



ORIGINAL  
ARTICLE

## 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.

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## 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* (Fringillidae) 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*, síndromes 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; Búrquez, 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; Búrquez, 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 *et al.*, 1989) and Hawaiian crow in the Hawaiian Islands (Cox, 1983), and several small passerines in Trinidad, Tobago (Feinsinger *et al.*, 1982), and Canary Islands and Madeira (Vogel *et al.*, 1984; Olesen, 1985; Valido *et al.*, 2002; Olesen & 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, 2003b). 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. melanocephala* Gmelin, and *Phylloscopus collybita* Vieillot (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 (Martín & 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 plants 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 *I. sceptrum*. Their visits fail because the corolla becomes slippery and sticky from nectar oozing out of the corolla. The Madeiran *Musschia 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.* ssp. *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 novaeseelandiae*, 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 *Strelitzia*, *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

**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 (*Lotus* spp.) according to Vogel et al. (1984), Olesen (1985), and personal observations. Furthermore, we include *E. pininana* because the Tui (*Prothemadera 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)  $\pm$  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

	Distribution and habitat	Flower characteristics			Birds					
		Colour	Max. vol. ( $\mu$ L)	% Sugar	Scan	Pcoll	Smel	Satri	Scons	Pcae
<b>Boraginaceae</b>										
<i>Echium decaisnei</i> Webb	C; semidesert	White-blue	–	10 (1)	–	6	6	–	3	–
<i>Echium pininana</i> Webb & Berthel.	C; laurel and pine forest	Light-blue	1.4	26 $\pm$ 3 (20)	–	–	–	–	–	–
<i>Echium virescens</i> DC.	C; pine forest	Purple-blue	–	–	6	–	–	–	–	–
<i>Echium wildpretii wildpretii</i> Pearson ex. Hook. f.	C; subalpine shrub and pine forest	Red	21	15 $\pm$ 3.8 (286)	4	4	–	–	–	4
<i>Echium wildpretii trichosiphon</i> (Svent.) Bramwell	C; subalpine shrub	Pink	–	18.2 $\pm$ 4.2 (8)	–	–	–	–	–	–
<b>Campanulaceae</b>										
<i>Canarina canariensis</i> (L.) Vatke	C; laurel forest	Red-orange	53	12.2 $\pm$ 2.0 (110)	–	1	2	–	2	–
<i>Musschia wollastonii</i> Lowe	M; laurel forest	Purple-yellow	149	12.5 $\pm$ 1.2 (15)	–	–	–	–	5	–
<b>Crassulaceae</b>										
<i>Aeonium arboreum</i> (L.) Webb & Berthel.	C; pine forest	Yellow	–	20.7 $\pm$ 4.9 (30)	6	6	–	–	–	–
<b>Fabaceae</b>										
<i>Lotus berthelotii</i> Masf.	C; pine forest	Red	49	24 $\pm$ 15 (18)	–	–	–	–	–	–
<i>Lotus eremiticus</i> A. Santos	C; pine forest	Orange	14.5	48	–	–	–	–	–	–
<i>Lotus maculatus</i> Breitf.	C; xerophytic lowland	Yellow	5.4	33	–	–	–	–	–	–
<b>Malvaceae</b>										
<i>Lavatera phoenicea</i> Vent.	C; transition to laurel forest	Salmon	112	24 (1)	–	6	–	–	–	6
<b>Scrophulariaceae</b>										
<i>Isoplexis canariensis</i> (L.) J.W. Loudon	C; laurel and pine forest	Orange	–	32.3 $\pm$ 10 (28)	–	1	2	6	–	6
<i>Isoplexis chalcantha</i> Svent. & O'Shan.	C; laurel forest	Orange	14	28.1 $\pm$ 3 (8)	–	6	–	–	–	–
<i>Isoplexis isabelliana</i> * (Webb & Berthel.) Masf.	C; pine forest	Orange	–	29.1 $\pm$ 12 (28)	–	6	3	–	–	–
<i>Isoplexis scyptum</i> (L. fil.)	M; laurel forest	Orange	81	40 $\pm$ 15 (10)	–	–	–	–	5	–

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. argyroides* 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 arboreum*). 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

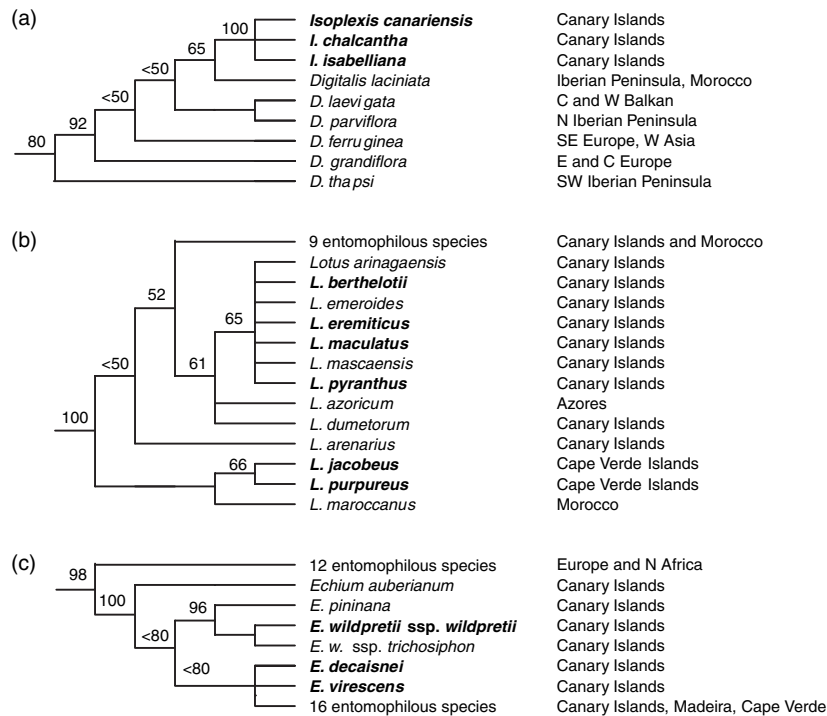
Molecular phylogenies now exist for the majority of Macaronesian plant genera containing bird-flower species: e.g. Böhle et al. (1996) for *Echium*, Carvalho & Culham (1998) for *Isoplexis*, Fuertes-Aguilar et al. (2002) for *Lavatera*, Allan et al. (2004) for *Lotus*, and J.M. Olesen & B.K. Ehlers (unpubl. 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*

*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. Ehlers, unpubl. data). *Canarina canariensis* is sister to the two African species, thus ornithophilous traits in *C. canariensis* may be plesiomorphic 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. Bräuchler, pers. comm., Fig. 1a). The closest relatives of Macaronesian *Lotus* spp. 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* species 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 alcoveri*, 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 takes 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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