Pollination on islands: examples from the Macaronesian archipelagos

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Introduction

Remote islands created by undersea volcanoes are first-class natural laboratories for the study of ecological and evolutionary processes and patterns involved in the origin and maintaining of the diversity of organisms, life histories, structures, and functions (e.g. Carlquist, 1974; Grant, 1998; Grant & Grant, 2007; Whittaker & Fernández-Palacios, 2007; Losos & Ricklefs, 2009). By their very nature and relative isolation from a source pool, oceanic islands can be considered as discrete and simple unities of biodiversity (microcosms) compared to the nearest mainland areas, which makes them a remarkable setting for the study of interactions of species with respect to both biotic (e.g. Linhart & Feinsinger, 1980; Inoue, 1993; Olesen & Jordano, 2002; Pafilis *et al.*, 2009) and abiotic factors (e.g. Grant *et al.*, 2000; Illera *et al.*, 2006; Padilla *et al.*, 2009).

In relation to biotic interactions occurring on oceanic islands such as the pollination of flowering plants by animals (or other kinds of mutualistic interaction among species, e.g. seed dispersal, facilitation and symbiosis, but also predation and competition), species dispersing and colonizing new habitats on remote oceanic islands left behind on their source mainland part of their well established mutualistic network and food web. This is an obvious consequence of the differential long-distance dispersal abilities of taxa, which arrive to remote islands (e.g. Carlquist, 1974; Gillespie & Roderick, 2002). Arthropods vary a lot in their abilities to colonise islands. Some of them are good long-distance dispersers, e.g. ballooning spiders and migrating Lepidoptera. Wood-living beetles and bees, such as Cetoniidae and carpenter bees (*Xylocopa*, Apidae), may also be transported by floating vegetative islets to distant oceanic islands (e.g. Gulick, 1932; Simberloff, 1978; Woodell, 1979; Gillespie &

Roderick, 2002). Others seem to be poor oceanic colonizers such as some of the typical flower-visiting groups (e.g. long-proboscid bees and flies), which are absent or poorly represented on islands (e.g. Simberloff, 1978; Inoue, 1993; Barret, 1998; Gillespie & Roderick, 2002). Besides, natural dispersal of colonies or swarms of highly social bees (e.g. Apis mellifera, Apidae) across wide oceans seems to be impossible without human assistance (Michener, 1979; Hohmann et al., 1993), and it is not inconceivable that only a few native social Hymenoptera species (excluding ants) are native to oceanic islands (see e.g. Hohmann et al., 1993; Arechavaleta et al., 2005, 2010; Borges et al., 2005, 2008 for specific examples from the Macaronesian archipelagos). The oceanic barrier can also act as a colonizing filter for relatively strong-flying insects. For example only 59% and 85% of the families of Lepidoptera and Hymenoptera from the Iberian Peninsula have representatives on the Canary Islands. Thus, the biota of oceanic islands is clearly depauperate and disharmonic compared to adjacent mainland areas (e.g. Baur, 1891; see also specific island-mainland comparative examples with arthropod communities in e.g. Allan et al., 1973; Janzen, 1973; Abbott, 1976; Tanaka & Tanaka, 1982; Becker, 1992; Gillespie & Roderick, 2002; Patiny et al., 2009).

Island pollination systems have distinctive and idiosyncratic ecological characteristics (i.e. Insular Pollination Syndromes) compared to mainland systems, because of the differential pool of species inhabiting insular habitats. For example, island plant species are often pollinated by new, even novel flower-visitors (lizards: e.g. Elvers, 1978; Whitaker, 1987; Olesen & Valido, 2003a; Menezes de Sequeira et al., 2007; Valido & Olesen, 2007; opportunistic passerine birds: Vögel et al., 1984; Olesen, 1985; Valido et al., 2004; Rodríguez-Rodríguez & Valido, 2008; Orthoptera: Micheneau et al., 2010). Besides, insular plant species are also visited by fewer pollinator species than their mainland populations or close relatives (e.g. Linhart & Feinsinger, 1980; Spears, 1987; Inoue, 1993; Delgado, 2000; Olesen & Jordano, 2002; Lázaro & Traveset, 2005; Abe, 2006a,b; Wheelwright et al., 2006; Pérez-Bañón et al., 2007a,b) and large flower–visiting insects are clearly underrepresented or even absent (Inoue, 1993; Barret, 1998). Although insular pollination systems are characterized by generalist pollinators, i.e. insects collecting pollen and nectar from a wider array of plant species than their mainland representatives (e.g. Olesen et al., 2002; Olesen & Jordano, 2002; Dupont et al., 2003; Philipp et al., 2006; Kaiser-Bunbury et al., 2009), some studies have demonstrated high species-specific pollination relationships in insular systems (e.g. Elmqvist et al., 1992; Ecroyd et al., 1995; Kato et al., 2003; Temeles & Kress, 2003; Kawakita & Kato, 2004a,b; Martén-Rodríguez & Fenster, 2008; Micheneau et al., 2010). Furthermore, and as a consequence of the distinct ecological characteristics, island pollinator

systems are also more extinction-prone and vulnerable to habitat disturbance and invasive species than mainland ones (e.g. Vaughton, 1996; Butz, 1997; Kato et al., 1999; Cox & Elmqvist, 2000; Goulson et al., 2002; Hansen et al., 2002; Valido et al., 2002; Goulson, 2003; Moritz et al., 2005; Paini & Roberts, 2005; Abe, 2006b; Patiny et al., 2009; Winfree et al., 2009).

Then, since the early (and famous) prediction of Darwin (1862) and Wallace (1867) about the presumably extreme specialisation of the long-spurred epiphytic orchid Angraecum sesquipedale (Orchidaceae) to, at that time, unknown long-tongued hawkmoth in Madagascar (later described as Xanthopan morgani; see Wasserthal, 1997) some of these Insular Pollination Syndromes have got the attention of researchers interested in the biogeography, ecology, evolution and conservation of these plant-animal mutualistic interactions from different islands and archipelagos around the world (e.g. Carlquist, 1974; Linhart & Feinsinger, 1980; Spears, 1987; Hohmann et al., 1993; Inoue, 1993; Adler & Dudley, 1994; Inoue et al., 1996; Barrett, 1998; Bernadello et al., 2001; Traveset, 2001; Hansen et al., 2002; Olesen et al., 2002; Olesen & Jordano, 2002; Traveset, 2002; Dupont et al., 2003; Olesen & Valido, 2003a,b; Dupont et al., 2004a; Valido et al., 2004; Lázaro & Traveset, 2005; Abe, 2006b; Philipp et al., 2006; Wheelwright et al., 2006; Pérez-Bañón et al., 2007a,b; Cronk & Ojeda, 2008; Dalsgaard et al., 2008; Rodríguez-Rodríguez & Valido, 2008; Hansen & Müller, 2009; Kaiser-Bunbury et al., 2009; McMullen, 2009; Ollerton et al., 2009).

The Macaronesian archipelagos (Azores, Madeira, Salvages, Canaries, and Cape Verde) are situated in a remarkably geographical position in the Northern part of the Atlantic Ocean and they provide powerful biological models in the study of the ecology and evolution of plant-animal mutualistic interactions, taking into account hypotheses and predictions formulated on the basis of these Insular Pollination Syndromes. In addition to the fact that these archipelagos present a high percentage of endemic plants and animals (Arechavaleta et al., 2005, 2010; Borges et al., 2005, 2008), they are also characterized by a considerable number of relict species (i.e. ancient lineages formerly distributed in southern Europe and northern Africa, which went extinct during the Tertiary and Quaternary severe climatic and geological changes; e.g. Cronk, 1992; Hohmann et al., 1993; Vargas, 2007). Besides, in the last decades, a large number of molecular studies have revealed the evolutionary relationships among insular species and some show examples of spectacular ecological radiation involving a considerable number of lineages, and in addition, the closest mainland relatives are known for many of them (see reviews in e.g. Juan et al., 2000; Kim et al., 2008). These data are extremely useful in our efforts to understand the adaptive consequences of pollinator shifts

both in relation to plant mating system and floral trait evolution (e.g. Bradshaw & Schemske, 2003; Fenster et al., 2004). Of special interest are the cases with remarkable changes in the pollination system from mainland to islands (e.g. Inoue, 1993; Inoue et al., 1996; Sun et al., 1996; Dupont et al., 2004a; Valido et al., 2004; Micheneau et al., 2006; Rodríguez-Rodríguez & Valido, 2008; Micheneau et al., 2010).

The goal of this chapter is: i) to review the scanty literature on Macaronesian islands, focusing on pollination or flower–visitation studies and presenting some case studies; ii) to synthesise some common patterns from these islands, and iii) to suggest future avenues in the study of plant-animal mutualistic interactions on these archipelagos.

Azores Islands

These islands are the most isolated Macaronesian archipelago, about 1340 km from any mainland and with a total area of 2,332 km^2 (nine main islands). The archipelago is relatively recent in origin (8 My) and about 7% (72 species) of their vascular plants are endemic (Caujapé-Castells et al., 2010). To take into account only the most important flower visitor/pollinator groups (Coleoptera, Diptera, Lepidoptera, and Hymenoptera), Borges et al. (2005) estimated that a total of 1,201 species - of which about 14% were endemic - could be found on these islands (Table I). Coleoptera (528 spp.) and Diptera (393 spp.) had the highest number of species. Besides, it is necessary here to include the introduced Madeiran lizard Podarcis (Teira) dugesii (Lacertidae) as a potential pollinator, since it visits flowers of Azorina vidalii, Campanulaceae (Olesen & Valido, 2003b) and the introduced herb Salpichroa origanifolia, Solanaceae (M.J. Pereira, pers. com.). In relation to potential ornithophily by passerine birds, neither the Blackcap (Sylvia atricapilla, Sylviidae) nor the Canary (Serinus canarius, Fringillidae) haven been reported as flower visitors on these islands although they have been frequently reported as flower visitors on some Canarian and Madeiran endemic and introduced plant species (see below).

The Azorean bullfinch (Pyrrhula murina, Fringillidae) at Pico da Vara (São Miguel) eats flower buds from male plants of Ilex perado (Aquifoliaceae) during September, when other preferred food resources are scarce (Ramos, 1995). Although the Azorean bullfinch acts as a florivore and does not pollinate these flowers, we cannot discard it completely as a putative pollinator of other plant species. For example, in the Canary Islands the granivorous S. canarius visits efficiently some flowers for nectar in e.g. Echium spp. (Boraginaceae) and

Table I. - Number of species, and percentages of endemic taxa (in parenthesis) of the principal orders of insects recorded as flower visitors and pollinators (Hexapoda: Coleoptera, Diptera, Lepidoptera, Hymenoptera) from the Macaronesian archipelagos. Values are compiled from published checklists from the Azores (Borges *et al.*, 2005), Cape Verde (Arechavaleta *et al.*, 2005), Madeira (Borges *et al.*, 2008), and Canary Islands (Arechavaleta *et al.*, 2010). We also include the number of passerine birds and lizards observed visiting flowers for nectar and pollen on each archipelago.

Orders[1]	Azores	Madeira	Canary	Cape Verde
Coleoptera	528 (35)	1011 (51)	2069 (57)	452 (31)
Diptera	393 (28)	554 (10)	1110 (27)	260 (21)
Lepidoptera	149 (18)	330 (10)	649 (31)	192 (4)
Hymenoptera	131 (5)	610 (14)	1009 (24)	250 (24)
TOTAL species	**1201**	**2505**	**4837**	**1154**
TOTAL Insecta	**2209**	**3266**	**6138**	**1686**
Passerine birds[2]	-	1	7	1
Lacertid lizards[3]	1	1	3	-

[1] Other insect orders recorded as flower visitors are: Collembola, Dermaptera, Dictyoptera, Psocoptera, Odonata, Orthoptera, Plecoptera, Hemiptera, Neuroptera, Mecoptera, Trichoptera, and Thysanoptera (Proctor *et al.*, 1996).

[2] Passerine birds include *Phylloscopus canariensis, Sylvia melanocephala, S. conspicillata, S. atricapilla, Serinus canarius, Parus* (*Cyanistes*) *caeruleus, Fringilla coelebs* from the Canary Islands (Valido *et al.*, 2004; Rodríguez-Rodríguez & Valido, 2008; Rodríguez-Rodríguez *et al., in prep.*), and *S. atricapilla* from Madeira (Olesen & Valido, 2003b).

[3] Lacertid lizards include *Gallotia atlantica, G. galloti and G. caesaris* from the Canary Islands, and *Podarcis* (*Teira*) *dugesii* from Madeira, and Azores (where it is introduced) (Valido & Olesen, *submitted*).

Isoplexis canariensis (Scrophulariaceae), but destroys flowers of *Chamaecytisus proliferus* (Fabaceae), when it tries to rob nectar. Other classical granivorous bird species feeding in the dry season on nectar/pollen and acting as potential pollinators are the Darwin's finches (Grant & Grant, 2007).

Unfortunately pollination studies of the Azorean flora are really scarce. Detailed cases are the endemic *Azorina* (Olesen *et al.*, *submitted*) and *Vaccinium* (Pereira, 2008), and a pollination network from Flores (Olesen *et al.*, 2002).

The Azores Bellflower (*Azorina vidalii*) is a rare, small shrub, endemic to the Azores. It is growing on all islands, except Graciosa. Its habitat is rocky sea cliffs and deposits. Although

pollination by wind possibly can take place, this species is mainly animal pollinated but flower visitors vary among islands. For example, on plants from the islands of Santa Maria (populations from São Lourenço and Ponta do Castelo) and Terceira (Porto Martins), the introduced lizard Podarcis (Teira) dugesii was observed to drink nectar and to eat pollen and stylar hairs from the stigmatic pollen brush. The hawkmoth Macroglossum stellatarum (Sphingidae) was also recorded as flower visitor on the two Santa Maria populations, and it arrived very early in the morning to the flowers, well before any lizard began to forage. On these two islands, the introduced honeybee Apis mellifera, the monarch butterfly Danaus plexippus (Nymphalidae) and some unidentified Muscidae, Calliphoridae and Sepsidae (Diptera) were observed as flower visitors too. They consumed pollen from the pollen brush and drank nectar. However, at the two western islands no lizards were observed in the three studied populations (one in Terceira and two in Flores), and the only flower visitors were Apis mellifera and Sepsis spp. (Sepsidae, Diptera). The flower visitation rate of these insects was also high.

In a pollination network study carried out in an open herb community from Flores (Olesen et al., 2002), Azorina was the more generalist plant species in a community composed of ten flowering plant species. The Bellflower was visited by eight of 12 flower visitors registered in this community. One native species of Halictus, Apidae (which also visited five other plant species) and the introduced Apis mellifera had the highest percentage of visits (30R and 27R, respectively). The remaining plant species had only 1-4 flower visitors. Both Azorina and Halictus were considered as super-generalist species (i.e. species that have more links with other mutualistic partners than the average in the community). Thus, A. vidalii was potentially pollinated by lizards, insects and wind on the eastern islands, and insects and wind only on the western ones. As an extension of these observations, it would be interesting to know fruit and seed set for plants being visited by the introduced lizard and the honeybee compared to those only being visited by native insects to test the impact of the introduced pollinators on the reproductive ecology of this endemic plant species.

The endemic Azores Blueberry (Vaccinium cylindraceum, Ericaceae) is a deciduous shrub growing above 300 m a.s.l. with declining populations on all islands, except Graciosa, where it is now extinct. Its breeding system, studied by Pereira (2008) in 13 populations from seven islands, is facultative xenogamy (i.e. fruit set was only 0.6-6.3R, if pollinators were excluded). Pereira also detected that one species of Microlepidoptera (Scoparia semiamplalis, Crambidae) is the main flower visitor/pollinator of these highly nectariferous red flowers except on Santa Maria, where it was absent in the flower censuses. The copious nectar of

these flowers was also used by ants (only on Santa Maria) and some Macrolepidoptera (*Hipparchia* spp., Nymphalidae). The domestic honeybee can visit these flowers as well (observations from Santa Maria), but only larger flowers in low–altitude populations. Interestingly, no other solitary bees and the bumblebee *Bombus ruderatus* visit these red flowers, possibly because of size or morphological mismatches (but see data from the Madeiran Blueberry below).

These flower-visiting Microlepidoptera use the endemic *Juniperus brevifolia* (Cupressaceae) as their host plant. Thus, since these two plant species coexist in the same habitat, it would be interesting to test positive indirect interactions (i.e. pollination facilitation) between neighbouring individual *Juniperus* plants on the reproduction of *Vaccinium*. This issue is important to future conservation strategies alongside the use of *in vitro* micropropagation techniques (Pereira, 2006). Besides, these Microlepidoptera species match very well the size of the flower (about 10 mm) and, from an evolutionary point of view, it would be interesting to test if differences in the corolla-tube diameter found by Pereira (with the most narrow and wide flower diameter from Pico and Santa Maria, respectively) is related to the importance of these Microlepidoptera as pollinators.

Madeiran Islands

These islands (Madeira, Deserta, Porto Santo, and Selvagens), with a total extension of 796 km^2, are about 630 km from the mainland and have a maximum geological age around 18 My. 13% (136 species) of their vascular flora is endemic (Caujapé-Castells *et al.*, 2010). Borges *et al.* (2008) estimated that these islands had a total of 2505 species of Coleoptera, Diptera, Lepidoptera and Hymenoptera and about 25% are endemic (Table I). Beetles (1011 spp.) and hymenopterans (610 spp.) had the highest number of species. Besides, the Blackcap (*Sylvia atricapilla*), and the endemic lacertid lizard *Podarcis* (*Teira*) *dugesii* are flower visitors (and possibly act as effective pollinators too) of some endemic Madeiran plants (Elvers, 1977, 1978; Beyhl, 1990, 1997; Sziemer, 2000; Olesen & Valido, 2003a,b; see below). In addition, the Canary (*Serinus canarius*) visits flowers of the introduced ornamental plants *Aloe arborescens* (Agavaceae) and *Strelitzia reginae* (Strelitziaceae) (Sziemer, 2000).

Specific studies about pollination or systematic flower-visitor censuses on Madeiran plant species are practically absent (see below), but some insect-flowers interactions have been reported (e.g. Fellendorf *et al.*, 1999; Smit & Smit, 2003; Smit *et al.*, 2004; Wakeham-

Dawson et al., 2004; Fernandes et al., 2007). From these sources, and also from personal observations, we mention some pollination interactions occurring in these islands. For example: Hylaeus maderensis (Apidae) is a common flower visitor of the endemic Aeonium glutinosum (Crassulaceae) and Rubus sp. (Rosaceae) (Fellendorf et al., 1999). However, Smit & Smit (2003) detected that H. maderensis also visits the introduced Ageratina adenophora (Asteraceae) and the native Torilis arvensis (Apiaceae), among others. It lives in both lowland and mountains. The introduced Hylaeus signatus is an oligolectic species feeding only on Reseda luteola (Resedaceae). The solitary bee Lasioglossum wollastoni (Apidae) and the hoverfly Eumerus hispidus (Syrphidae), both endemic species from Madeira and Porto Santo, also visit the flowers of A. glutinosum. The endemic Andrena maderensis (Apidae) visits the native herbs: Brassica sp., Rapistrum rugosum and Raphanus raphanistrum (Brassicaceae). In contrast, the also endemic Andrena wollastoni is found on Madeira and Porto Santo as well, and it visits the endemic Echium candicans and Echium nervosum (Boraginaceae) but also Cakile maritima, Sinapis sp. (Brassicaceae), Reseda luteola (Resedaceae) and Euphorbia sp. (Euphorbiaceae). Amegilla maderae (Apidae) is another interesting endemism of the archipelago. It is one of the most abundant bees in gardens, maybe being active all year round. It is a super-generalist pollinator visiting many plant species, e.g. Echium candicans, E. nervosum, E. plantagineum (Boraginaceae), Brassica sp., Cakile maritima (Brassicaceae), Galactites tomentosa, Cichorium endivia (Asteraceae), and Agapanthus praecox (Liliaceae). Madeira Island has two bumblebees, the widespread Bombus ruderatus and the endemic B. maderensis. Both species are super-generalists and many food plant species are known (e.g. the endemic Vaccinium padifolium). The former bumblebee is also found on the Azores, but it does not visit the endemic Azorean Blueberry (Pereira, 2008). The fly Melanostoma wollastoni (Syrphidae) is endemic to Madeira, and it has been registered visiting flowers of Ranunculus cortusifolius (Ranunculaceae) in forested areas (Wakeham-Dawson et al., 2004). The also endemic hoverfly from the laurel forest Myathropa usta (Syrphidae) visits several Ranunculus species, but also the endemic Asteraceae Tolpis macrorhiza (from Madeira), T. succulenta (Macaronesia), and Pericallis aurita (Madeira). In general, the introduced honeybee (Apis mellifera) is the most common bee visiting flowers on these islands. More specific pollination studies have been made on the Madeiran Giants, the Bellflowers (Musschia spp., Campanulaceae) and Foxglove (Isoplexis sceptrum, Scrophulariaceae), and also on several species of orchids.

The genus Musschia is endemic to Madeira and consists of the species M. wollastonii, M. aurea, and the recently discovered M. isambertoi (yellowish-green flowers) from the island of

Deserta Grande (Menezes de Sequeira et al., 2007). M. wollastonii is a rare, unbranched shrub with 45-90 cm long leaves which grows in the laurel forest (700-1000 m). The species is monocarpic, i.e. individual plants die after one flowering episode, which happens after a plant has reached an age of 4-5 years. Flowering plants are on average 270 cm tall (range 180-390) and have only one inflorescence with an average of 570 flowers (range 120-1050). Plants are dimorphic with respect to flower colour (purple or yellow). The species has secondary pollen presentation on the underside of the four stigmatic lobes, and the papillae may get in contact with the pollen on the presenter on the underside of the lobes, resulting in selfing. In the morning, the corolla tube is full of nectar. Standing crop of nectar is on average 95 !l and sugar concentration is 13% (Olesen, 2003; Olesen & Valido, 2003b; Olesen et al., submitted).

In the laurel forest at Ribeiro Frio, flowers were frequently visited by insects and also birds (Sylvia atricapilla) (Olesen & Valido, 2003b). Nectar-drinking insects were the abundant bumblebee Bombus maderensis, abundant Vespidae spp., the endemic butterfly Lycaena phlaeas phlaeoides (Lycaenidae), and also the introduced Pieris rapae (Pieridae). The insects were only nectar thieves because the distance between the nectar and the underside of the stigmatic lobes is much larger (1.8 cm) than the height of the insects. However, pollen-collecting Syrphidae and abundant Muscidae might function as pollinators because they forage for both pollen and nectar. The other two Musschia (M. aurea and M. isambertoi) are rare endemic species, growing on vertical cliffs facing the sea at lower altitudes on Madeira and Deserta Grande (M. aurea), and on only two localities from Deserta Grande at almost sea level (M. isambertoi). The endemic lizard (Podarcis –Teira- dugesii) visits and presumably pollinates the flowers of both species. The first observations of lizards as pollinators happened more than 30 years ago (Elvers, 1977, 1978). In Madeira, Elvers noted several incidences of lizards visiting cultivated and native plants for floral nectar. Early in the morning, the lizards begin to climb the inflorescences of this species with its many beautiful yellow-greenish flowers. They drink the nectar and lick the long stigmatic lobes for pollen (Olesen et al., submitted). Lizards also visit the flowers of other natives: e.g. Echium nervosum and Aeonium sp., and also some introduced species: e.g. Cynara cardunculus (Compositae), Euphorbia pulcherrima (Euphorbiaceae), Nicotiana glauca (Solanaceae), Pelargonium sp. (Geraniaceae), and Foeniculum vulgare (Apiaceae) (Beyhl, 1990, 1997; Sziemer, 2000; Olesen & Valido, 2003b). They share these plants with other flower visitors, e.g. Bombus spp. and Apis mellifera.

The Giant Madeiran Foxglove (Isoplexis sceptrum, Scrophulariaceae) is another enigmatic plant species from the Madeira laurel forest. It has red-orange flowers visited by opportunistic

passerine birds, such as Sylvia atricapilla (Olesen & Valido, 2003b). The bumblebee Bombus maderensis often try to visit its flowers too but visits fail because the corolla becomes very slippery and sticky from nectar oozing out of the corolla of neighbouring flowers. Average standing crop of nectar in a flower was 37 !l and sugar concentration was 15%. As a consequence of their flower morphology, several other Madeiran plant species may candidate as being bird-lizard pollinated as well, e.g. the endemics Lotus argyrodes, L. macranthus, L. loweanus, Vicia costae (Fabaceae), Teucrium betonicum and T. abutiloides (Lamiaceae).

A systematic study of pollinator species attracted by essential oils and volatiles was carried out on the Madeiran rare endemic, scented orchids Goodyera macrophylla and the native and widespread Gennaria diphylla, both growing in the laurel forest (Fernandes et al., 2007). In these species, 29 and 32 volatile components were isolated, respectively. The first species is visited (but not very frequently) by Bombus maderensis possibly attracted by linalool in the scent. However, the presence of 9-pinene in the scent preludes some nocturnal pollination by moths too. In G. macrophylla, the major compounds of the volatile fraction are terpenes, which play important attractive roles for nocturnal pollinators. The flower visitors are the noctuids Chrysodeixis chalcites, Phlogophora wollastoni and Mythimna unipuncta.

Canary Islands

The by far largest number of studies about flower visitors and plant reproductive ecology on any Macaronesian archipelago, have been made on the Canary Islands. They are the oldest (20.6 My for Fuerteventura), largest (7545 km^2; seven main islands) and closest to mainland (about 95 km) of all Macaronesian archipelagos. This may explain their high habitat diversity and number of species and percentage of taxa (flora and fauna) being endemic. Approximately 45% (607 species) of the Canarian vascular flora is endemic (Caujapé-Castells et al., 2010). The Canary Islands also harbour the highest number of classical flower-visitor species in the orders Coleoptera, Diptera, Lepidoptera, and Hymenoptera, compared to other Macaronesian archipelagos (Table I). For example, Arechavaleta et al. (2010) reported a total of 4837 species in these taxonomic groups. Beetles (2069 spp.) and flies (1110 spp.) had the highest number of species. Apart from these insect groups, several passerine birds such as Phylloscopus canariensis, Sylvia atricapilla, S. melanocephala, S. conspicillata (Sylviidae), Parus -Cyanistes- caeruleus (Paridae), Serinus canarius and Fringilla coelebs (Fringillidae), and the endemic lizards Gallotia galloti, G. atlantica, and G. caesaris (Lacertidae) have been

registered as common flower visitors consuming nectar and pollen in both native and introduced plant species (e.g. Vogel *et al.*, 1984; Olesen, 1985; Eades, 2001; Olesen & Valido, 2003a; Valido *et al.*, 2004; Rodríguez-Rodríguez & Valido, 2008; Ollerton *et al.*, 2009; Valido & Olesen, *in prep.*). In the Canary Islands, this association between vertebrates and flowers has received some attention since early last century, especially with respect to opportunistic passerine birds (Porsch, 1924; Schmucker, 1936), and more recently lizards (Speer, 1994; Font & Ferrer, 1995; Beyhl, 1997; Olesen & Valido, 2003a). These vertebrates are frequent flower visitors of the Canarian classical bird-flower elements such as *Isoplexis canariensis, I. chalcantha, I. isabelliana,* (Scrophulariaceae), *Canarina canariensis* (Campanulaceae), *Echium wildpretii* (Boraginaceae), *Lavatera* (*Navaea*) *phoenicea* (Malvaceae), *Teucrium heterophyllum* (Lamiaceae), and being anecdotically regarded as pollinators of *Lotus berthelotii* (Fabaceae) (Vogel *et al.*, 1984; Olesen, 1985; Westerkamp, 1990; Valido *et al.*, 2004; Rodríguez-Rodríguez & Valido, 2008; Ollerton *et al.*, 2009; and *pers. obs.*). In addition, these lizards and birds frequently take nectar/pollen from insect-pollinated plants as well. For example, different species of *Lotus*, *Scrophularia*, *Euphorbia*, *Teucrium, Echium*, *Rhamnus*, and *Aeonium*, among others (Elvers, 1978; Valido *et al.*, 2004; Rodríguez-Rodríguez *et al.*, *in prep.*). However, the quantitative role of these vertebrates as effective pollinators has only been documented in the case of *Canarina canariensis* and *Isoplexis canariensis* (Rodríguez-Rodríguez & Valido, 2008; Ollerton *et al.*, 2009; Rodríguez-Rodríguez & Valido, *in prep.*). Opportunisitc birds/lizards visiting flowers by nectar/pollen has been explained as being a result of several ecological processes operating on islands *i.e.* a low number of vertebrate species, low interspecific competition, low predation risk and also poor arthropod-food supply and, on the other hand, high intraspecific competition due to density compensation in bird/lizard populations. As a consequence, these two groups of vertebrates amplify their dietary niche and become new potential mutualistic agents of a considerable number of island plant species (Olesen & Valido, 2003a,b; Valido & Olesen, 2007).

All these plants are not exclusively visited by birds or lizards. Their nectar/pollen are also used by insects. However, the visitation rate of these is very low (and anecdotically) in the case of the classical bird-flower element. For example, the red-purple flowers of the extremely rare *Lotus berthelotii* are visited, though very sporadically, by *Lasioglossum* spp. (Apidae), an unidentified Lycaenidae, and a few ants in their natural population (Valido *et al.*, 2004). The Canarian chiffchaff (*Phylloscopus canariensis*) and the Blue Tit (*Parus - Cyanistes- caeruleus*) were observed a few times as flower visitors but only to cultivated plants in a public park in Tenerife (Ollerton *et al.*, 2009). Practically nothing is known about

flower visitors and breeding ecology in the other putative ornithophilous and critically endangered endemic Lotus from La Palma, L. eremiticus and L. pyranthus, where only 10 and 20 individuals are known, respectively. The Canarian bellflower Canarina canariensis is visited too, but only sporadically, by the introduced Apis mellifera and by the natives Paravespula germanica (Vespidae), the butterfly Gonepteryx cleobule (Pieridae), and Lasioglossum spp., among others (Hohmann et al., 1993; Valido et al., 2004; Ollerton et al., 2009; Rodríguez-Rodríguez & Valido, in prep.). This low attraction to insects can be partially explained since flowers of Canarina and L. berthelotii (Ollerton et al., 2009), but also those of L. eremiticus and L. pyranthus (A. Valido, in prep.), reflect light predominantly above 600 nm and being poorly detected by bees on a background contrast made up of foliage. However, flowers of Isoplexis canariensis having a moderate detectability for bees are visited, but only very infrequently, by insects. For example Lasioglossum cf. loetum have been detected collecting pollen and also some small ants visit flowers, but they act as nectar robbers. The Canarian bumblebee (Bombus canariensis) though being abundant in the habitat of I. canariensis, does not visit the flowers (Rodríguez-Rodríguez & Valido, 2008). In addition to petal colour, other flower traits like nectar composition and flower accessibility to insects are also responsible for this pattern. All these species have hexose-dominant nectar (which is associated with bird visitation in contrast to sucrose-rich nectar, which is related to insect pollination; Dupont et al., 2004a). However, the role of these insects as pollinators, if they have any, is insignificant in comparison to birds, according to exclusion experiments in Isoplexis (Rodríguez-Rodríguez & Valido, 2008). In contrast to the previous species, Lavatera (Navaea) phoenicea flowers are also frequently visited by insects, e.g. native ants, bumblebees, and domestic honeybees, among others. We have no data about flower colour in L. (Navaea) phoeniceae, but this species, together with the supposedly entomophilous L. acerifolia, has a dominance of hexose-nectar too. Thus, flowers of the latter species would be potentially visited also by birds (Dupont et al., 2004a). Future research will be needed to confirm the role of lizards and birds as effective pollinators in the remaining species being visited by vertebrates, and also in some cases a comparison to insects is needed.

In relation to insect-flower mutualistic interactions in the Canaries, Hohmann et al. (1993) reported 221 taxa of bees and wasps (Hymenoptera) visiting up to 428 Canarian plant species (native and introduced). This impressive data set (compiled since 1981 by Herbert Hohmann and Francisco La Roche) includes observations on all islands from lowland to high mountain habitats. The domestic honeybee was by far the most generalist flower visitor. It collects pollen and nectar from 126 of the plant taxa (from 37 plant families) listed in this database.

Domestic honeybees were the predominant flower visitors in practically all habitats and islands (except in Fuerteventura and Lanzarote where there are no beekeeping activities because of the aridity). This human mediated plant-animal interaction has its maximum during the short spring in the high mountain scrubland in the Teide National Park (Tenerife, >2000 m a.s.l.). In this protected area, the authorized massive introduction of beehives (up to 2426 in 2009, OAPN 2010) makes Apis extremely abundant and it visits the great majority of flowering plants in the area. Besides, at the time when beekeepers introduce their beehives, Apis expels by exploitative competition some native pollinators from their food species. For example, the mutualistic interactions between native birds with the emblematic Red Bugloss (Echium wildpretii) disappeared after the introduction of Apis (Valido et al., 2002; Dupont et al., 2004b). The impact of this anthropogenic activity is also detected at pollination network level, affecting the great majority of flowering plant species in the community (Dupont et al., 2003; Valido et al., in prep.; see below), and negatively affecting the reproductive success (i.e. seed set) is some plant species (e.g. Spartocytisus supranubius, Fabaceae; Valido et al., in prep.).

The data from Hohmann et al. (1993) mention other native bees being super-generalists (sensu Olesen et al. 2002), especially the endemic Lasioglossum loetum (up to 113 plant taxa) and L. viride (96), Bombus canariensis (90), and Anthophora alluaudi (79), among others. On the other hand, although more data are needed in order to obtain strong conclusions, species-specific interactions between bees and plants have not been detected. However, Tetralonia hohmanni (Apidae) visits almost exclusively Allagopappus dichotomus (Asteraceae) on Tenerife and Gran Canaria. Other cases are Heliophila pulverosa (Apidae) visiting Heliotropium ramosissimum (Boraginaceae) in the central islands and on Lanzarote and Fuerteventura, and Andrena aegyptiaca visiting Launaea arborescens (Asteraceae) on Gran Canaria and the eastern islands. From this database, L. arborescens was also the most generalist plant species (receiving 91 insect taxa), followed by Hirschfeldia incana, Brassicaceae (58), Heliotropium ramosissimum, Boraginaceae (55), and Plocama pendula, Rubiaceae (53), among others.

Specific pollination studies on Canary plant species in which the identity of insect flower visitors is included have been made for several species in the genus Echium (Olesen, 1988; Kraemer & Schmitt, 1997; Valido et al., 2002; Dupont & Skov, 2004; Dupont et al., 2004a,b), Laurus azorica, Lauraceae (Forfang & Olesen, 1998), Cedronella canariensis, Lamiaceae (Olesen et al., 1998), Lavandula buchii, Lamiaceae (Delgado, 2000), Phoenix canariensis, Arecaceae (Meekijjaroenroj & Anstett, 2003), Withania aristata, Solanaceae (Anderson et al.,

2006b), Solanum lidii and S. vespertilio, Solanaceae (Anderson et al., 2006a; Dupont & Olesen, 2006), Erysimum scoparium, Brassicaceae (Ollerton et al., 2007), and in some species of Aeonium, Crassulaceae (Esfeld et al., 2009; Olesen, unpubl. data). Besides, some studies using a pollination-network approach have been made in the high mountain scrubland in the Teide National Park (Dupont et al., 2003; Valido et al., in prep.), in the laurel forest in Garajonay National Park in La Gomera (Olesen et al., 2005, 2007), and in the lowland xerophytic scrubland in Tenerife (Stald, 2003; Olesen et al., 2005, 2007; Padrón et al., 2009). Below we summarize some of the main results obtained from these studies.

The genus Echium has one of the most spectacular radiations (28 species) in Macaronesia. According to a molecular analysis, all Canarian species originated from a single colonization event by an herbaceous ancestor from the mainland, followed by secondary colonizations, single or multiple to Madeira and possibly a single one to Cape Verde (Böhle et al., 1996; García-Maroto et al., 2009). Although very closely related, these species exhibit a remarkable variation in both life form (with short-lived annuals and monocarpic, rosette herbs and long-lived woody shrubs) and floral traits (in morphology and colour), which could explain the variation in flower visitors. However, the results of the study of Dupont & Skov (2004) of 20 Echium species from the Canary Islands showed that, irrespectively of flower morphology, the altitudinal distribution range of each plant species was the strongest predictor of richness of bees visiting their flowers. Eighty percent of the visitors were native bees (Hylaeus, Andrena, Lasioglossum, Anthophora, Osmia, Amegilla) but also Bombus canariensis and the introduced Apis mellifera, among others. Echium strictum (with 18 bee taxa), E. aculeatum (12), E. acanthocarpum (11), and E. decaisnei (11) were the most generalist species. Thus, the Canarian Echium species are not highly specialized. Surprisingly, two alien species accumulated the highest number of mutualistic interactions (i.e. super generalists). They are the introduced Mediterranean herbaceous E. plantagineum (which is widely naturalized in the central and western Canary Islands) with 25 bee taxa as visitors and the domestic honeybees (Apis mellifera), which visited up to 15 Echium species. Echium plantagineum usually co-occurs with some of the other Echium species in many habitats, and they also share practically all their pollinator species (Dupont & Skov, 2004). The increase in this pattern of sharing pollinators could also be positively related to the size of flower patches of E. plantagineum. For example, Guitián et al. (1993) found a strong increase in number of flower-visitor species (from two to 13) in mainland populations of E. plantagineum in concordance with flower abundance within patches (from around 250 to 64,000 flowers/patch). Thus, it would be interesting to test the ecological implications of E. plantagineum patch-size on the

reproductive biology of some native Echium species. A reduced fertilization by interspecific pollen contamination from native Echium is expected to increase local population size of E. plantagineum. On the other hand, the domestic Apis mellifera is also a superabundant flower visitor of both alien and native Echium species. Besides, it also excludes, by resource competition, native pollinators from Echium (see below the specific well known case of E. wildpretii). Thus, when interacting alien species co-occur in the same habitat, they can develop invader complexes (D'Antonio & Dudley, 1993), in which such super generalist species interact more with each other than expected by chance (see e.g. Corbet & Delfosse, 1984 for a specific case in Australia where the introduced Apis is almost the only flower visitor of the alien E. plantagineum; but see Olesen et al., 2002). Thus, in this situation, both species are facilitating each other in their ecological integration into their new communities. However, these alien species can also have a strong negative impact by decreasing the native species interactions (Valido et al., 2002; Dupont et al., 2004b; Valido et al., in prep; see also Aizen et al., 2008 and Morales & Traveset, 2009 for a general discussion about the impact of alien species on mutualistic systems). Thus, because of the potential impact of alien species on native Echium pollination in the Canary Islands (but also on endemic taxa from Madeira and Cape Verde), e.g. competition among plants for pollinators, exclusion of native pollinators by resource competition, but also pollen contamination, risk of hybridization and genetic introgression, future studies focusing on these conservational aspects would be of high priority to protect endemic Echium species (Valido et al., 2002; Dupont et al., 2004b; Dupont & Skov, 2004). In the Canary Islands, Echium has a relatively high frequency of hybridization (Bramwell, 1972), many populations are suffering strong introgression and e.g. E. handiense (Fuerteventura) is under risk of extinction and seven other species are classified as vulnerable. On the other hand, pollen from E. plantagineum was detected in 95% of the analyzed farmhouse honey samples collected in Tenerife, La Gomera, El Hierro and La Palma (La Serna et al., 1999; Santos et al., 2004; La Serna & Gómez, 2006; Pardillo & La Serna, 2007). From Tenerife, Santos et al. (2004) also listed pollen from other 22 introduced plant species from honey.

More detailed studies of the pollination ecology have been made on the monocarpic Echium wildpretii in the Teide National Park (Tenerife; E. w. wildpretii) with some preliminary data about flower visitors in the other subspecies from Taburiente National Park (La Palma; E. w. trichosiphon). This species has a mixed pollination strategy. According to flower morphology and ultraviolet spectra they are associated with insect pollination, whereas their red-pink corolla, relatively large amount of nectar with low sugar concentration

dominated by hexose, are traits more associated to bird pollination. Although potential bird pollination was suspected by Olesen (1988), some insects have been repetitively registered visiting their flowers (e.g. Olesen, 1988; Kraemer & Schmitt, 1997). However, today we know for E. w. wildpretii that 37 species including bees (15), flies (12), butterflies (3), and beetles (3) visit the flowers, but also three species of opportunistic passerine birds and one lizard make up their pollinator guild (Valido et al., in prep.). The passerine birds (Phylloscopus canariensis, Serinus canarius, Parus -Cyanistes- caeruleus) and lizards (Gallotia galloti) and also some insect species are practically only detected early in the flowering season, coinciding with the total absence of Apis in the National Park. Only insects were observed visiting its sister subspecies E. w. trichosiphon (with pink flowers) in the sub-alpine scrubland on the island of La Palma. However, we do not discard the possibility of observing bird pollination in this subspecies as well (Valido et al., 2002).

E. wildpretii constitutes a well-supported monophyletic group together with two other monocarpic-rosette species with white-blue flowers, E. pininana from La Palma and E. simplex from Tenerife (García-Maroto et al., 2009). The former is only visited by the bees Lasioglossum spp., Anthophora alluaudi, Bombus canariensis and Eucera gracilipes in its forest habitats (Dupont & Skov, 2004), but E. simplex, apart from these bees, is also visited by birds (Serinus canarius and Parus -Cyanistes- caeruleus; J.M. Olesen, pers. obs.). Thus, in the future and in order to expand the research initiated by Dupont & Skov (2004) in Echium, it would be interesting to include (and using a phylogenetic context) data about vertebrates, flies, and also butterflies visiting these plant species and including simultaneously also the colour spectra (300-700 nm) of these flowers. It is known that these groups of pollinators have different spectral sensitivities, and differential selective regime exerted for each functional group on flower colour is expected. However, phylogenetic branch length (i.e. species age) and number of flower visitor species are not correlated in Echium (J.M. Olesen, unpublished).

The genus Aeonium (Crassulaceae) comprises the largest Canarian plant species radiation. Thirty-six of the 42 species in the genus are endemic to the archipelago, while Madeira has two species, Cape Verde Islands one, Morocco one, and East Africa two species. The flowers are small, open and the nectar is easily accessible. Some species, however, do not have any nectar (Esfeld et al., 2009). Floral colours are yellow, white or reddish and the inflorescences are panicles varying a lot in size. Reproductive structures are weakly differentiated among species, which mainly differ in size of flower and inflorescence (range in genus: 20-5500 flowers/inflorescence), but also in their pollen:ovule ratio (range: 100-300). Thus floral biology indicates that the genus has a rather random pollinator fauna (Jorgensen & Olesen,

2001). An unpublished study (J.M. Olesen) of A. arboreum on Tenerife supports this argument. Sixty-two percent of the species (Coleoptera, Hymenoptera, Diptera and Lepidoptera) observed to visit the plants in the habitat of A. arboreum visited the flowers of this species. On the Ladera de GKímar, the species is also visited by the birds Parus (Cyanistes) caeruleus, Sylvia melanocephala and Phylloscopus canariensis. A few of the Aeonium species are monocarpic, and their inflorescences are larger than that of polycarpic species, e.g., the monocarpic A. urbicum (endemic to Tenerife) and A. hierrense (endemic to La Palma and El Hierro) have a considerably higher flower number per inflorescence than closely related polycarpic species. Many plant species on islands poor in insects may experience a selection pressure for larger floral display, either as larger flowers or larger inflorescences (Wallace, 1878). Phylogenetic constraints may determine which strategy is followed. This seems to be the case for many Canarian species. Plants on other archipelagos may evolve towards more selfing as seen in the flora of Galápagos (McMullen, 1987). Thus Aeonium, in general, attracts a large sample of local pollinators. This may cause hybridization between sympatric species. However, a pollen transfer study by Esfeld et al. (2009) demonstrated that this rarely happens. They attribute this to pollinator constancy within one foraging bout.

From this high mountain scrubland habitat in Tenerife, Dupont et al. (2003) also studied the local pollination network structure (among 11 plant species and 37 flower visitors). These authors concluded that the level of mutualistic generalization in this community was positively correlated with abundance of species, and the structure of these plant-animal interactions was also nested (rather than random). According to this, a few generalists (corresponding to the most abundant) interact with a large number of species while the rest (lower abundance) interact with only a subset of them (i.e. more specialized). Consequently, the more generalist species are the most abundant in the community. This type of pollination network structure may reduce interspecific competition and allows a greater biodiversity within communities (e.g. Bastolla et al., 2009). Thus, this ecological pattern underlines the importance of preserving not only rare species, but also the more abundant ones since they are also keystone species within this community (Dupont et al., 2003). For plants, one way to establish interactions with local mutualistic species would be to increase their visual attraction to pollinators. As a way to do this, some plant species present modified structures (i.e. coloured bracts) whereas others can maintain and change the colour of their 'old' flowers in order to intensify the visual cues. This last option is found in Erysimum scoparium (Brassicaceae), an endemic shrub inhabiting high mountain habitats in Gran Canaria, Tenerife and La Palma. Individual plants may simultaneously present early white phase and late purple

phase flowers, and it was demonstrated experimentally to retain purple flower (with almost no nectar) as a way to increase its visual signal in order to attract their principal pollinator in the study area (Anthophora alluaudi) (Ollerton et al., 2007).

In another Canarian habitat, the laurel forest in the Garajonay National Park, La Gomera, Forfang & Olesen (1998) studied the reproductive ecology (including flower insect censuses) in the dioecious and abundant Macaronesian endemic tree Laurus azorica (Lauraceae). To produce their fleshy-fruited seeds which are dispersed mainly by blackbirds and endemic pigeons Laurus requires cross-pollination. Small solitary bees (Halictidae spp., Hymenoptera) and Tachina canariensis (Diptera) made 67U and 30U of the flower visits, respectively. Tachina canariensis made about twice as many visits to male flowers as to females, whereas halictids made seven times as many visits to males. Individuals of halictids carried an average of 22 times as much Laurus pollen as individuals of T. canariensis. Other flower visitors, constituting the last 3U of visitors, were Hymenoptera species: Lasioglossum spp., Bombus canariensis, and Ichneumonidae spp.; Diptera species: Eristalis tenax (Syrphidae), Dasyphora albofasciata (Muscidae), Bibio elmoi (Bibionidae); Lepidoptera species: Vanessa vulcania (Nymphalidae); and the Coleoptera species Brachypterus sp. (Nitidulidae). The importance of flies and beetles as pollinators in phylogenetically basal angiosperms, such as L. azorica, has been pointed out repeatedly, and bee pollination is very rare and only a few cases are known (Endress, 2010). The mainland Laurus nobilis is most often visited by Diptera (e.g. Musca spp., Syrphus spp.) but also some bees such as Apis, Bombus, and Andrena, and the wasps Polistes have been registered as frequent flower visitors (Knuth, 1909; Ricciardelli & Torini, 1982; F. Rodríguez-Sánchez, pers. com.). However, it is remarkable that in the laurel forest of La Gomera, only two taxa accounted for nearly all (97U) flower visits in L. azorica (Forfang & Olesen, 1998). The fruit-set of this insular plant was as low as 18U (Forfang & Olesen, 1998). For L. nobilis in Italy the fruit-set was much higher (53U; Ricciardelli & Torini, 1982). In Cádiz (Iberian Peninsula), a similar high value was found too (F. Rodríguez-Sánchez, pers. com.). It would be interesting to test if the difference in the functional diversity of pollinators on island vs. mainland is the principal reason for this variation in fruit-set.

Another well-studied case from this protected laurel forest area in La Gomera concerns the Macaronesian endemic Cedronella canariensis (Lamiaceae) (Olesen et al., 1998), which probably, as Laurus, diverged from an ancestral mainland line in the Tertiary. This species encompasses two chemo-varieties: var. canariensis smells like camphor and the dominant essential oils are pinocarvone (47U) and α-Pinene (10U), and var. anisata like aniseed has mainly a presence of p-Ally1 anisole (76U) and pinocarvone (12U) (López-García et al.,

1992). These varieties can grow sympatrically, but in Gara=onay var. canariensis dominates in the north-western part of the park, while var. anisata is most frequent in the south-eastern corner. According to this field study, these flowers were visited by at least 27 insect species. The most frequent flower visitors (accounted for 95% of all visits) were the endemic Bombus canariensis (which can also act as nectar robbers in some periods), Macroglossum stellatarum (Sphingidae) and several Halictidae spp. The bumblebees clearly preferred var. canariensis and the hawkmoth did not differentiate between varieties. Interestingly, the fruit set did not differ among the varieties, but outcrossed plants had seeds of a higher weight than selfed and since half of the visits realized by Bombus did not result in pollination, M. stellatarum could be a more effective pollinator of Cedronella than Bombus. Other, but very infrequent flower visitors were Anthophora alluaudi, Vanessa vulcania and Argynnis pandora (Nymphalidae), and Gonepteryx cleobule (Pieridae). Besides, some beetles (Attalus sp., Melyridae) and Thysanoptera were also found frequently inside flowers. During some nocturnal censuses only a few, and very infrequently, unidentified moth species (Geometridae and Noctuidae) were observed (Olesen et al., 1998).

From this forest area (Gara=onay), an analysis of pollination at community level was also made (Olesen et al., 2005, 2007). Field observations of 55 insect species visiting flowers of 29 plant species resulted in a total of 145 mutualistic interactions. Similar to the pattern observed in the high mountain scrubland in Tenerife, the structure of these mutualistic interactions was significantly nested. Halictidae sp., Bombus canariensis, Anthophora alluaudi, and Vanessa vulcania were the insects which made most of the links to the plants (16, 14, 7 and 7, respectively). Thus, they are the most generalized pollinators in this pollination network. The domestic honeybee, although it is not extremely abundant in forested areas, is also present in the laurel forest. It visited six plant species, viz. the two introduced Echium plantagineum and Galactites tomentosa, but also the endemics Cedronella canariensis, Andryala pinnatifida (Asteraceae), Geranium reuteri (Geraniaceae) and the native Erica arborea (Ericaceae). Among the plants, Cedronella canariensis was the species receiving most flower visitors (24 species). The second-most important one was the introduced herb Galactites tomentosa.

Another case study from the laurel forest focused upon Solanum species. In the Canary Islands three endemic, small woody shrubs belong to Solanum: S. lidii, S. vespertilio and S. nava (actually considered as Normania nava). The last one has been extinct from the laurel forest in Gran Canaria and Tenerife since 1984. The other two species are still present (though under threats) in some mesic areas in Gran Canaria (S. lidii) and in the laurel forest in

Tenerife and are also represented by some individuals in Gran Canaria (S. vespertilio). They constitute a phylogenetic clade closely related to African Solanum (Anderson et al., 2006a). Both species are andromonoecious (individual plants have both male and hermaphrodite flowers) and self-compatible. Flowers have no nectar, and pollen is the only reward to flower visitors. They present a special mechanism of pollination termed ‖buzz pollination‖. Pollen is contained in sac-like poricidal anthers, and it can only be removed from the anthers by thoracic muscle vibration by bees. Only some medium-large sized bee species are capable of buzzing, which might be a more specific pollination interaction than previously described from the Macaronesian islands. In a field study made by Dupont M Olesen (2006) only Amegilla sp. was observed buzzing the flowers in S. lidii. In S. vespertilio, Bombus canariensis was the most abundant flower visitor, and another buzzing visitor, but less frequent was Anthophora alluaudi. Hohmann et al. (1993) also observed Amegilla canifrons in S. vespertilio. These four species also made contact with the stigma. Other flower visitors, which did not buzz-pollinate, were Apis mellifera, Lasioglossum spp., and small beetles (Meligethes sp., Nitidulidae). Thus, the Canarian endemic Solanum species have a specialised pollination system, which could have evolved on the islands. The closest relative is Solanum melongena in Kenya, which has been observed to be visited by nine species of bees, although only three of these are relatively frequent as flower visitors: Xylocopa caffra, Amegilla calens (Apidae) and Macronomia rufipes (Halictidae) (Gemmill-Herren M Ochieng, 2008).

The lowland areas in the Canaries with their xerophytic vegetation is the habitat for another studied Solanaceae: the endemic shrub and functionally dioecious Withania aristata (Anderson et al., 2006b). Its flowers are characterized by an "inflated calyx syndrome" (Chinese lantern) that could have a selective advantage by maintaining a suitable microclimate within the lantern for the developing fleshy fruit in its dry habitat (Khan et al., 2009). The male flowers offer pollen and the females offer nectar to insects. Four species of bees have been observed visiting these flowers: Lasioglossum viride, L. loetum, Amegilla quadrifasciata and less frequent, measured in visitation rate, Apis mellifera (Hohmann et al., 1993Y Anderson et al., 2006b). According to the observed high fruit set, it is assumed that these insects generate a high rate of cross-pollination (Anderson et al., 2006b). In the mainland, the hermaphrodite Withania somnifera, Kaul et al. (2005) found a high fruit set too, but mainly due to the self-compatible system of this species. Here, the flower visitors were Apis dorsata, A. florea, and some Lepidoptera and Diptera.

Another shrub, the Tenerife-endemic Lavandula buchii also from the xerophytic lowland was studied by Delgado (2000). About 80% of all visits were performed by Amegilla

quadrifasciata and *A. canifrons*. Other relatively frequent visitors (>1% of all visitors) were the flies *Anastoechus latifrons* (Bombyliidae) and several unidentfied species of Calliphoridae and Syrphidae (Diptera). This result contrasts with those obtained from the Mediterranean mainland species of *Lavandula*. Here, e.g. *L. latifolia* is visited by around 80 insect species, and 13 of these made 75% of all visits. For two other Canarian endemic *Lavandula,* Hohman *et al.* (1993) registered 15 species of bees from *L. canariensis* and five for *L. minutolii.*

Two pollination networks in the xerophytic lowland on Tenerife were studied by Stald (2003) and Olesen *et al.* (2005, 2007). Both were nested in their link structure. One of them had 35 insects visiting the flowers of 14 plant species and made a total of 86 mutualistic interactions. The bees *Lasioglossum* cf. *viride* and *Eucera gracilipes* were the most generalized insects (visiting eight and seven plant species, respectively). *Euphorbia lamarckii* was the plant which received the highest number of insects (17). The endemic ant *Camponotus feai* is a very generalist flower visitor too (7 spp.). It visited frequently flowers of *Euphorbia lamarckii* and *E. canariensis*, but also *Convolvulus floridus* (Convolvulaceae)*, Plocama pendula*, *Periploca laevigata* (Asclepiadaceae), *Echium bonnetii,* and also *Neochamaelea pulverulenta* (Cneoraceae). Although generally not considered as good pollinators, their role as effective pollinators was experimentally demonstrated in the last species, (Valido & Olesen, *in prep*.). In the Canary Islands, from the coast to the high mountain zones ants frequently visit flowers for nectar from different plant species. For example, in Teide National Park all except one of the studied plant species (17 in total) were visited by ants (Valido *et al., in prep*.). However, their role as pollinators is unknown. This pattern needs more research, since ant pollination (*myrmecophily*) is poorly represented in mainland habitats, and could be included as another example of an insular mutualistic phenomenon. Other interesting mutualistic interactions observed in this arid habitat were lizards *Gallotia galloti* (Lacertidae) visiting flowers of the endemic *Echium bonnetii*; the hawkmoth *Macroglossum stellatarum* on *Euphorbia canariensis,* and *Cyclyrus webbianus* (Lycaenidae) on *Lavandula buchii*, among others.

Another studied example was made on the endemic palm *Phoenix canariensis*. This species was earlier suspected to be only wind pollinated, but Meekijjaroenroj & Anstett (2003) demonstrated that the weevil *Neoderelomus piriformis* may pollinate its flowers, but they also injure some flowers and cause flower abortions. However, this study was realized on ornamental plants in France. The weevil is also native in some of the Canary Islands (Arechavaleta *et al.*, 2010). Thus wind *vs.* beetle pollination in natural stands of *P. canariensis* needs future consideration.

Cape Verde Islands

This archipelago is about 576 km away from mainland Africa and has a total area of 4,033 km^2 (nine main islands). Their maximum geological age is about 7.6 My and the islands harbour a vascular flora, which is about 34% (82 species) endemic (Caujapé-Castells et al., 2010). Arechavaleta et al. (2005) estimated that these islands had a total of 1154 species in the Coleoptera, Diptera, Lepidoptera, and Hymenoptera, and the first two orders being the more diverse - Coleoptera (452) and Diptera (260) (Table I).

Only very scant information about the pollination of the plants is available. For example, Alexander (1898) reported that the resident Blackcap (Sylvia atricapilla) usually feed on orange blossoms. This suggests that other cases of ornithophily by blackcaps on the Cape Verde Islands are possible. For example, and similar to the stories from Madeira and the Canaries, some plants, which might be visited by this bird could be some of the native and endemic Echium (e.g. E. vulcanorum), Lotus purpureus and L. jacobaeus, and also Campanula (e.g. C. bravensis, C. jacobaea, Campanulaceae; however, these two species are probably only one, according to C. Roquet et al. unpubl.). However, future field observations would be necessary to confirm this. Besides, we do not discard the possibility of future flower observations of the Mabuya skinks (Scincidae) on these plants too. Six species of this lizard genus are recognized in Cape Verde, and it is known that some insular skinks (e.g. Eutropis atlanticus formerly considered Mabuya atlantica) usually visit flowers for nectar on island plants (Sazima et al., 2009). For C. jacobaea/C. bravensis, Leyens & Lobin (1994) suggested it to be pollinated by the carpenter bee Xylocopa modesta. They have a conspicuous UV reflection on the inner surface of their corolla and pollination by some Sphingidae is proposed. It has also been observed to be visited by small solitary Halictidae bees, but sometimes and in some populations, visitation rate is so low that selfing seems more likely (Olesen et al., submitted).

Conservation remarks

The potential impact of biological invasions on insular native mutualistic systems is a major concern (e.g. Bond, 1994; Kearns et al., 1998; Traveset & Richardson, 2006; Aizen et al., 2008; Padrón et al., 2009). One of the more recurrent example is related to the human-induced massive presence of the domestic honeybee and their consequences on mutualistic

native plant-animal interactions on islands (e.g. Kato et al., 1999; Craig et al., 2000; Barthell et al., 2001; England, 2001; Roubik & Wolda, 2001; Hansen et al., 2002; Goulson et al., 2002; Valido et al., 2002; Goulson, 2003; Dupont et al., 2004b; Kato & Kawakita, 2004; Abe, 2006b; Kaiser-Bunbury et al., 2009; Dohzono & Yokoyama, 2010; Valido et al., in prep.). The principal conclusion obtained from these authors is that the extreme local abundance of honeybees, influenced by beekeeping activities, reduces considerably the flower–visitation rates of native pollinators (predominantly insects but also birds and lizards). Direct consequences of this mutualistic disruption have been detected in e.g. a significant reduction in fruit and seed set, a reduction of outcrossing rates, an increased probability of hybridization, a different altered gene flow pattern by pollen, the pollination of exotic weeds, the reduction in native pollinator fecundity, and possibly the transmission of parasites or pathogens to native organisms (see also e.g. Michener, 1979; Westerkamp, 1991; Kearns et al., 1998; Gross, 2001; Goulson, 2004; Moritz et al., 2005; Paini & Roberts, 2005; for others mainland examples where Apis was introduced: New World, Asia and Australia). As we have exposed before from the Macaronesian islands, the introduced honeybee is one of the most generalistic flower-visitors, both in terms of number of plant species visited within community and in the extent of its geographic range. One reason is its remarkably efficient communication system and large colony size, enabling them to effectively use nectar and pollen resources from an extensive area around their nests (up to 15 km as maximum distance has been detected). The honeybee originated in Africa and naturally expanded to Europe and Asia at least twice (Whitfield et al., 2007), but it has been introduced in most parts of the world to improve crop pollination and to produce honey (e.g. Moritz et al., 2005). It is not fully domesticated and swarms usually escaped into the wild and established feral colonies. Actually the establishment of wild colonies in the Macaronesian islands is limited by the presence of the ectoparasitic mite Varroa destructor, Varroa-associated viruses, and some bacteria and/or fungi (De la Rúa et al., 2009). In Macaronesia honeybees are present in all archipelagos but not on all islands. For example, in Cape Verde it is only present on Santiago. In the Canaries it is present on all the islands except Fuerteventura and Lanzarote. In Madeira it is absent from Selvagens and Desertas islands, and in the Azores it is present on all islands. Since they have been domesticated for millennia, their native range is, in some instances, difficult to define and their taxonomic status (native vs. introduced) is still controversial in some places. For example, for the Canary Islands Arechavaleta et al. (2010) cited Apis mellifera as 'possibly native' while Hohmann et al. (1993) assumed it being 'introduced'. Some doubts are also expressed for the cases concerning the Azores and Cape Verde

(Arechavaleta et al., 2005; Borges et al., 2005). For Madeira, Borges et al. (2008) added 'introduced'. Based on morphology, the Canarian honeybees are closest related to those in S. Spain (Ruttner, 1988), although Ruttner (1988) states that N. African and Spanish bees are very similar. On the other hand, genetic studies point towards a North African origin of Canarian honeybees (De la Rúa et al., 2001, 2002), and if any specific line of Canarian honeybees can be termed 'native' it is probably the Canarian black morph (De la Rúa et al., 1998). However, these particular mitochondrial DNA haplotypes (from the African lineage) firstly found in the Canaries were detected later in Southern Spain and Portugal, as well (De la Rúa et al., 2002, 2006). However, due to the obligate composition of its dispersal propagule (a queen and some workers together), it certainly very rarely, if ever, colonizes remote islands such as Macaronesia. Maybe a floating tree trunk containing a nest could have brought the honeybee to some of these islands. Thus, for Apis mellifera no definitive answer can be given to the question about the origin of Macaronesian honeybees, whether they are Iberian or North African, and native or introduced by humans, but the option most plausible is that it has been introduced by humans in these islands as it has happened to most other oceanic islands around the world (Michener, 1979; Moritz et al., 2005). For example, when the Macaronesian islands were discovered by Europeans in the 15th century, only the Canaries were inhabited (by guanches); they probably arrived from North-western Africa in the first millennium BC (e.g. Santos et al., 2010). The first Europeans reported that they already used honey from Apis (e.g. Morales-Padrón, 1993), and possibly they already introduced honeybees as they had done with goats, dogs, pigs and several cultivated plants as well. Honey collection is an ancient activity. Crane (1983) states that humans began hunting for honey at least 10,000 years ago. Her evidence is a Mesolithic rock painting at Valencia (Spain), showing two women honey-hunters collecting honey and honeycomb from a bee nest. Beekeeping activity evidences from prehistoric times are also illustrated in paintings from Africa, India, and in illustrations made between 2400 and 600 BC in Egypt. In Greece hives used in ancient times have been excavated, the earliest being from 450 BC. 3000 BC. Egyptians kept written records of beekeeping activities: their hives were transported down the Nile on barges to get to the floral sources. Ancient Romans wrote much about beekeeping and honey production during the Roman expansion (400 BC - AD 200). Thus, beekeeping activities in North Africa were well known at the time when aborigines arrived to the Canary Islands. Bumblebees (Bombus spp.) are also social bees but, in contrast to the honeybee, fertilised queens alone establish new colonies. Thus, pollination interactions in these islands probably evolved in the complete absence of honeybees. However, if guanches introduced Apis in the Canaries, it would be

necessary to know if "2000 years is sufficient time to evolve specific mitochondrial haplotypes (e.g. sublineages A_{14}, A_{15}) detected for the Canarian black morph by artificial selection. In this respect, it is known that Canarian goats, clearly being introduced by guanches, have also particular mitochondrial haplotypes (D-loop HpaII RFLP), which differ from North African and European goats (Amills et al., 2004).

Field and experimental evidences support that alien pollinators disrupt native plant-animal interactions. Their impact can vary among pollination systems, but usually they reduce the fitness of some native plants and have also some implications on native pollinators. Besides, a long-term change in population genetic structure may be expected because different foraging behaviour between native pollinators and honeybee affect mating systems and gene flow, as well. These four archipelagos harbour a considerable number of species being endemic, with e.g. 30-49% of vascular plants listed as being under some kind of threat (e.g. CauʃapT-Castells et al., 2010). Thus, independently of a clarification of the native vs. introduced status of Macaronesian Apis, it would be urgent to focus on conservation studies to know the potential implications of the local, and human-mediated, extreme abundance of Apis in some situations on the endemic and threatened plant (but also animal) species in these archipelagos. For example in the Canaries, the beekeeping activities have increased significantly during the last decade (up to 25,000 beehives censused in 2006) with the help of some institutional supports (program POSEI, European Union). This means that the average density of managed hives for the Canaries (excluded Fuerteventura and Lanzarote) is around 4.9/km^2. This value is similar to those observed for mainland Spain (De la R[a et al., 2009). However, for Tenerife this density is relatively higher (5.4/ km^2) than average for European countries (4.04/ km^2). The extreme case is known from Teide National Park (Tenerife) with 12.7 beehives per km^2. This density of honeybee colonies is higher than in any other locality across its natural range in Africa, Europe and Asia (]affT et al., 2010).

Acknowledgements

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