en asociación con aves especializadas en libar néctar en el continente. Para el resto de especies con afinidad mediterránea, el origen de la ornitofilia es menos clara, pero las evidencias presentadas señalan igualmente hacia un origen continental, y que posiblemente tuvo lugar cuando elementos de la flora mediterránea estuvieron en contacto con la vegetación etiópica en el pasado. En este escenario, aves nectarívoras especializadas posiblemente visitaron asiduamente las flores de los ancestros de esta flora ornitófila macaronésica. Posteriormente, y como consecuencia de fluctuaciones climáticas severas en el continente, dichos elementos se extinguieron, y únicamente aquellos taxones que colonizaron y se establecieron en estas islas, sobrevivieron hasta nuestros días. Finalmente, la hipótesis de novo parece explicar mejor el caso de los tajinastes rojos (g. Echium), el cual es considerado como un neo-endemismo, y cuyas flores presentan rasgos mixtos de polinización por insectos y aves.

Palabras clave
Ornitofilia, Islas Canarias, Madeira, evolución insular, Paseriformes generalistas libadores de néctar, Isoplexis, Lotus, Lavatera, Canarina, Echium, sindromes de polinización por aves.
INTRODUCTION

Thousands of species of flowering plants rely on birds as pollinators and about 50 families of birds are reported as flower visitors (Proctor et al., 1996; Renner, 1996). The largest diversity of specialist nectarivorous birds is found in tropical and subtropical regions (Proctor et al., 1996). In addition to these groups, several generalist birds occasionally include nectar in their diet. This behaviour is observed in Australia (e.g. Franklin & Noske, 1999, 2000; Franklin, 1999), Africa (e.g. Oatley & Skead, 1972; Pettet, 1977), Europe (e.g. Thake, 1980; Kay, 1985; Bürquez, 1989; Thiede, 1998), and Central and South America (e.g. Fisk & Steen, 1976). Generally, opportunistic nectarivory is observed when preferred resources (insects, fruits and seeds) are in short supply and nectar from typical bird plant species is also abundant (e.g. during winter, early cold spring or dry seasons; Pettet, 1977; Thake, 1980; Bürquez, 1989; Franklin & Noske, 1999).

Whereas opportunistic nectarivory by generalist passerines is considered casual in mainland ecosystems (but see Ford, 1985), it is a relatively frequent phenomenon on oceanic islands. Examples include Darwin Finches in Galápagos (Grant & Grant, 1981), red-whiskered bulbul (Olesen et al., 1998), Madagascar fody (Safford & Jones, 1998), Mauritius grey and olive white-eyes in Mauritius (Hansen et al., 2002), Japanese white-eye (Pimm & Pimm, 1982; Lammers & Valido, 2003a). The phenomenon may be related to certain characteristics of island biota. Compared with mainland areas, few species inhabit oceanic islands. Thus, interspecific competition is reduced. Some insular species respond to competitive release by increasing their abundance (density compensation; MacArthur et al., 1972). In lizards, nectarivory on islands may be a result of competitive release and density compensation, combined with a general shortage of arthropod food on islands (Olesen & Valido, 2003a). A similar mechanism may explain nectarivory in generalist passerine birds (Olesen & Valido, 2003a).

Since early last century, the association of birds and flowers in the Macaronesian islands has received interest (e.g. Porsch, 1924; Schmucker, 1936). Generalist passerine bird species, which regularly visit flowers for nectar include Sylvia atricapilla L., S. conspicillata Temminck, S. melanopephala Gimelin, and Phylloscopus collybita Vicillot (Sylviidae), Parus caeruleus L. (Paridae), and Serinus canarius L. (Fringillidae). The Palearctic P. collybita, P. caeruleus and Sylvia spp. are known to be insectivorous and/or frugivorous in mainland habitats (see references in Cramp, 1992; Cramp & Perrins, 1994). The Macaronesian-endemic S. canarius is mostly granivorous (Martin & Lorenzo, 2001). No specialized nectarivorous bird species are present in the Macaronesian islands, and no fossils indicate an earlier presence (Pieper, 1985; Tyrberg, 1998, 2003; H. Pieper & J.C. Rando, pers. comm.). Nevertheless, a small group of endemic plant species show typical ornithophilous traits such as red-orange-yellow floral corolla, plenty of dilute nectar and absence of scent (Faegri & Pijl, 1971). Typical ornithophilous plants are absent from the nearest mainland floras in S Europe and NW Africa.

Here, we review records of bird–flower interactions in the Macaronesian islands including new field observations. We discuss two hypotheses to explain origin and evolution of ornithophily in the Macaronesian flora. Floral traits in the bird-pollinated plants could have evolved on the islands from mainland colonizers (‘island de novo hypothesis’). Alternatively, these plants may originate from bird-pollinated mainland species (‘relict hypothesis’). For the various lineages of Macaronesian ornithophilous plants, we discuss both hypotheses using four different approaches: molecular phylogenies, the fossil record, historical biogeography and ecological patterns.

RESULTS

At least six generalist passerine bird species visit flowers for nectar in 11 native plant species in Macaronesia (Table 1). The floral traits of most of these plant species includes typical ornithophilous traits. The three Canarian species of Isoplexis (Scrophulariaceae) and Canarina canariensis (Campanulaceae) are visited almost exclusively by birds. A few insects (solitary bees, e.g. Lasioglossum spp., Halictidae) too small to act as pollinators, have been observed visiting these large flowers. Furthermore, in secondary open forest, the Canarian-endemic lizard (Gallotia galloti Oudart, Lacertidae) drinks nectar from Isoplexis canariensis. Bumblebees often try to visit the Madeiran L. sceptrum. Their visits fail because the corolla becomes slippery and sticky from nectar oozing out of the corolla. The Madeiran Muschia wollastoni is visited by birds and insects. The extremely rare Lotus berthelotii (Fabaceae) certainly looks like an ornithophilous flower. However, apart from a few individuals of Lasioglossum spp., a Lycaenidae sp. and a few ants, no flower visitors have been observed. In Tenerife, Echium wildpretii ssp. wildpretii (Boraginaceae) is visited frequently by both insects, passerines and occasionally by lizards. On the other hand, only insects were observed visiting its sister subspecies E. w. trichosiphon in the sub-alpine scrubland on the island of La Palma. Only insects have been recorded visiting the Canarian-endemic E. pininana in its natural habitats in La Palma. However, in New Zealand, where this species is introduced, the endemic Tui (Prosthemadera novaezeelandiae, Meliphagidae) takes its nectar. Furthermore, the Macaronesian flower-visiting birds (the six species mentioned above plus Passer hispaniolensis) forage for nectar in introduced plant species of Streptizia, Hibiscus, Aloe, Nicotiana and Agave. These species originate from S Africa and S and C America where they are pollinated by sunbirds and hummingbirds.

DISCUSSION

We show that in the Macaronesian islands, six species of birds feed regularly on nectar in seven typical ornithophilous plant
species. Several other Macaronesian plant species have red, purple or orange flowers indicating potential bird pollination or perhaps a mixed bird/insect pollination system, e.g. the Canarian Scrophularia calliantha Webb & Berthel. (Scrophulariaceae), Lotus pyranthus P. Pérez, L. berthelotii Masf., L. maculatus and L. eremiticus A. Santos, the Macaronesian Teucrium heterophyllum L’Her. (Lamiaceae), the Madeiran L. argyrodes R. P. Murray, and T. abutiloides L. Hér, and the Cape Verdean L. purpureus Webb and L. jacobaeus L. These species may be candidates for future observations of bird pollination. In addition, three plant species without evident ornithophilous floral traits are visited by Macaronesian birds (Echium decaisnei, E. virescens and Aeonium arboresum). We conclude that bird flowers and nectar feeding are relatively frequent phenomena in the Macaronesian islands compared with the nearest mainland. In the following, different non-exclusive lines of evidence are used to discuss the origin and evolution of these typical bird flowers.

### Phylogenetic evidence

Molecular phylogenies now exist for the majority of Macaronesian plant genera containing bird-flower species: e.g. Böhle et al. (1996) for Echium, Carvalho & Culham (1998) for Isoplexis, Fuertes-Aguilar et al. (2002) for Lavatera, Allan et al. (2004) for Lotus, and J.M. Olesen & B.K. Ehlers (unpubl. data) for Canarina and Musschia spp. According to this information, ornithophilous floral traits of Lavatera phoenicea and Canarina canariensis could be plesiomorphic (Fuertes-Aguilar et al., 2002; J.M. Olesen & B.K. Ehlers, unpubl. data). Lavatera

### Table 1

Bird–plant interactions in the Macaronesian islands (M: Madeira; C: Canary). Scan: Serinus canarius; Pcoll: Phylloscopus collybita; Smel: Sylvia melanocephala; Satri: S. atricapilla; Scons: S. conspicillata; Pcae: Parus caeruleus. We also add some putatively ornithophilous plant species (Lottus spp.) according to Vogel et al. (1984), Olesen (1985), and personal observations. Furthermore, we include E. pininana because the Tui (Prosthemadera novaeseelandiae, Meliphagidae) was observed visiting plants introduced in New Zealand (pers. obs.). *Data from greenhouse plants. Sugar content of nectar is given as average sugar percentage (g sugar per 100 g nectar) ± SD, sample size between brackets. References of bird–plant interactions: 1: Vogel et al. (1984); 2: Olesen (1985); 3: Trujillo (1992); 4: Valido et al. (2002) and Dupont et al. (2004a,b); 5: Olesen & Valido (2003a); 6: present study.

<table>
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<tr>
<th>Family</th>
<th>Distribution and habitat</th>
<th>Flower characteristics</th>
<th>Max. vol. (IL)</th>
<th>% Sugar</th>
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<th>Pcoll</th>
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<td>Echium decaisnei Webb</td>
<td>C; semidesert</td>
<td>White-blue</td>
<td>10 (1)</td>
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<td>Echium pininana</td>
<td>C; laurel and pine forest</td>
<td>Light-blue</td>
<td>1.4 26 ± 3 (20)</td>
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<td>Echium virescens DC.</td>
<td>C; pine forest</td>
<td>Purple-blue</td>
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<td>Echium wildpretii</td>
<td>C; subalpine shrub and</td>
<td>Red</td>
<td>21 15 ± 3.8 (286)</td>
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<td>Echium wildpretii</td>
<td>C; subalpine shrub</td>
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<td>18.2 ± 4.2 (8)</td>
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<td>Canarina canariensis</td>
<td>C; laurel forest</td>
<td>Red-orange</td>
<td>53 12.2 ± 2.0 (110)</td>
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<td>Musschia wollastonii</td>
<td>M; laurel forest</td>
<td>Purple-yellow</td>
<td>149 12.5 ± 1.2 (15)</td>
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<td>Aeonium arboresum</td>
<td>C; pine forest</td>
<td>Yellow</td>
<td>20.7 ± 4.9 (30)</td>
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<td>(L.) Webb &amp; Berthel.</td>
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<td>Lotus berthelotii Masf.</td>
<td>C; pine forest</td>
<td>Red</td>
<td>49 24 ± 15 (18)</td>
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<td>Lotus eremiticus A. Santos</td>
<td>C; pine forest</td>
<td>Orange</td>
<td>14.5 48</td>
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<td>Lotus maculatus Breitf.</td>
<td>C; xerophytic lowland</td>
<td>Yellow</td>
<td>5.4 33</td>
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<td>Lavatera phoenicea Vent.</td>
<td>C; transition to laurel</td>
<td>Salmon</td>
<td>112 24 (1)</td>
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<td>Isoplexis canariensis</td>
<td>C; laurel and pine forest</td>
<td>Orange</td>
<td>32.3 ± 10 (28)</td>
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<td>Isoplexis chalectanha</td>
<td>C; laurel forest</td>
<td>Orange</td>
<td>14 28.1 ± 3 (8)</td>
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<td>Isoplexis isabelliana*</td>
<td>C; pine forest</td>
<td>Orange</td>
<td>29.1 ± 12 (28)</td>
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<td>(Webb &amp; Berthel.) Masf.</td>
<td>Isoplexis sceptrum (L. fil.)</td>
<td>Orange</td>
<td>81 40 ± 15 (10)</td>
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L. phoenicea may be an example of a relict bird-pollinated species because it occupies a stem-basal lineage of the Lavatera–Malva complex. Furthermore, some floral traits (e.g. a specialized system for nectar delivery) are shared with the southern African sister plant species (Fuertes-Aguilar et al., 2002). Thus, L. phoenicea may belong to an old bird-pollinated clade, which may have been pollinated by African nectar birds. The continental origin of the ornithophilous characters appears more evident in C. canariensis because their closest extant relatives C. eminii Ascherson ex Schweinf. and C. abyssinica Engler grow in E. African, and are visited by various sunbirds (J.M. Olesen & B.K. Ellers, unpubl. data). Canarina canariensis is sister to the two African species, thus ornithophilous traits in C. canariensis may be pleistomorphic traits shared with its African relatives in conjunction with specialist nectar-feeding birds in the mainland.

The origin of bird-pollination traits in the remaining plant taxa is less clear according to actual phylogenetic information. Ornithophily in the derived species of Isoplexis and Lotus may have either a mainland or a Macaronesian origin. Phylogenies suggest that the woody Isoplexis belongs to a clade which is derived from the continental herbaceous Digitalis (Carvalho & Culham, 1998; C. Braüchler, pers. comm., Fig. 1a). The closest relatives of Macaronesian C. eminii are Moroccan species (Allan et al., 2004, Fig. 1b). Ornithophilous Isoplexis and Lotus species seem to have evolved from lineages, which are insect-pollinated and of a Mediterranean origin (Fig. 1a,b; see also Carine et al., 2004). However, in these cases the origin of ornithophily remains obscure and an interpretation of evolutionary patterns is blurred by incomplete knowledge of potential plant–pollinator interactions in the past. For instance, bee-pollinated Digitalis spp. introduced to NW America are frequently visited by hummingbirds (David, 1996; C. Barr, pers. comm.) and by sunbirds in South Africa (Fry et al., 2000; Y. Wijk, pers. comm.). Isoplexis spp. have hexose-dominated nectar, whereas studied Digitalis spp. have sucrose-rich nectar (Best & Bierzychudek, 1982; Dupont et al., 2004a). Specialist nectarivorous birds can assimilate sucrose, whereas some opportunistic nectar feeders can only digest hexoses (Nicolson, 2002). Thus, sucrose-tolerant African nectar-feeding birds may have visited ancestors of the Digitalis–Isoplexis lineage (see below).

Finally, the molecular phylogeny of Echium (Böhle et al., 1996) combined with observations of flower visitors (Dupont & Skov, 2004) suggest that the bird-visited Echium wildpretii and E. decaisnei evolved within a mainly entomophilous lineage. Moreover, ornithophily most likely evolved after colonization of the Canary Islands (Fig. 1c). Thus, in the neo-endemic Echium wildpretii bird pollination and ornithophilous traits evolved de novo on the islands, possibly in association with resident nectar-drinking passerines. However, additional phylogenetic information will be necessary to resolve these issues because limited utility of these phylogenetic studies alone. For example, for some clades it is required to

Figure 1 Parsimony trees of three plant lineages containing Macaronesian bird–flower species. Trees have been redrawn from (a) Isoplexis/Digitalis (Carvalho & Culham, 1998), (b) Lotus (Allan et al., 2004), and (c) Echium (Böhle et al., 1996). Ornithophilous and putatively ornithophilous species are in bold face, the remaining species are entomophilous. Geographical distribution of the plants is indicated to the right.
include all the putative relatives (in particular the positions of close relatives of Macaronesian species), and for others, new studies are needed using high-resolution molecular markers to increase phylogenetic resolution and bootstraps values (Allan et al., 2004; Andrus et al., 2004).

**Fossil evidence**

Specialist flower visitors are important as selective factors on floral morphology. In continental Africa, specialist nectarivorous birds belong to the Promeropidae, Zosteropidae and especially the Nectariniidae. None of these families have Macaronesian representatives, and presently the closest locality of specialist nectarivorous birds is the Acacia steppe in Senegal (Moreau, 1966; Fry et al., 2000). The Macaronesian and NW African fossil small-bird fauna is virtually unknown (Pieper, 1985; Tyrberg, 1998, 2003; Rando, 2003). Evidence exists that some Canarian passerine species have gone extinct (Emberiza aloveri, Rando et al., 1999). On the other hand, some nectar-feeding bird species repeatedly colonized African offshore islands (e.g. Comoros Islands), which are more isolated than the Canary Islands. Thus, we cannot completely exclude the possibility that specialist nectar-drinking birds were present in Macaronesia in the past. If so, they may have influenced floral evolution (Vogel et al., 1984).

**Historical biogeography of African flora and avifauna**

Although the fossil record is incomplete, indirect evidence tentatively suggests that specialist nectarivorous birds never inhabited the Macaronesian islands. The NW African bird fauna, like that of Madeira and Canary Islands, has a Palearctic affinity, whereas the NE African avifauna (bounded by the Nile) has an Ethiopian affinity (Moreau, 1966). Small forest passerines of the Ethiopian avifauna have never been found as far west as NW Africa (Moreau, 1966; Tyrberg, 1998, 2003; Fry et al., 2000). At least since the Pliocene, birds of W Africa have been separated from the Ethiopian avifauna by the Sahara desert (Blondel & Mourer-Chauviré, 1998). Moreover, although some Macaronesian islands have a mid-Miocene origin, the main woody species of the laurel and pine forests (Wang et al., 1999; Arroyo-García et al., 2001), and associated fauna and flora (Brunton & Hurst, 1998; Sturmbauer et al., 1998; Caujapé-Castells et al., 1999; Emerson et al., 2000a,b; Helfgott et al., 2000; Pestano et al., 2003), may not have been present until geologically recently. Thus, we find it unlikely that specialist nectar-feeding birds were present in Macaronesia in the past.

However, the expansion of a Mediterranean vegetation southwards during cool periods (possibly as far south as to Lake Chad; Moreau, 1966), may have brought sunbirds, white-eyes and/or sugarbirds into contact with the Mediterranean flora in N Africa. This flora does not contain bird flower elements, and thus ornithophily becomes a ‘new’ condition derived from entomophily. Sunbirds and white-eyes forage opportunistically and often explore new resources of food, e.g. the nectar of numerous exotic plants (Vogel, 1954; Fry et al., 2000). It is plausible that these birds visited the ancestors of the Macaronesian ornithophilous plants, exerting a phenotypic selection on floral traits. A similar scenario of intermingling floras and hummingbirds is described by Grant (1994) to explain the origin of ornithophily in North America. Thus, for extended time-spans, ancestors of the Macaronesian bird flowers may have lived in contact with sunbirds and other nectar-feeding birds from continental Africa.

**Associations with generalist passerines in islands**

If specialist nectar birds never inhabited the Macaronesian islands, and ornithophily did evolve de novo on the islands, ornithophilous traits might have evolved as a response to resident generalist nectar-feeding birds. This could be the case for the neo-endemic E. wildpretii. In contrast to mainland regions, directional selection in response to generalist pollinators may be possible in island environments. Low species numbers, density compensation and the use of nectar as an alternative food resource, may make generalized passerine birds important pollinators exerting selective pressure on some plant species on islands (Olesen et al., 2002). If these birds are the only effective pollinators in the insular environment, floral evolution may occur in response to these birds, even within a generalist pollination regime (‘most effective pollinator principle’, Stebbins, 1970). On the other hand, there is no clear evidence that Phylloscopus collybita or other generalist passerines induce a selective pressure to drive evolution of ornithophilous traits. For instance, these birds also take nectar from flowers, which are not typically ornithophilous.

**CONCLUDING REMARKS**

According to the available evidence, we suggest that the origin and evolution of ornithophilous traits in the Macaronesian bird flowers mostly took place in continental Africa prior to colonization of the islands. However, no single hypothesis can explain all cases of ornithophily in Macaronesia as each plant group have a unique biogeographic and evolutionary history.

For Lavatera, ornithophily may be a relict condition, which evolved in association with African nectarivorous birds (Fuertes-Aguilar et al., 2002). During glaciations and dry periods the relative mainland plant species disappeared allowing these climatic changes during Quaternary (Quézel, 1978), and only relative survived in island refuge (Tenerife). A similar scenario may apply to Canarina canariensis, whose closest relatives are still extant. The mainland relatives became isolated in mountain ‘island’ refuges in E Africa, where they are pollinated by sunbirds.

For Isoplexis, the most plausible explanation is that the Macaronesian species are derived from an ancestor in the Isoplexis–Digitalis clade, which may have been visited by specialist nectar-feeding birds in continental Africa. The
present distribution of red-flowered species of Digitalis around the Mediterranean Basin, outside the distribution range of specialist nectarivorous birds, may explain why only insects visit these flowers today. Similarly, ornithophily may have evolved in African continental ancestors of Lotus. However, more information about the pollination biology of the continental African species is needed to explain the occurrence of ornithophilous traits in this clade. Finally, ornithophily may have evolved by island de novo evolution in Echium wildpretii. The association with generalist birds in an insular setting may have induced directional selection, even in a generalist pollination regime. However, there is no evidence that island generalistic passerines are sufficient selective agents acting on floral variation and driving evolution of a set of bird pollination-related traits.

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