Differences in flower visitation networks between an oceanic and a continental island

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Two important biological differences between oceanic and continental islands are that the former usually have lower species richness and a higher degree of taxonomic disharmony than the latter. Although there is some evidence of less complex interaction networks on oceanic islands, only a few studies have compared island communities with each other or with mainland communities. Here, we analyse the species composition and structural properties of quantitative flower visitation networks in two communities of each of two different island systems: the Canary Islands (oceanic origin) and the Balearic Islands (continental origin). We compared different network parameters to inform us about their vulnerability in the face of different types of disturbance. The number of species was greater in the Balearic than in the Canarian networks but, contrary to expectations, the total number and diversity of interactions did not differ between them. Moreover, a greater number of opportunistic species and the presence of super-generalist species on the oceanic island led to significantly higher values of quantitative connectance and nestedness relative to those on the continental island. Given that these two parameters are associated with network stability, our findings support the hypothesis that oceanic island communities are less vulnerable to perturbations than are those of continental islands, although further studies with a network approach are needed to determine whether this is a general pattern. © 2014 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2014, **174**, 478–488.

ADDITIONAL KEYWORDS: Balearic Islands – Canary Islands – mutualistic interactions – nestedness – pollination networks – similarity index – specialization – super-generalist species.

INTRODUCTION

Islands are ideal ecosystems for the study of certain ecological processes owing to their relatively low species richness, high level of endemicity and limited area relative to mainland regions. Two of the main types of island, based on their geological traits, are oceanic and continental islands (continental fragments *sensu* Whittaker & Fernández-Palacios, 2007), which differ strongly in their initial resident biota: continental islands bear an initial biota that is identical to that of mainland areas (Thornton, 2007), whereas oceanic islands, generally formed from submarine volcanic activity, are initially devoid of life and thus their biota is entirely the result of long-distance dispersal and *in situ* speciation.

The biota of oceanic islands also shows strong disharmony relative to that of mainland areas, containing different proportions of taxa found in the mainland source areas and lacking entire groups of taxa (e.g. large terrestrial mammals). This disharmony is mainly caused by the abilities of different species for long-distance dispersal and establishment on islands. For example, flower visitors with long proboscises, especially bees, are typically under-represented in oceanic island environments (Inoue, 1993), whereas small insects (flies, beetles, wasps and small moths) are over-represented, possibly because of their higher probability of arrival facilitated by strong winds (Barrett, 1996). Therefore, oceanic island pollination networks show an impoverishment of potential animal pollinators (Gillespie & Roderick, 2002), which results in a low ratio of animal to plant species ($A : P$; Trøjelsgaard & Olesen, 2012). On continental islands, the disharmony in biota composition is less pronounced because of their mainland origin, although it may increase over time, depending on isolation, as a result of the extinction of ancestral taxa from the

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source (Gillespie & Roderick, 2002). Another characteristic of oceanic communities is the presence of 'super-generalist' species (*sensu* Olesen, Eskildsen & Venkatasamy, 2002), i.e. species with very high generalization levels (large number of interacting species) relative to co-occurring species (e.g. Kaiser-Bunbury, Memmott & Müller, 2009; Padrón *et al.*, 2009; Traveset *et al.*, 2013). No comparisons have been made between the two types of island with regard to the selectivity of species in the use of resources, which depends on their availability. The complementary specialization index (d') (Blüthgen, Menzel & Blüthgen, 2006) provides this information. According to this parameter, a pollinator that visits a plant species proportionally to its availability in the community is considered to be opportunistic, whereas a pollinator that visits rare plants disproportionately more often than common ones is considered to be selective. We might expect that a pollinator reaching a new island, regardless of its origin (continental or oceanic), and assuming no morphological restrictions to interactions with flowers, will infiltrate the pollination network by linking to the most abundant plant species (thus acting as opportunistic, i.e. showing low selectivity). However, species might be expected to be more opportunistic on oceanic islands because of the phenomena of 'density compensation' and niche expansion, which are caused by the lower interspecific competition relative to continental islands or mainland areas (MacArthur, Diamond & Karr, 1972; Blondel, Chessel & Frochot, 1988).

In the last decade, the application of network techniques to the study of community patterns has allowed the identification of some general properties, their ecological and evolutionary consequences and the role of each species in the community (Bascompte & Jordano, 2007; Blüthgen *et al.*, 2008; Ings *et al.*, 2009; Vázquez *et al.*, 2009). This network approach has also contributed to a realization of the importance of maintaining and restoring the integrity of species interactions if we wish to preserve the biodiversity on islands (Kaiser-Bunbury, Traveset & Hansen, 2010), where species are more vulnerable to human disturbance because of their naturally small population sizes and ranges (Cox & Elmqvist, 2000; Simberloff, 2000). Despite the importance of a network approach, most conservation and restoration projects do not incorporate this information as indicators of community structure, ecosystem function and resilience of restored communities to future perturbations (Memmott, 2009; Kaiser-Bunbury *et al.*, 2010; Menz *et al.*, 2011; Devoto *et al.*, 2012).

Here, we used this network perspective to compare species composition and the structure of different pollination communities between oceanic (Lanzarote) and continental (Mallorca) islands. We focused on coastal communities because they represent the habitat in which most immigrant species arrive (Whittaker & Fernández-Palacios, 2007). Despite island differences in origin, area, age and colonization sources, we expected some similarities in species composition between communities, as a result of species adaptation to coastal habitats and the close proximity to a common source area (Africa), although strong differences in the predominant group of flower visitors could be hypothesized; specifically, we expected a higher fraction of bees in the Balearics and a higher fraction of small flies in the Canaries (Inoue, 1993; Barrett, 1996). We also predicted a greater diversity of interactions and more specialist (low linkage level) and selective (high d') species in the Balearics (Trøjelsgaard & Olesen, 2012). Moreover, because of the smaller communities on oceanic islands and the presumed presence of super-generalist species (Kaiser-Bunbury *et al.*, 2009; Padrón *et al.*, 2009; Traveset *et al.*, 2013), we further envisaged higher connectivity and nestedness in the Canaries than in the Balearics, the latter with values probably more similar to those found in studies conducted on mainland areas (Trøjelsgaard & Olesen, 2012). Comparison of patterns of plant–animal interactions between oceanic and continental islands have been performed only with seed dispersal communities (González-Castro, Traveset & Nogales, 2012); therefore, this is the first time that pollination networks have been contrasted between these two types of island.

MATERIAL AND METHODS
STUDY SITES
The study was carried out in four coastal areas, two in Mallorca (continental island) and two in Lanzarote (oceanic island) (Fig. 1). The distance between each island and the mainland is rather similar (approximately 125 km for Lanzarote and 180 km for Mallorca), but an important biogeographical difference is the geographical location of the archipelagos. The Canary Islands are located in the Atlantic Ocean, Africa being the only nearby mainland, whereas the Balearic Islands are located in the western Mediterranean Sea and are surrounded by different nearby landmasses acting as potential sources of colonization (e.g. Africa, Iberian Peninsula). Moreover, the area and island age differ considerably between the two islands: Lanzarote has a surface area of 846 km^2 and its oldest volcanic areas are aged 15.5 Myr, whereas Mallorca has a surface area of 3625 km^2 and its age is *c*. 5 Myr.

On Mallorca, the largest of the Balearic Islands, the two study sites were Son Bosc (SB) (39°46′28.11″N, 3°07′45.34″E, 3.9 ha) and Cala Mesquida (CM)
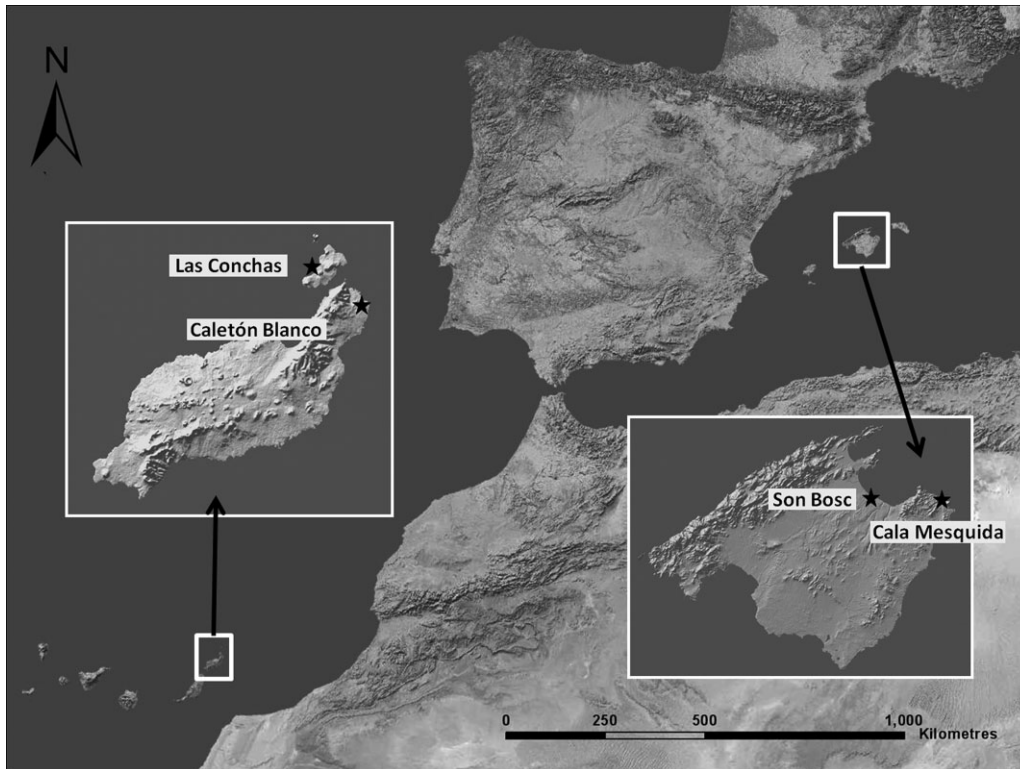
Figure 1. Map showing the location of the study sites.

(39°44′37.63″N, 3°26′02.12″E, 1.4 ha). SB is a dune marshland (Fig. 2), located in the north of the island, with a high diversity of plants; the predominant vegetation consists of *Daucus carota* L. (Apiaceae), *Helichrysum stoecha*s DC. (Asteraceae), *Lotus corniculatus* L. (Fabaceae), *Lotus cytisoides* L. (Fabaceae), *Scabiosa atropurpurea* L. (Dipsacaceae) and *Teucrium dunense* Sennen (Lamiaceae). CM, in the north-east, is one of the best preserved dune areas on Mallorca (Fig. 2); it is dominated by typical dune vegetation, including *Euphorbia paralias* L. (Euphorbiaceae), *Helichrysum stoechas*, *Scrophularia canina* L. (Scrophulariaceae), *Teucrium capitatum* L. (Lamiaceae) and *Lotus cytisoides*.

On Lanzarote, in the north-east of the Canary Islands, the study took place in Caletón Blanco (CB) (29°12′15.20″N, 13°25′26.07″W, 6 ha) and Las Conchas (LC) (29°16′32.13″N, 13°30′53.34″W, 4.3 ha). CB is also one of the best preserved dune areas of Lanzarote (Fig. 2), located in the north-east and included in the protected area of 'La Corona Natural Monument'. The dominant vegetation in this area consists of *Tetraena fontanesi* (Webb & Berthel.) Beier & Thulin (Zygophyllaceae), *Launaea arborescens* Murb. (Asteraceae), *Euphorbia paralias*, *Senecio leucanthemifolius* Poir. (Asteraceae) and *Polycarpaea nivea* Webb (Caryophyllaceae). LC is a dune area (Fig. 2) located in the

north-west of La Graciosa islet (29.05 km^2), approximately 1.1 km from Lanzarote. This small island is a protected area included in the 'Archipiélago Chinijo' Natural Park. The vegetation is dominated by *Astydamia latifolia* Baill. (Apiaceae), *Launaea arborescens*, *Lotus lancerottensis* Webb & Berthel. (Fabaceae), *Ononis hesperia* (Maire) Förther & Podlech (Fabaceae) and *Polycarpaea nivea*.

The climatic conditions on the two study islands differ strongly. Mallorca has a mean annual temperature of 16 °C and a mean annual rainfall of 410 mm, occurring mostly from September to December. In contrast, Lanzarote has a mean annual temperature of 20.7 °C and a mean annual rainfall of 110 mm, occurring mostly from December to March (Agencia Estatal de Meteorología, AEMET).

SAMPLING PROCEDURE

Flower–visitor interactions were recorded in April–July 2010 on Mallorca and in January–April 2011 on Lanzarote, which covered the entire flowering spring season for both islands. Sampling started early in the year on Lanzarote because of the tight association between rainfall and plant flowering on this dry island.

Flower density was estimated every 2 weeks at each study site by counting the number of open flowers of

Figure 2. Images of each of the study coastal sites.

each flowering plant observed along each of the ten (50×2 m²) permanent belt transects established in SB and in each of the 30 (0.5×0.5 m²) random plots located in the other three sites. Random plots instead of transects were used in these sites to capture the high heterogeneity of each area. Flower density was calculated for each species as the number of open flowers divided by the total area surveyed. For species with tightly clustered inflorescences (e.g. Asteraceae), we scored each inflorescence as a flower.

On each census day at each community, all plants in bloom were observed, and censuses were performed once or twice a week at each site. We made randomized focal censuses, i.e. observing individuals of each flowering plant species at a time, between 10:00 and 17:00 h on sunny and low-wind days. Interactions were recorded from a distance of approximately 1 m from the focal plant species to minimize interference with insect behaviour during sampling. We recorded contacts between insects and flowers during 3-min periods at SB, 6-min periods at CM and 7.5-min periods in both sites on Lanzarote. Longer censuses were carried out in the last three locations because of the lower number of simultaneous species in bloom than at SB. During each census, we recorded: (1) the identity of flowering plant species; (2) the number of open flowers of each individual plant observed; (3) the identity of each flower visitor (species name if possible or morphotype otherwise); (4) the number of individuals of each species visiting flowers; and (5) the number of flowers visited by each individual flower visitor. Insects that could not be identified in the field were collected for further identification by taxonomists.

The total time spent censusing flower–visitor interactions was 49:39 h at SB, 84:45 h at CM, 56:38 h at CB and 80:53 h at LC. Differences in total observation times among sites were a result of differences in the duration of the flowering period of their constituent plant species.

SPECIES COMPOSITION AMONG SITES

In order to assess the similarity in species composition among all study sites, we calculated the Bray–Curtis dissimilarity index (Bray & Curtis, 1957), which ranges from zero, when species are very similar among sites, to unity, when no single species is shared among them. The Bray–Curtis dissimilarity was calculated for plants and animals separately, and at two different levels of species identification: species and genus level. Likewise, this index was calculated separately for each island, i.e. unifying information for the two sites.

NETWORK PARAMETERS

Quantitative interaction networks were constructed using flower visitation rate (FVR) as the interaction weight, a measure of the intensity of mutual interaction strength between partners. The FVR of species was calculated as the number of flowers contacted by each flower visitor species during a census, standardized by the number of flowers observed, the total number of censuses per plant species and the specific flower abundance (as in Castro-Urgal et al., 2012).

We calculated quantitative network parameters, as they are more robust to sampling bias than qualitative ones (Dormann et al., 2009), and are thus more conservative for comparisons among different sites. We chose five parameters at the network level and three parameters at the species level which are often used to describe network structure.

At the network level, we calculated:

1. *Quantitative connectance* (C_q); this is the fraction of realized interactions in the network weighted by the interaction strength of each species, and was calculated following Bersier, Banašek-Richter & Cattin (2002) (see also Kaiser-Bunbury et al., 2009). It is a measure of the network generalization level that tells us how connected are all species in the community. In contrast to the unweighted connectance, weighted connectance is robust against variation in sampling intensity, network size and level of asymmetry.

2. *Weighted NODF* (WNODF; Weighted Nestedness based on Overlap and Decreasing Fill; Almeida-Neto & Ulrich, 2011); this is a measure of the degree of nestedness for quantitative data. Networks are nested if those species with fewer interactions are preferentially associated with a subset of species that interact with the most connected ones. It ranges from zero (not nested network) to 100 (highly nested network).

3. *Interaction evenness* (IE); this is a measure of the uniformity of interactions between species in a network, based on Shannon's evenness (Tylianakis, Tscharntke & Lewis, 2007). An uneven network has a high skewness in the distribution of interaction weights. It ranges from zero (completely uneven) to unity (completely uniform).

4. *Interaction diversity* (ID); this provides a measure of the complexity of associations in the community, separately for plants and flower visitors (e.g. Albrecht et al., 2007). It is the Shannon diversity of interactions of a species averaged across all species, in our case flower visitors (ID_{fv}) or plant species (ID_p).

5. *Network specialization H_2'* (Blüthgen et al., 2006); this is a measure of the level of network selectiveness; it is also derived from Shannon entropy and is related to the weighted d' (described in detail below) across all species. It ranges between zero (opportunistic, high niche overlap) and unity (selective, high niche differentiation).

At the species level, we calculated:

6. *Species specialization d'* (Blüthgen et al., 2006); this is a measure of the level of selectiveness of a species. In contrast with the linkage level (see next parameter), it accounts for the available resources provided by its interaction partners. It also ranges from zero (highly opportunistic) to unity (highly selective). This index increases with the deviation from random selection of the available interaction partners based on their abundance. Thus, for instance, a flower visitor that visits flowering plant species proportionally to their availability in the community is considered to be opportunistic, whereas a flower visitor that visits rare plants disproportionately more often than common plants is considered to be selective. Given that d' is influenced by network asymmetry [which can be calculated as $(A-P)(A+P)^{-1}$, so that it ranges from zero (total symmetry) to unity (maximum asymmetry), where A is the number of animals and P is the number of plants in the network] (Blüthgen et al., 2007), we used a corrected metric (d'_{corr}) (see Trøjelsgaard et al., 2013). This metric is derived from the residuals of the linear regressions of d'_p and d'_{fv} against network asymmetry in order to compare the four sites.

7. *Linkage level* (L); this tells us the level of generalization of each species, i.e. the number of species with which each species interacts. Although this is a qualitative parameter, we considered it here as it is frequently used when describing ecological networks, and mainly to compare it with other published pollination networks.

Finally, we also obtained a *normalized linkage level* (also named the normalized degree, ND), which is L divided by the number of possible partners. When

Table 1. Qualitative web parameters for all studied sites: oceanic island (Lanzarote) and continental island (Mallorca). P (number of plant species), A (number of flower visitor species), S (total number of species), $A : P$ (animal to plant ratio), T_{int} (total number of interactions), L_p (mean plant linkage level ± SD), L_{fv} (mean flower visitor linkage level ± SD), max. L_p (maximum number of partners of a plant species in each site), max. L_{fv} (maximum number of partners of a flower visitor species in each site). The percentage of interactions of the most generalist species relative to the total number of interactions observed is shown in parentheses

	Continental island		Oceanic island	
	Son Bosc	Cala Mesquida	Caletón Blanco	Las Conchas
P	69	42	18	25
A	143	131	62	62
S	212	173	80	87
$A : P$	2.07	3.12	3.44	2.48
T_{int}	2739	1466	1008	1913
L_p	7.33 ± 6.42	8.36 ± 7.97	7.61 ± 6.34	8.16 ± 6.84
Max L_p	28 (20%)	42 (32%)	24 (39%)	29 (47%)
L_{fv}	6.42 ± 6.4	4.76 ± 3.98	4.22 ± 3.16	4.33 ± 3.66
Max L_{fv}	32 (46%)	16 (38%)	13 (72%)	14 (56%)

calculating the mean of these two parameters, all flower visitors observed less than three times were not considered. The rationale was to avoid the over-estimation of singletons and doubletons (species observed only once or twice, respectively) which might bias the true L and ND averages.

For each of the four networks, we also obtained the number of plant species (P), number of flower visitor species (A), total number of species (S), animal/plant ratio ($A : P$), total number of interactions (T_{int}), mean plant linkage level (L_p), mean flower visitor linkage level (L_{fv}), maximum number of partners of a plant species in each community (max. L_p) and maximum number of partners of a flower visitor species in each community (max. L_{fv}).

All network parameters and Bray–Curtis dissimilarity indices were calculated using the *bipartite* package version 1.17 (Dormann *et al.*, 2009) run in *R 2.11*. Generalized linear mixed effect models were used to compare species specialization parameters across sites, employing site nested within island as a random factor. Tukey's test, with the general linear hypothesis function (glht; 'many-to-one comparison procedure'; Dunnett, 1955), was employed to detect differences among study sites. These analyses were performed using the packages *lme4* (Bates, Maechler & Bolker, 2011) and *multcomp* (Hothorn, Bretz & Westfall, 2008).

In order to confirm that our results described patterns that are different from random, we compared them with an appropriate null model (Dormann *et al.*, 2009). We generated 1000 null versions (null model) of each community matrix using the *Patefield* algorithm implemented in the *bipartite* package with method *r2d*

(Patefield, 1981) (see Supporting Information, Table S1).

RESULTS

DIFFERENCES IN SPECIES COMPOSITION WITHIN AND BETWEEN ISLANDS

Species richness in the Balearic sites was more than twice as high as that in the Canarian sites. However, the total number of interactions (total number of insects observed visiting the flowers) was context dependent (Table 1). Thus, CM on Mallorca had fewer interactions than LC on Lanzarote, despite the fact that the number of species in the former was more than twofold higher than that in the latter. The ratio between flower visitors and plants also varied among sites and, on average, was higher on the oceanic than on the continental islands (Table 1).

The two islands differed significantly in species composition (Table 2); they had < 8% of species and < 30% of genera in common. At the island level, species similarity between sites was lower on Mallorca than on Lanzarote, but similarity between sites at the genus level was comparable between the islands (about 50% of genera were shared by the two sites on each island). Three plant species [*Cakile maritima* Scop., *Euphorbia paralias* and *Reichardia tingitana* (L.) Roth] were present in three of four study sites, and one bee (*Amegilla quadrifasciata*) and two butterflies (*Colias croceus* and *Vanessa cardui*) were present in all sites. At the genus level, species of *Euphorbia* L. and 12 flower visitors (five bees: *Amegilla* sp., *Andrena* spp., *Chalicodoma* spp., *Lasioglossum* spp., *Osmia* spp.; three beetles: *Dasytes* spp., *Meligethes* spp., *Mordellis-*

Table 2. Bray–Curtis dissimilarity index for each two possible community combinations. This dissimilarity index ranges from zero, when species are similar among sites, to unity, when no single species is shared among them. Values in bold show the similarity in species composition between sites on the same island

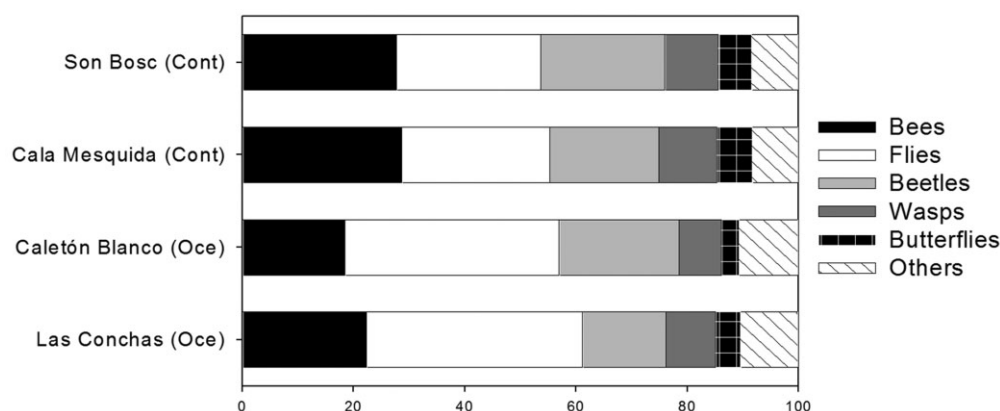|	Species level		Genus level	
	Plants	Flower visitors	Plants	Flower visitors
SB (Cont) vs CM (Cont)	**0.73**	**0.55**	**0.59**	**0.44**
SB (Cont) vs CB (Oce)	0.98	0.95	0.92	0.75
SB (Cont) vs LC (Oce)	0.96	0.92	0.86	0.75
CM (Cont) vs CB (Oce)	0.95	0.94	0.87	0.74
CM (Cont) vs LC (Oce)	0.96	0.91	0.8	0.72
CB (Oce) vs LC (Oce)	**0.55**	**0.51**	**0.54**	**0.44**
Continental vs oceanic	0.95	0.92	0.84	0.7

Figure 3. Proportions of flower visitor taxonomic groups at each study site.

tena sp.; two flies: *Sphaerophoria* spp., *Sarcophaga* spp.; and two butterfly taxa; *Vanessa* sp. and *Colias* sp.) were observed at all study sites.

The main taxonomic group of flower visitors also varied between the two islands: bees were predominant on Mallorca [46 species (27.7%) at SB and 41 species (28.7%) at CM] and flies on Lanzarote [26 species (38.8%) at LC and 25 species (38.5%) at CB] (Fig. 3). With regard to plant taxa, Asteraceae was the family with the greatest species representation in all study sites: 17 species (54.8%) at CM, 12 species (35.3%) at SB, eight species (44.4%) at LC and four species (33.3%) at CB. This was followed by Fabaceae present in three of the sites: eight species (23.5%) at SB, six species (19.3%) at CM and four species (22.2%) at LC.

SPECIES SPECIALIZATION AND SELECTIVITY

The plant linkage level (L_p) was rather similar among all four communities (Table 1). Likewise, the linkage level of flower visitors (L_{fv}) did not differ significantly between continental and oceanic communities,

although SB (the most diverse area, with the largest number of species and interactions) showed higher L_{fv} than the other three communities (CM: $z = 3.85$, $P = 0.001$; CB: $z = 3.72$, $P = 0.01$; LC: $z = 4.42$, $P = 0.001$) (Table 1). When accounting for partner availability, and thus comparing ND among communities, similar results were obtained; however, in this case, SB only showed higher ND_{fv} than CB ($z = -2.74$, $P = 0.01$). The most generalist plant was *Euphorbia paralias* from CM on Mallorca, being visited by 42 different flower visitors, and the most generalist flower visitor was the beetle *Meligethes* sp. from the other Mallorcan community, SB, visiting 32 plant species.

On the Canaries, the most generalist species were native species, which had a disproportionately higher number of links than the rest, thus acting as supergeneralist species. These were represented by two plants, *Euphorbia balsamifera* Aiton (Euphorbiaceae) at CB (with 24 links, involved in 39% of all network interactions) and *Astydamia latifolia* (Apiaceae) at LC (with 29 links, involved in 47% of all network interactions), and one flower visitor (a fly), *Tethina* sp. (Tethinidae), with 13 (72%) and 14 (56%) links at CB and LC, respectively.

Table 3. Quantitative network parameters for all studied sites: oceanic island (Lanzarote) and continental island (Mallorca). d'_p (mean plant selectivity ± SD), d'_{fv} (mean flower visitor selectivity ± SD), H_2' (community-level selectivity), C_q (quantitative connectance), ID_p (plant interaction diversity), ID_{fv} (flower visitor interaction diversity), IE (interaction evenness), WNODF (Weighted Nestedness based on Overlap and Decreasing Fill)

	Continental island		Oceanic island	
	Son Bosc	Cala Mesquida	Caletón Blanco	Las Conchas
d'_p	0.56 ± 0.22	0.57 ± 0.14	0.41 ± 0.17	0.46 ± 0.18
d'_{fv}	0.54 ± 0.23	0.45 ± 0.20	0.37 ± 0.13	0.37 ± 0.18
H_2'	0.73	0.61	0.46	0.52
C_q	0.02	0.03	0.06	0.05
ID_p	0.39	0.46	0.35	0.51
ID_{fv}	1.01	1.20	1.14	1.22
IE	0.42	0.73	0.79	0.71
WNODF	10.41	11.66	19.91	21.73

With regard to species selectivity, both plants and flower visitors were overall more opportunistic (showed lower values of d' and H_2', Table 3) at the oceanic than at the continental sites. However, when using d'_{corr}, differences were significant only between the two Mallorcan sites and LC on Lanzarote for flower visitors (CM: $z = -4.17$, $P = 0.001$; SB: $z = 3.83$, $P = 0.001$) and between CM on Mallorca and the two sites on Lanzarote for plants (differences from CB: $z = 2.83$, $P = 0.05$; from LC: $z = -2.73$, $P = 0.01$). When we classified all species into different groups according to their d' value (highly selective, $d' > 0.75$; selective, $0.75 > d' > 0.5$; opportunistic, $0.5 > d' > 0.25$; highly opportunistic, $d' < 0.25$), we observed a clear predominance of selective species at the two Mallorcan sites and a predominance of opportunistic species at the two oceanic sites; on Lanzarote, highly selective species were almost absent (Fig. 4).

DIFFERENCES IN NETWORK-LEVEL PARAMETERS WITHIN AND BETWEEN ISLANDS

The interaction diversity of both plants and flower visitors (ID_p, ID_{fv}) and the interaction evenness (IE) were similar for three of the four sites, which resulted in similar values for these parameters between islands (Table 3). The most uneven site and that showing a slightly lower interaction diversity, for either plants or flower visitors, was SB on Mallorca. By contrast, both quantitative connectance (C_q) and nestedness (WNODF) were almost twice as high at the oceanic than at the continental island sites (Table 3).

DISCUSSION

Despite the greater species richness in the continental than oceanic pollination communities, $A : P$ ratios were rather similar between Lanzarote ($A : P = 2.96$) and Mallorca ($A : P = 2.60$), reaching intermediate values to those previously reported from other islands ($A : P = 2$) and from mainland communities ($A : P = 4$) (Trøjelsgaard & Olesen, 2012). The close proximity of our two study islands to the mainland source areas might partly explain the high pollination richness relative to other islands with a more depauperate pollinator fauna. Probably because of this similar distance to the mainland, the coastal areas of Mallorca and Lanzarote analysed in this study shared up to 30% of the genera of flower visitors, a high value considering that the two sites within each island shared only 56% of the genera. By contrast, plants shared only 16% of genera between the two islands, possibly because of their lower capacity for dispersal and establishment than flower visitors. Within islands, the two Canarian sites were more similar in species composition than the two Mallorcan sites. This translated into more similar qualitative parameters (total number of species, total number of interactions, mean and maximum species linkage level) and quantitative parameters (H_2' and IE) in the former. As expected, bees constituted the richest taxonomic group on the continental island, as found in continental communities (Kaiser-Bunbury *et al.*, 2010). By contrast, dipterans were the group with the largest number of species in the oceanic communities, a pattern commonly observed in island pollination assemblages (Kaiser-Bunbury *et al.*, 2009; Padrón *et al.*, 2009; Traveset *et al.*, 2013).

Contrary to expectations (Barrett, 1996; Padrón *et al.*, 2009), we found that the number of links per species, for plants or flower visitors and accounting for partner availability or not, was rather similar between the two oceanic and continental island sites. Only flower visitors at SB tended to be more linked than those observed at the other three sites. Similar linkage levels between an oceanic and a continental
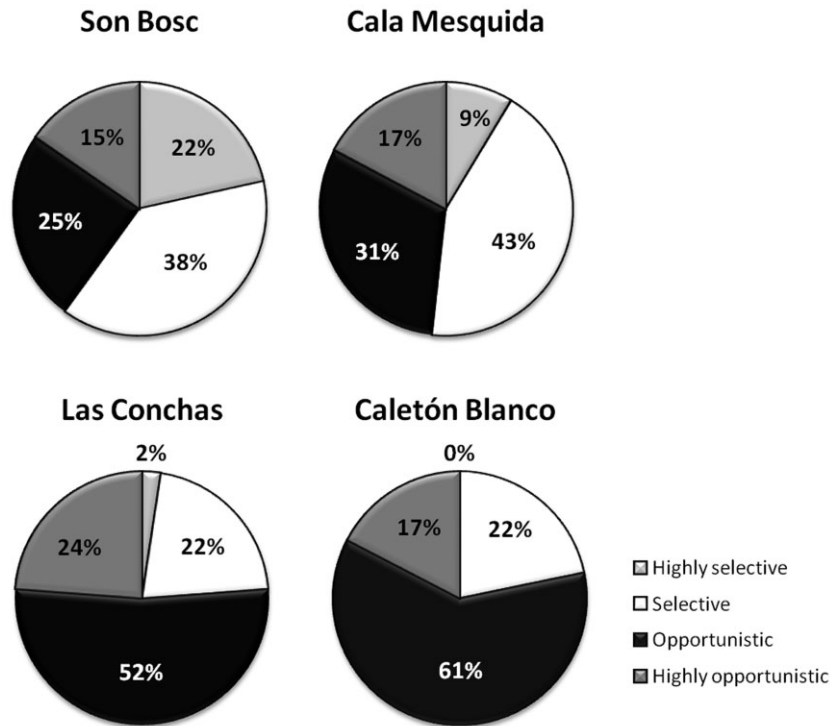
Figure 4. Proportions of species in the different categories of selectivity at each of the study sites. The degree of selectivity is calculated based on the d' parameter (highly selective, $d' > 0.75$; selective, $0.75 > d' > 0.5$; opportunistic, $0.5 > d' > 0.25$; highly opportunistic, $d' < 0.25$).

island were also found by González-Castro *et al.* (2012) for vertebrate seed dispersal interactions. When contrasting our results with those obtained by Bartomeus, Vila & Santamaria (2008), pooling all data from their coastal mainland study areas (which did not involve the entire community), we found that our island plants had lower linkage levels. However, accounting for the number of available partners (i.e. comparing normalized degrees; results not shown), these differences disappeared, being similarly generalized as continental plants. Regardless of the lack of differences in the generalization level between the oceanic and continental island communities, we detected a small group of super-generalist species in the former. *Euphorbia balsamifera* and *Astydamia latifolia* are two such species, which have open flowers with nectar resources easily available for flower visitors and are widely distributed across all of the Canary Islands. All super-generalist species were involved in asymmetric interactions, i.e. links between specialist and generalist species, which are known to be common in small networks and important for the long-term survival of rare plant populations as they provide stable interaction partners (Bascompte *et al.*, 2003; Kaiser-Bunbury *et al.*, 2009; Memmott, 2009). However, the loss of any of these native, highly connected species could be detrimental

to overall network stability, causing possible secondary cascading extinctions and resulting in a decline of diversity (Memmott, Waser & Price, 2004; Tylianakis *et al.*, 2010). Thus, in a conservation context, the identification, management and restoration of species that interact strongly with others should be a principal objective (Dupont, Hansen & Olesen, 2003).

In contrast with the findings on the generalization level, differences in the level of species selectivity were detected between the two islands. The two Mallorcan networks were more selective, i.e. less opportunistic (higher H_2' values) than the two Canarian networks. In the latter, > 75% of species were opportunistic or highly opportunistic, but none was highly selective. These results contrast in part with those obtained by Trøjelsgaard *et al.* (2013), who found an increased d' for plants (but not for flower visitors) with island age in the Canaries. Using data from other coastal networks of another oceanic archipelago, the Galápagos (Traveset *et al.*, 2013), we found that the oldest island, San Cristobal (2.4–4.0 Myr), showed the lowest d' values, with 70% of species also being opportunistic or highly opportunistic, whereas the youngest island, Fernandina (0.035–0.07 Myr), showed the highest d', with 58% of species being selective or highly selective. Data from more archipelagos are thus needed to assess how this index varies with island age and complexity

of interactions. A higher proportion of opportunistic, generalized species on older islands might translate into a greater redundancy in species interactions, thus implying that they are less vulnerable to perturbations. In contrast, in the Mallorcan communities, > 50% of species were selective or highly selective, which might be associated with the higher niche competition described on continental islands (Whittaker & Fernández-Palacios, 2007). This high level of selectiveness in continental island networks may indicate a reciprocal dependence between interacting partners, thus increasing the vulnerability of interactions to perturbations (Blüthgen *et al.*, 2008).

Finally, the diversity of interactions in each community was similar between the two islands, despite their differences in species richness. However, a small oceanic network size with a large number of interactions, combined with the presence of opportunistic and also super-generalist species, results in a more connected community, as found on other oceanic islands (Kaiser-Bunbury *et al.*, 2009). Greater connectivity may, in turn, result in greater nestedness (González-Castro *et al.*, 2012; Trøjelsgaard & Olesen, 2012; Traveset *et al.*, 2013), which has been reported to provide stability and resistance to perturbations (Bascompte *et al.*, 2003; Memmott *et al.*, 2004; Burgos *et al.*, 2007; Tylianakis *et al.*, 2010). Islands are of particular importance for the conservation of global diversity. However, the human pressure on ecosystems is likely to increase in the near future, as the introduction of invasive alien species and habitat alteration and destruction, the main threats to endemic biodiversity in many island ecosystems (Kaiser-Bunbury *et al.*, 2010), increase. The small population sizes and the high level of endemism make islands particularly susceptible to anthropogenic change. However, in the light of our results, small oceanic island communities might be less vulnerable to disturbance than previously thought, being buffered by some of the network traits (e.g. connectivity and nestedness) that provide stability to communities. Further research is certainly necessary from more archipelagos to establish the generality of our findings.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Results of a null model analysis to confirm that our results described patterns that are different from random. Observed network parameter values were compared with the 1000 null version of each island community, calculated using the *Patefield* algorithm (method *r2d*) implemented in the *bipartite* package of R.