


Divergence in floral trait preferences between nonflower-specialized birds and insects on the Galápagos

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PREMISE OF THE STUDY: The characteristic scarcity of insects on remote oceanic islands has driven nonflower-specialized vertebrates to broaden their trophic niches and explore floral resources. From our previous studies in the Galápagos, we know that native insectivorous and frugivorous birds visit a wide range of entomophilous flowers and can also act as effective pollinators. Here, we tested whether opportunistic Galápagos birds show any preference for specific floral traits, and if so, this preference differs from that of insects.

METHODS: Sixteen floral morphology and nectar traits of 26 native species were studied, as well as the frequency with which they are visited by birds and insects. Nonmetric multidimensional scaling (NMDS) was used to evaluate the distribution of flower traits values along two main dimensions and measure the similarity between the plants visited mostly by birds versus those by insects.

KEY RESULTS: NMDS of floral traits resulted in two species groups: (1) bell-shaped, white flowers with wider corollas at nectary level and higher nectar volume, associated with high bird visitation rates; and (2) bowl and tubular-shaped flowers with narrower corollas at nectary level and lower nectar volume, associated with high insect visitation rates.

CONCLUSIONS: Despite the divergence in floral trait preferences between opportunistic Galápagos birds and insects, bird-visited flowers display mixed traits not fitting the classical ornithophilous syndrome. This finding is compatible with the existence of a transitional or bet-hedging phenotype between insect and bird visitors and underscores the importance of coevolution and floral diversification in nonspecialized plant–visitor interactions.

KEY WORDS corolla size; entomophilous species; floral diversification; floral syndromes; flower shape; interaction frequency; nonmetric multidimensional scaling (NMDS); nonspecialized plant–visitor interactions; opportunistic birds; ornithophilous traits.

For plant species that rely on pollinators for successful reproduction, flower–visitor interactions are considered to be important drivers of plant trait diversification (Crepet and Niklas, 2009 and references therein; Emel et al., 2017; but see Souto-Vilarós et al., 2018). Such diversification can be expected when a functional group of pollinators shows preferences for a particular floral syndrome, i.e., suites of floral morphology and reward traits related to the attraction of a specific pollinator group. For example, small, bowl-shaped, white–yellow–blue–UV-colored flowers (entomophilous syndrome) are commonly associated with insect pollination, whereas large, tubular, red–orange flowers (ornithophilous syndrome) tend to be pollinated by birds (Proctor and Yeo, 1973; Fenster et al., 2004; Willmer, 2011). However, these syndromes have been described for specialized nectarivorous species, and they cannot fully encompass

the vast number of angiosperms regularly visited by nonflower-specialized animals (Waser et al., 1996; Ollerton et al., 2009a; da Silva et al., 2014).

There is now solid evidence that pollination tends to be more generalized on oceanic islands, likely as a result of more depauperate and disharmonic pollinator faunas, when compared to continents (Anderson et al., 2001; Olesen et al., 2002; Traveset et al., 2016; Stuessy et al., 2017). The shortage of suitable prey for insectivorous birds, the low abundance of insect pollinators, and the availability of underexploited flower resources have impelled nonflower-specialized birds to broaden their trophic niches to include nectar and pollen (Rodríguez-Rodríguez and Valido, 2008; Cecere et al., 2011; Traveset et al., 2015b). One of the most remarkable examples of such interaction release (*sensu* Traveset et al.,

2015b) is found in the Galápagos, where native granivorous and insectivorous birds commonly visit flowers and are known to be effective pollinators even of plants displaying a typical entomophilous syndrome (Traveset et al., 2015b; Hervías-Parejo and Traveset, 2018). Nevertheless, whether opportunistic Galápagos birds show any preference for specific floral traits remains totally unknown. Studies addressing floral preferences are important because flower visitors can be selective agents acting upon plant traits. Networks have proven to be a most effective tool to evaluate the intricacy of species interactions and their effects on community functioning and evolution (Heleno et al., 2014; Delmas et al., 2019). Here we used a network approach to evaluate whether Galápagos birds show any preference for specific floral traits and to compare their floral choices with those of insects. To the best of our knowledge, this is the first community-wide study assessing the floral preferences of opportunistic birds on otherwise entomophilous plant species. Under the floral syndrome framework, we would expect to see certain trait values linked with nonflower-specialized visitors (e.g., wide corollas).

MATERIALS AND METHODS

Study area, plant species, and nonflower-specialized birds

Fieldwork was carried out in the Tortuga Bay area (0°45'02.5"S 90°19'24.2"W; 100 m a.s.l.), west of Puerto Ayora on the Island of Santa Cruz (Galápagos), with its characteristic arid vegetation. The arid zone is dominated by two Cactaceae species *Opuntia echios* and *Jasminocereus thouarsii*, and trees such as *Bursera graveolens*. This zone is the most widespread habitat in the archipelago (≈60% of total land area), and it includes the greatest plant diversity and most endemic species (Guézou et al., 2010). The hot–wet season (January–May) is associated with frequent rain and coincides with the peak of the flowering period. In contrast, the arid zone becomes extremely dry during the cold–dry season (June–December) (mean rainfall: 277 mm, mean temperature: 24°C; Trueman and d'Ozouville, 2010).

Nearly 900 angiosperm species have been recorded in the Galápagos (Guézou et al., 2014), of which, 29% are endemic, 36% are non-endemic natives and 35% are introduced (Lawesson et al., 1987; Trueman et al., 2010). Most angiosperms that have been studied are considered entomophilous (McMullen, 1999, 2012; Chamorro et al., 2012; Traveset et al., 2015a). There are 24 land birds, including the remarkable radiation of 15 finch species. A recent study revealed that all species examined across the main islands feed on the flowers of at least 106 plant species (Traveset et al., 2015a). Pollination effectiveness has been confirmed for eight nonflower-specialized feeders: three ground finches (*Geospiza fuliginosa*, *G. fortis*, and *G. magnirostris*), the cactus finch (*G. scandens*), one tree finch (*Camarhynchus parvulus*), a Galápagos mockingbird (*Mimus parvulus*), the yellow warbler (*Setophaga petechia*), and the Galápagos flycatcher (*Myiarchus magnirostris*) (Grant and Grant, 1981; Hervías-Parejo and Traveset, 2018).

Observation of flower visitors

Data on bird and insect visitation to the flowers of the 26 native plant species studied here were retrieved from Traveset et al. (2015a,

respectively). A total of 144 h were spent recording diurnal and nocturnal insect visits to flowers of the studied species within an area of about 1 km² from April 2010 to May 2011 (as detailed by Traveset et al., [2015a]). For birds, mist nets were operated for a total of 234 h (from 06:00 to 12:00 hours) to evaluate pollen transport by captured birds by swabbing a 3-mm³ cube of glycerin jelly stained with fuchsin on their bill, throat, and forehead from March 2010 to February 2011 (as detailed by Traveset et al., [2015b]). For each of the 26 studied plant species, visitation frequency (hereafter, interaction frequency) of insects was quantified as the number of censuses with at least one legitimate visit of any insect species with respect to the total number of censuses. “Legitimate visit” means that the visitor enters the corolla and comes into contact with the reproductive organs of the flower. Illegitimate visits were not included in the analysis. Interaction frequency of birds was quantified as the number of birds sampled that transported pollen grains from each plant species with respect to the total number of birds sampled. Both data sets were standardized by dividing each interaction frequency by the minimum observed interaction score; thus, the weakest interaction in each matrix was assigned the value of 1, and all pairwise interactions were scored in relation to that value. These values of relative interaction frequency were then related to floral traits to explore flower preferences by birds and insects.

Floral traits

For the 26 plant species, 16 floral morphology and nectar traits were measured, whenever possible, on five fresh flowers from five individuals by the same observer (S. Hervías-Parejo). Seven morphological traits were measured with a digital caliper: corolla length and diameter at opening, corolla bell diameter at nectary level, corolla–stigma distance, stamen length, pistil length, and either stigma surface diameter or stigma lobe length (Fig. 1). The sepals, petals, stamens, and stigmatic lobes were counted. Flower color was assigned into one of three categories, according to the predominant petal color: (1) completely white, (2) green and intermediate (blue and yellow) or (3) orange and intermediate (purple). For flower shape, species were coded as (1) bowl, (2) bell, or (3) tubular (Appendix S1). Nectar volume was determined as the length of the liquid column inside microcapillary tubes (0.5 µL) measured between 06:00 and 09:00 hours, and nectar concentration was measured with a refractometer, standardized to 20°C. Concentration could not be measured in nectar volumes lower than 0.5 µL. In such cases, 1 µL of distilled water was added, and the concentration was then corrected to account for the dilution factor (Appendix S2). In addition, plant origin was coded as (1) endemic or (2) non-endemic native.

Data analysis

Nonmetric multidimensional scaling (NMDS) was used to evaluate the dispersal of floral trait values along two main dimensions and to measure the similarity between the plants visited mostly by birds versus those visited mostly by insects. This technique makes no assumption about the distribution of the species, and its outcome depicts relationships wherein morphologically (including nectar characteristics) similar species are located near each other, whereas dissimilar species are proportionately located further apart (Hout et al., 2013). Because our data set included different types of quantitative variables, we used the Gower distance metric implemented in packages *vegan* and *cluster* in R version 3.4.3 (R Core Team, 2017). The first

two dimensions of the ordination space were then correlated (Spearman's test) with floral traits, whether each plant species was endemic or non-endemic native, and visitation frequencies of birds and insects (package Hmisc). Correlation coefficients were reported significant at $p < 0.05$, after sequential Bonferroni corrections to adjust for multiple comparisons. Spearman correlation analyses were also performed to confirm the association among floral traits and plant origin.

RESULTS

Plant species and flower visitors

Of the 26 plant species (18 families) studied here, 12 (46%) were visited either exclusively (6) or mainly (6; based on mean interaction frequency) by birds, whereas the remaining 14 were mostly visited by insects (Table 1). Most plant species we studied were non-endemic native (58%) to the archipelago, the remaining were endemic. The largest differences in floral traits were found in corolla length (mean 8.3 ± 9.2 mm, range 0.7–34.4 mm), corolla diameter at opening (13.2 ± 16.6 mm, 1.3–67.5 mm), stamen length (9.9 ± 11.5 mm, 1.4–49.2 mm), pistil length (10.5 ± 12.2 mm, 0.8–49.6 mm), and number of stamens (14.2 ± 21.4 , 2–100) (Appendix S2).

The flowers of the 26 plant species studied were visited by nine passerine bird species (Appendix S3), the most frequent visitors being *G. fuliginosa* (24% of samples with pollen), *G. fortis* (22%), and *M. magnirostris* (20%). Regarding insects, at least 85 species visited the flowers studied here (Appendix S4). The most frequent visitors were six native species—a wasp (*Toxomerus crockeri*), three butterflies (*Atteva hysginiella*, *Leptotes parrhasioides*, and *Urbanus dorantes*), a moth (*Pseudoplusia includens*) and the Galápagos carpenter bee (*Xylocopa darwini*), and eight introduced species—three ants (*Brachymyrmex heeri*, *Paratrechina longicornis*, and *Tapinoma melanocephalum*), two wasps (*Polistes versicolor* and *Brachygastra lecheguana*), one fly (*Ornidia obesa*), one butterfly (*Hemiargus ramon*), and one moth (*Disclisioprocta stellata*).

Floral trait ordination

NMDS revealed that plant species mostly visited by birds and insects segregated well into two non-overlapping groups (Fig. 2). The first and second dimensions of the ordination trait space condensed 98% of the variation (stress=0.14) and were correlated with six and three floral traits, respectively. Dimension 1 also correlated with plant origin. The group of plants mostly visited by birds was composed of endemic species with a predominance of wider corollas at nectary level, more stamens, more, longer but narrower stigma lobes, and higher nectar volume (dimension 1). In contrast, all these morphological traits tended to be smaller in the species visited mostly by insects, except the stigma surface diameter. Specifically, insects visited more non-endemic species with narrower corollas at

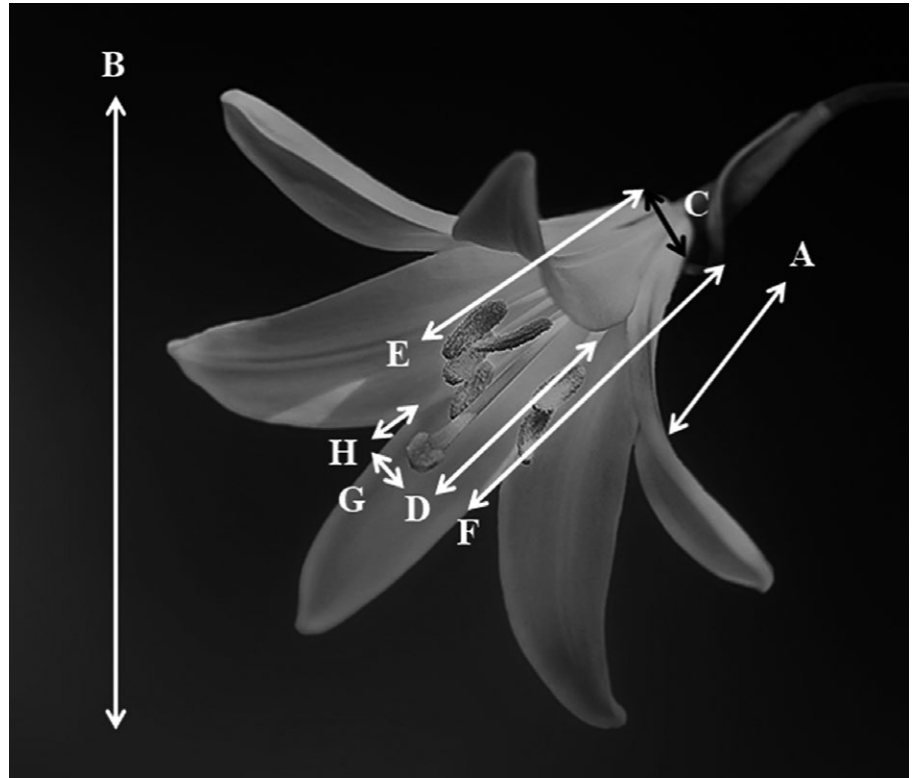


FIGURE 1. Morphological traits measured (in mm) in 26 native plant species from March 2016 to April 2017 on Santa Cruz, Galápagos. A: corolla length, B: corolla diameter at opening, C: corolla bell diameter at nectary level, D: corolla–stigma distance, E: stamen length, F: pistil length, G: stigma surface diameter, H: stigma lobe length.

nectary level, less stamens, less, shorter but wider stigma lobes and lower nectar volume. Species mostly visited by birds also tended to have more bell-shaped, white flowers, and fewer petals, whereas insects visited more bowl and tubular-shaped flowers with more petals (dimension 2).

Correlation analyses confirmed the association among several floral traits (Table 2). For example, flowers with large, wide corollas also tended to have a greater distance between corolla and stigma, longer stamens, pistils, and stigma lobes, a higher number of stamens and stigmatic lobes. Moreover, endemic species correlated with flowers with more stamens, longer stigma lobes, and higher nectar volume (as observed in bird-visited species), whereas these traits had smaller values for non-endemic native species (as observed in insect-visited species).

DISCUSSION

This study shows that Galápagos birds and insects prefer different flower types. However, flowering species mainly visited by opportunistic birds do not display a typical ornithophilous syndrome. Flower shape, corolla size, and nectar volume seem to be important for bird visitation in the plant community of the Galápagos arid zone.

Floral preferences of opportunistic Galápagos birds

Legitimate flower visitation by nonflower-specialized birds, such as most forest passerines, is a known phenomenon on oceanic

TABLE 1. Interaction frequencies (IF) of birds and insects recorded for 26 native Galápagos plant species on Santa Cruz from 2010 to 2011. For each plant species, insect interaction frequency was quantified as the number of census with at least one legitimate visit of any insect species with respect to the total number of censuses. “Legitimate” visit means that the visitor enters the corolla and physically contacts the reproductive organs. Bird interaction frequency was quantified as the number of bird samples with pollen grains with respect to total number of samples.

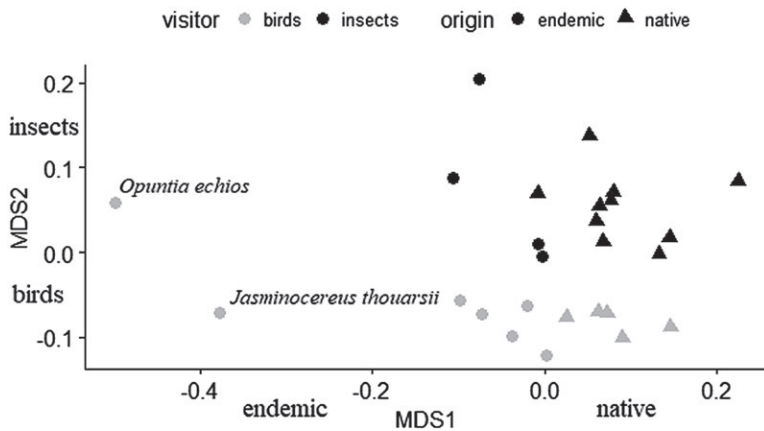
Species	Family	Origin	Color	Shape	Insect IF	Bird IF
<i>Abutilon depauperatum</i>	Malvaceae	Endemic	Yellow-orange	Bowl	2.26	0.00
<i>Acacia rorudiana</i>	Mimosaceae	Endemic	Yellow-orange	Tubular	1.21	3.00
<i>Alternanthera echinocephala</i>	Amaranthaceae	Non-endemic native	White	Tubular	1.00	0.00
<i>Bastardia viscosa</i>	Malvaceae	Non-endemic native	Yellow-orange	Bowl	1.39	0.00
<i>Boerhavia caribaea</i>	Nyctaginaceae	Non-endemic native	Yellow-orange	Bowl	2.20	0.00
<i>Bursera graveolens</i>	Burseraceae	Non-endemic native	White	Bell	2.23	14.00
<i>Cardiospermum galapageium</i>	Sapindaceae	Endemic	White	Bowl	2.78	5.50
<i>Clerodendrum molle</i>	Verbenaceae	Non-endemic native	White	Tubular	2.81	0.00
<i>Cordia leucophlyctis</i>	Boraginaceae	Endemic	White	Bell	3.12	3.00
<i>Cordia lutea</i>	Boraginaceae	Non-endemic native	Yellow-orange	Bell	2.09	0.00
<i>Croton scouleri</i>	Euphorbiaceae	Endemic	White	Bowl	2.80	16.50
<i>Cryptocarpus pyriformis</i>	Nyctaginaceae	Non-endemic native	White	Bowl	2.89	2.00
<i>Hippomane mancinella</i>	Euphorbiaceae	Non-endemic native	White	Bowl	0.00	10.00
<i>Jasminocereus thouarsii</i>	Cactaceae	Endemic	Blue-green	Bell	0.00	2.50
<i>Lantana peduncularis</i>	Verbenaceae	Endemic	White	Tubular	1.95	1.50
<i>Maytenus octogona</i>	Celastraceae	Non-endemic native	Blue-green	Bell	0.00	3.50
<i>Nolana galapagensis</i>	Solanaceae	Endemic	White	Bell	0.00	18.00
<i>Opuntia echios</i>	Cactaceae	Endemic	Yellow-orange	Bowl	2.63	48.00
<i>Passiflora foetida</i>	Passifloraceae	Endemic	Yellow-orange	Bowl	1.12	1.00
<i>Plumbago scandens</i>	Plumbaginaceae	Non-endemic native	White	Tubular	1.15	2.00
<i>Rhynchosia minima</i>	Fabaceae	Non-endemic native	Yellow-orange	Bell	2.86	9.00
<i>Scutia spicata</i>	Rhamnaceae	Non-endemic native	Blue-green	Bowl	1.78	0.00
<i>Tournefortia psilostachya</i>	Boraginaceae	Non-endemic native	Yellow-orange	Bowl	2.49	0.00
<i>Tournefortia pubescens</i>	Boraginaceae	Endemic	White	Bell	1.42	3.50
<i>Vallesia glabra</i>	Apocynaceae	Non-endemic native	White	Tubular	1.01	1.00
<i>Waltheria ovata</i>	Sterculiaceae	Non-endemic native	Yellow-orange	Bowl	3.06	0.00

islands (Rodríguez-Rodríguez and Valido, 2008; Dalsgaard et al., 2016; Hervías-Parejo and Traveset, 2018). However, it can also occur on continents where this niche is vacant (da Silva et al., 2017). Galápagos passerines are not specialized flower visitors, either in feeding habits (they are typically insectivorous, frugivorous, and granivorous) or in terms of morphology, but bird–flower visitation seems to be very common across the entire archipelago and all year round (Traveset et al., 2015a). Understandably, previous studies on floral trait preferences by nonflower-specialized birds have focused on ornithophilous plants (Dupont et al., 2004; Botes et al., 2008; Ollerton, 2009a; Brown et al., 2011), while non-ornithophilous species have been overlooked. This study represents the first community-wide assessment of floral preferences by nonflower-specialized birds and shows that some plants attract birds more often than others, mainly due to the interplay of flower shape, size, and nectar volume.

Specifically, birds tend to prefer bell-shaped, white flowers with wider corollas at nectary level, more stamens, more and longer stigma lobes and higher nectar volume, compared to those visited by insects. In South Africa, nonflower-specialized birds visit tubular-shaped flowers with shorter corollas and larger volume of nectar, compared to those visited by specialist nectarivorous birds (Botes et al., 2008; Brown et al., 2011). However, in the Galápagos, where ornithophilous traits are scarce or absent, opportunistic birds selected more bell-shaped corollas, while insects visited mainly bowl- and tubular-shaped flowers. Bell-shaped flowers with wider corollas may be more suitable for short-billed generalist birds, compared to those visited by insects that can easily

access narrower corollas (Botes et al., 2008). Moreover, flowers with more stamens likely facilitate pollen placement over a wide area of bill and forehead of birds when they probe for nectar, while small-sized visitors such as insects are poor pollinators of such flowers (Wang et al., 2018). Overall nectar volume was low (range 0.1–0.9 μL), but significantly higher among bird-visited species compared to insect-visited species. Last, birds visited mainly white flowers, consistent with an entomophilous syndrome, whereas insects visited white and yellow-orange flowers equally. The visitation of white flowers by both functional groups is not surprising as dull-colored, inconspicuous flowers are the most prevalent in the Galápagos and other pollinator-depauperate archipelagos such as Juan Fernández (Robinson Crusoe) (Anderson et al., 2001), Hawaii (Carlquist, 1974), in the southeastern and central Pacific Ocean, respectively, and the Mascarenes in the Indian Ocean (Jacquemyn et al., 2005). A plausible explanation for relatively small, dull-colored flowers (“typical” floral morphology of island angiosperms) from Galápagos is that they can be pollinated by the few insects present, as half of the bird-visited species were also visited legitimately by insects.

Overall, flowers visited mostly by opportunistic Galápagos birds displayed mixed traits not fitting any classical floral syndrome. For instance, white flowers are typical of entomophilous species, relatively high nectar volume is associated with ornithophilous species and bell-shaped flowers with large corollas resemble those of chiropterophilous species. Anderson et al. (2001) and Bernardello et al. (2001) pointed out that the floral morphology of the Juan Fernández angiosperms does not give an accurate indication of the pollination systems; instead, morphology



Floral traits	Dim 1	Dim 2
color	-0.21	0.52
shape	0.35	-0.36
corolla length	-0.15	0.33
corolla diameter at opening	-0.30	0.36
corolla bell diameter at nectary level	-0.39	0.35
corolla-stigma distance	-0.08	0.37
stamen length	-0.22	0.29
pistil length	-0.19	0.31
stigma surface diameter	0.47	0.24
stigma lobe length	-0.85	0.18
number of sepals	-0.20	0.30
number of petals	-0.29	0.53
number of stamens	-0.59	0.05
number of stigmatic lobes	-0.47	0.01
nectar volume	-0.67	0.19
sugar concentration	-0.34	0.08
Plant origin	0.84	0.15
Visitors		
insect interaction frequency	-0.05	0.31
bird interaction frequency	-0.37	-0.70

FIGURE 2. Nonmetric multidimensional scaling of 26 plant species based on 16 floral characters and plant origin. Spearman correlation coefficients are listed for associations of dimensions 1 and 2 with floral traits, plant origin, and visitor interaction frequencies. Coefficients in bold indicate significant correlations following sequential Bonferroni correction ($p < 0.05$). Along dimension 1, from left to right there were mainly endemic (the majority below the zero value) and non-endemic native species (mostly above the zero value). This gradient was related to positive correlations between six floral traits and the first dimension of the ordination plot. The correlations indicated that, moving toward the left along dimension 1, species have larger corollas at nectary level, more stamens, more and longer stigmatic lobes, and greater nectar volume. Moving toward the top along dimension 2, there were mainly bird-visited species (mostly below the zero value) and insect-visited species (mostly above the zero value). This gradient was related to positive correlations between three floral traits and the second dimension of the ordination plot. The correlations indicated that, moving toward the bottom along dimension 2, species have more bell-shaped, white flowers with fewer petals. The endemic *Opuntia echios* and *Jasminocereus thourarsii* (Cactaceae) were the most distinct species within the bird-visited species group.

may reflect retention of traits derived from the progenitors' reproductive systems. In systems relatively young in evolutionary time such as the Galápagos, mixed floral types might be related to establishment rather than to in situ selection (Crawford et al., 2011 and references therein). On the other hand, the mixed traits displayed by bird-visited species might potentially act to deter other forager groups, as recently documented in North America for the genus *Penstemon* (del Carmen Salas-Arcos et al., 2019). However, in the Galápagos, we still need to ascertain whether the ancestors of the study plants were pre-adapted to bird pollination or if the floral choices of opportunistic Galápagos birds could be an outcome of selection among species in the present flora through their foraging preferences. The correlation of bird visits and specific floral traits could lead to floral trait adaptation and diversification, as suggested for other nonspecialized plant-pollinator interactions on islands (Dupont et al., 2004; Ollerton et al., 2009b). Further work is needed to provide insights about the origins and evolutionary directions of the pollination systems of species visited by opportunistic birds in the Galápagos and other oceanic islands. These studies should focus on tracing evolutionary changes of floral traits and reconstructing ancestral characters and pollination systems. On the North Island of New Zealand, Biddick and Burns (2018) observed that small-billed

birds tended to visit small flowers and large-billed birds, large flowers. This size coupling relationship between bill length and flower size can also be tested on the Galápagos where bill size varies greatly across species (Grant et al., 1976). Moreover, it is therefore worthwhile to increase knowledge about the trophic behavior of other animal groups such as bats on oceanic insular ecosystems. Even though the two Galápagos bat species (Vespertilionidae: *Lasiurus* spp.) are considered insect-eaters and never recorded to visit flowers, a recent study suggested that they might also show interaction release, broadening their diets to include flower resources on these insect-poor islands (Olesen et al., 2018).

MAIN CONCLUSIONS AND FUTURE RESEARCH

While Galápagos flowering plants are frequently visited by nonflower-specialized birds, they do not fit a typical ornithophilous syndrome. Instead, we reported two main flower types among them: entomophilous species, which are as expected to be mostly visited by insects, and a second group mostly visited by opportunistic birds that display mixed floral traits. We tentatively interpret this segregation as representing a transitional phenotype driven by

TABLE 2. Spearman correlation coefficients among 16 floral traits of 26 native Galápagos plant species, collected on Santa Cruz, Galápagos, from 2016 to 2017. Numbers in bold indicate significant correlations after sequential Bonferroni correction.

Trait	Origin	Color	Shape	CL	CDO	CBD	CSD	SL	PL	SSD	SLL	NS	NP	NS	NSL	NV
Color	0.07															
Shape	0.30	-0.47														
Corolla length (CL)	-0.23	-0.06	0.38													
Corolla diameter at opening (CDO)	-0.21	0.08	0.15	0.80												
Corolla bell diameter at nectary level (CBD)	-0.34	0.07	0.01	0.73	0.90											
Corolla–stigma distance (CSD)	0.04	0.23	0.11	0.66	0.74	0.66										
Stamen length (SL)	-0.22	-0.02	0.27	0.91	0.91	0.80	0.77									
Pistil length (PL)	-0.25	0.09	0.19	0.81	0.76	0.65	0.61	0.85								
Stigma surface diameter (SSD)	0.18	0.13	0.07	0.31	0.12	0.19	0.31	0.19	0.15							
Stigma lobe length (SLL)	-0.61	0.73	-0.62	0.60	0.38	0.55	0.12	0.28	0.18	0.00						
Number of sepals (NS)	-0.04	0.31	-0.03	0.44	0.41	0.31	0.25	0.42	0.41	-0.06	0.46					
Number of petals (NP)	-0.07	0.41	-0.12	0.54	0.48	0.35	0.26	0.47	0.58	-0.17	0.68	0.69				
Number of stamens (NS)	-0.41	0.25	-0.13	0.40	0.51	0.46	0.53	0.48	0.33	-0.01	0.81	0.28	0.31			
Number of stigmatic lobes (NSL)	-0.36	-0.03	-0.29	0.42	0.51	0.52	0.33	0.42	0.49	0.06	0.77	0.14	0.36	0.55		
Nectar volume (NV)	-0.38	0.05	-0.33	0.11	0.32	0.29	0.22	0.25	0.09	-0.54	0.82	0.15	0.19	0.46	0.34	
Sugar concentration (SC)	-0.25	-0.09	-0.09	0.08	0.41	0.41	0.26	0.26	0.07	-0.35	0.35	-0.07	-0.19	0.31	0.07	0.69

the preferences of opportunistic birds and that can eventually lead to a classic syndrome. But an equally valid alternative explanation includes nondirectional selection, i.e., a random walk that will not lead to any particular floral syndrome. This result suggests that syndrome thinking is based on a shaky foundation, particularly on islands where decreasing resources can weaken specialization and blur the syndrome boundaries. The lack of molecular phylogenetic studies makes it difficult to determine whether those species mainly pollinated by birds have evolved in situ postcolonization and are therefore more specialized than their mainland relatives or whether this is a result of limited pollination in small, isolated and depauperated island systems such as the Galápagos. Plasticity of floral traits might “help” plants to adjust their reproductive strategy in response to these pollinator-poor environments, opening a window of opportunity for nonspecialized visitors, which might eventually lead to floral diversification.

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AUTHOR CONTRIBUTIONS

A.T., R.H., M.N., and J.M.O. conceived and designed the study, S.H.-P. performed the experiment, analyzed the data, and led the writing of the manuscript with valuable contributions from all authors.

DATA ACCESSIBILITY

The data set used by this article is available at FigShare: <https://doi.org/10.6084/m9.figshare.7258100.v1>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. Three predominant floral shapes in Galápagos plants: (A) *Opuntia echios* representing bowl-shaped flowers; (B) *Cordia lutea* representing bell-shaped flowers; and (C) *Acacia macracantha* representing tubular-shaped flowers.

APPENDIX S2. Floral traits (mean, SD, min, and max) of the 26 plant species measured in 2016–2017 on Santa Cruz, Galápagos ($n = 5$ flowers/species).

APPENDIX S3. Bird species captured in mist nets from March 2010 to February 2011 on Santa Cruz (Galápagos) and number of pollen grains transported.

APPENDIX S4. Species recorded during the census from April 2010 to May 2011 on Santa Cruz (Galápagos) and number of interactions with the study plant species.

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