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Bird–flower visitation networks in the Galápagos unveil a widespread interaction release

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Owing to food scarcity and to the high densities that vertebrates often reach on islands, typical insect- and seed-eaters widen their feeding niche and interact with a greater fraction of species than their mainland counterparts. This phenomenon, coined here ‘interaction release’, has been previously reported for single species but never for an entire community. During 4 years, we gathered data on bird–flower visitation on 12 Galápagos islands. We show that all sampled land birds exploit floral resources and act as potential pollinators across the entire archipelago, in all major habitats and all year round. Although species and link composition varies among islands, strong interaction release takes place on all islands, making their bird–flower network highly generalized. Interaction release is crucial to the survival of native birds but simultaneously threatens the unique biodiversity of this archipelago, as the birds also visit invading plants, likely facilitating their integration into pristine native communities.

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I took great pains in collecting the insects, but excepting *Tierra del Fuego*, I never saw in this respect so poor a country', goes the famous Darwin quote¹ about the insect fauna on the Galápagos. These islands, as well as other isolated oceanic islands, typically sustain a low diversity of, not just insects, but plants and animals in general, and thus have a more simple interaction structure compared with mainland biota^{2–5}. Consequently, island species experience a release in their interaction structure, promoting the exploitation of new interaction possibilities. Indeed, islands have a high proportion of generalist species showing novel and opportunistic interactions^{2,6,7}. We term this niche expansion process 'interaction release' (as one aspect of the wider concept 'ecological release'⁸), that is, island species wire up novel mutualists and prey as a response to mutualist and food shortage, and to reduced predation risk. To study the generality of this phenomenon at the community level, we adopted a network approach^{9–11}. Single species of insect-eating birds and lizards are known to supplement an insect-poor diet with nectar, pollen and fruit^{12–15}. Such interaction release is common, especially among density-compensators, that is, species that respond to low interspecific competition and reduced levels of predation and parasitism in their habitat by increasing their population size. Density-compensating vertebrates often behave as super-generalists and may exert strong directional selection on their interacting partners^{16–18}. In particular, super-generalist vertebrates may be important to plants suffering from reduced reproductive output due to a scarcity of insect pollinators. Empirical support for such a scenario is still scant but growing^{19,20}.

For most of the Galápagos land bird fauna (19 out of 23 species), we evaluated the extent of its interaction release towards the use of floral resources such as nectar and pollen. These birds are generally regarded as insect- and seed-eaters²¹, but a shortage of these resources, at least of insects, may force birds to expand their food niche to include floral rewards, abundant and widespread across all islands. We estimated pollen harvesting through direct observation of flower visits and inspection of pollen load on birds' beak and plumage. A recent literature review reported only a total of 20 interactions between Galápagos birds and flowering plants²², and at least one of them demonstrated effective pollination¹⁴. However, no study has screened any island bird fauna in the world for its potential importance as pollinators. In this respect, the most detailed available information is about flowers visited by New Zealand birds²³.

First, we built a qualitative archipelago-wide bird–flower interaction network based on data from 12 Galápagos islands to assess bird pollination patterns across the archipelago. In addition, based on a full year of pollination surveys in the two main habitats on two more intensively studied islands (Santa Cruz and San Cristóbal), we constructed one quantitative network per island, per habitat (lowland and highland) and per season (hot and cold). The strength of an interaction between plant species *i* and bird species *j* was scored as the frequency of occurrence of pollen from *i* in samples from *j*. Network structure was evaluated by a set of network descriptors. Note that, throughout the manuscript, we refer to birds as pollinators regardless of their effectiveness.

The land bird community on the Galápagos shows strong interaction release by exploiting floral resources and thus acting as potential pollinators across the entire archipelago. Birds—including virtually all finches, the yellow warbler and the Galápagos flycatcher—visit flowers extensively throughout the year, and both in the arid and humid zone, and a high spatio-temporal structural network consistency is found. At present, we expect it to be a general oceanic island phenomenon, but no comparable data are yet available. This behavioural response

across the whole bird community may be crucial to the survival of both native birds and plants, but unfortunately also catalyses the integration of invading plants into the natural systems of these unique islands.

Results

Archipelago-wide patterns. All of the 19 bird species examined (representing 83% of Galápagos native land birds) were found to feed on flowers and/or transport pollen of 106 plant species (Fig. 1). Such species are all endemic to Galápagos, except the native *Coccyzus melacoryphus* and *Dendroica (Setophaga) petechia* (Supplementary Table 1). Thus, irrespective of the main feeding guild of these 19 bird species, the whole bird community expanded its niche and included floral rewards into the diet. The other four land bird species could not be included in this study because they are either very rare or absent in the study areas (Supplementary Table 1). We know, however, that at least two of those four species, the critically endangered *Camarhynchus pauper* and *Mimus trifasciatus* from Floreana Island, do visit flowers (Supplementary Table 1). One hundred out of the 106 plant species were identified to species or genus level; 55 were trees or shrubs, 28 were herbs and 17 were vines; ~30% of these plants were endemics, 41% natives and 29% aliens to Galápagos (Fig. 1). Thus, birds visited both native and alien plants (Supplementary Table 2), with only a weak preference for natives (mean \pm s.d. = 4.48 ± 3.53 links to native species ($n = 46$) and

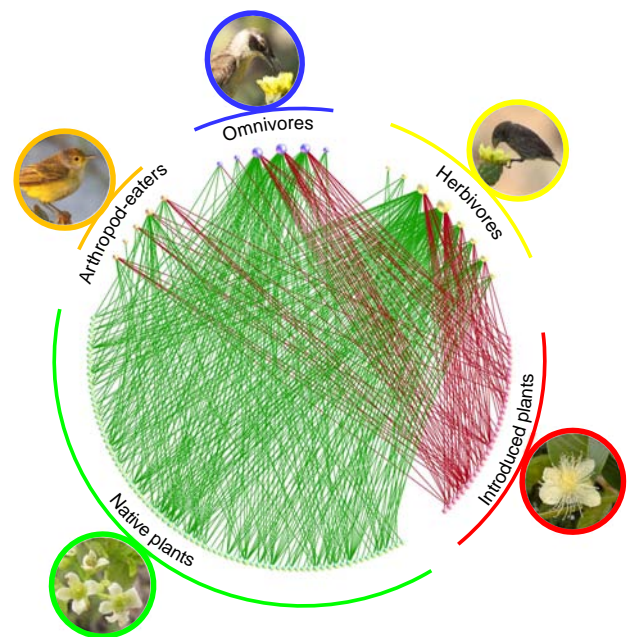


Figure 1 | Archipelago network in which all interactions observed on the 12 largest Galápagos islands were pooled. This network consisted of 19

land bird species (all but 2 being endemic to the islands) and 106 plant species, either native (green nodes) or introduced (red nodes) to the islands. Birds were classified into three functional groups depending on their main diet composition. Note that granivores, nectarivores and folivores (three groups frequently overlapping) are merged into the herbivore category. Most birds were highly generalized (their generalization level is proportional to node size), each pollinating an average of 22 plant species (range 1–77). Total number of network links was 421 (increasing 20 times the previously known number of flower–bird interactions in the archipelago). Among the main bird hubs were two finch species, the yellow warbler and the Galápagos flycatcher. Nearly a third of all identified plant species were introduced.

3.38 ± 3.58 links to alien species ($n=24$); GLM: $z=2.45$, $P<0.01$). Two of the most visited plants were highly invasive aliens: *Psidium guajava* and *Impatiens balsamina*, being visited by 14 and 12 bird species, respectively. The combined archipelago network had a connectance of 21% (Supplementary Table 2). Most bird individuals transported numerous pollen grains (mean ± s.d. = 233 ± 1,065 pollen grains; median = 5; maximum = 20,112; $n=769$ samples). About 65% of all sampled pollen loads were mixed, that is, included pollen from several plant species (mean ± s.d. = 2.45 ± 1.56 pollen species per sample; median = 2; max = 10; $n=502$). Two finches (*Geospiza fuliginosa* and *G. fortis*), the Galápagos flycatcher (*Myiarchus magnirostris*) and the yellow warbler (*D. petechia*) were the most abundant and generalized, being involved in 54% of all network links, that is, these four bird species showed the strongest interaction release. Almost all species-rich pollination networks are both nested²⁴ and modular²⁵. However, the archipelago network was only nested (NODF = 61.80, $P<0.001$), and not modular ($M=0.27$, $P>0.05$), that is, the whole network operated as one module.

Bird–plant interactions differed strongly among islands, that is, inter-island turnover of interactions was high. Of all scored interactions, 73.4% were from one island, whereas only 2% were found on four or more islands (Fig. 2). To assess to what extent such a finding was due to sampling incompleteness (that is, links missing due to insufficient sampling), we obtained rarefaction curves and asymptotic species richness estimators for each bird species (see Methods). We estimated that we had detected a large fraction (~70%) of all existing interactions (Supplementary Fig. 2, Supplementary Table 3); hence, more sampling would certainly have led to more interactions, but also to more plant species being included in the network. The same high turnover of interactions was found when considering only the interactions observed on a standardized 3-day period during the peak of the flowering season (February of 2010 and 2011) on five of the islands in which we invested an equivalent sampling effort.

Spatio-temporal variation in network parameters. Santa Cruz and San Cristóbal showed very similar network structure despite

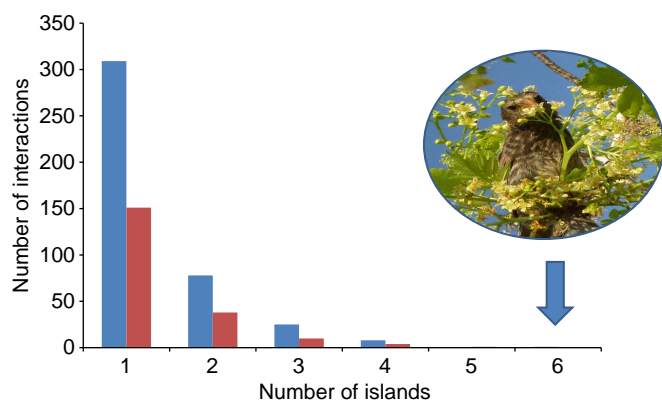


Figure 2 | Number of plant–bird interactions found on different number of islands. Blue columns correspond to the interactions pooled from all 12 islands (archipelago network), whereas red columns correspond to the 5 islands where our sampling effort was similar (Fernandina, Pinta, Santiago, Santa Cruz and San Cristóbal). Only one interaction—*Geospiza fuliginosa* and *Bursera graveolens* (photo inset)—was observed on a maximum of six islands. Each island had a high diversity of bird–flower interactions that were ‘single-island endemics’, strongly enhancing the uniqueness of each island. Despite this variation, the observation of ‘interaction release’ was general across the archipelago.

only 21% of all interactions being shared between them (that is, the same species pair interacting on both islands). Both networks had a high connectance (>30%), high interaction evenness, high species strength and low network specialization (H'_2)—Supplementary Table 4 and Supplementary Fig. 3. The interaction pattern was also very similar between the two habitats, although lowlands have higher species richness (Supplementary Table 4) and only 31% of the interactions were shared. On both islands and in both habitats, the endemic small ground finch *G. fuliginosa* and the alien plant *P. guajava* were the most connected species. Other plants frequently visited by birds were the endemic prickly pear cactus *Opuntia echios* and the non-endemic native tree *Bursera graveolens* in the lowland. The lowland and highland networks were, to some extent, coupled; some species of *Opuntia*, characteristic of the lowlands, were found in the bird samples from the highlands, suggesting that birds make altitudinal movements. Network structure was also similar between seasons, though the number of interactions was almost twice as high in the hot (wet) season, when most plants were in flower, than in the cold (dry) season (Supplementary Table 4). Only 25% of all interactions were present in both seasons. *G. fuliginosa* was the all-year-round network hub, together with two other finches (*G. fortis* and *Camarhynchus parvulus*) in the hot season, and the flycatcher *M. magnirostris* in the cold season. The main plant hubs were *P. guajava* in the hot season, whereas the native creeper *Galactia striata* and the alien herb *I. balsamina* were cold-season hubs.

Comparison between alien and native plants. Alien and native plants on Santa Cruz and San Cristóbal islands had a similar number of bird flower visitors (GLM: $z=0.92$, $P=0.36$; Supplementary Fig. 4) and they differed neither in specialization level d' ($t=0.93$, $P=0.35$) nor in species strength ($t=0.49$, $P=0.62$), indicating that alien species were fully integrated into the networks. Indeed, some of them had even achieved a central position as network hubs: *P. guajava* got 32% of all links on San Cristóbal and 14% on Santa Cruz (Supplementary Fig. 4).

Comparison across bird functional groups. Interaction release was observed in all three functional groups, that is, insectivores, herbivores and omnivores (Supplementary Table 1). The number of flowering plants included in their diet (linkage level) showed a higher average for herbivores (mean ± s.d.: 30.6 ± 19.6; $n=5$) than for arthropod-eaters or omnivores (17.8 ± 15.5 and 14.3 ± 11.3, $n=5$ and $n=4$, respectively) though differences were not significant (all P values >0.05). Likewise, no differences were found on the specialization level (d') and interaction strength across functional groups (Supplementary Fig. 5).

Discussion

We demonstrate that bird–flower visitation and pollen transport are very common on the Galápagos Islands. Almost all land birds in the archipelago are involved, visiting over a hundred flowering plant species. Such a massive food-niche widening—that is, interaction release—has never been described for any vertebrate community in the world.

Given the lack of similarly detailed studies on other parts of the world, it is too early to say if the massive interaction release we observed is unique to Galápagos or if it might be found elsewhere if detailed screening protocols were implemented. Unfortunately, bird pollination is still rarely reported at the community and network level. In a sample of 53 pollination networks, including ~10,000 plant and animal species, only 9 contained birds: a total of 26 species, of which 19 were hummingbirds (Supplementary Table 5). The vast majority of animals in those pollination

networks were insects. Thus, based on this set of networks, we have to conclude that bird pollination within a given habitat is either a rare phenomenon globally or systematically under-reported (perhaps exacerbated by human-caused reduction in bird densities). A massive interaction release might well occur in other archipelagos, where other phenomena like lizard pollination are known to be frequent¹². A lack of comparable data sets from other archipelagos precludes us from making further conclusions. However, we attempted to calculate similar network parameters for New Zealand, which is the archipelago with most studies of bird pollination. The New Zealand data originate from flower observations, and most of these are from specific plants and birds of high conservation priority, whereas our data mostly come from bird–pollen load analysis. Out of 35 New Zealand land bird species for which we obtained published information²³, 22 (63%) were observed to visit flowers (compared with the 83% we scored in Galápagos). The New Zealand birds visited 73 plant species, yielding a connectance of 12%, which is still considerably lower than the 21% found in the Galápagos network. Taking into account that the Galápagos network has more species than the New Zealand network, this difference in connectance becomes even larger (Supplementary Fig. 6). Without further information we cannot conclude whether this difference is real or methodological. However, one important characteristic of New Zealand bird biota, which should make flower visitation by birds more frequent, is its honeyeater birds, which belong to an old species-rich phylogeny of nectar-drinking and insect-eating birds. In spite of that, we have to conclude that the land birds of New Zealand seem to respond less massively to flowers than the Galápagos bird fauna. The reasons might be that Galápagos is more isolated, less disturbed and very likely poorer in insects than New Zealand. In addition, a review on the presumed diet of all extant and known extinct native birds in New Zealand concluded that there had been no extinctions from the major nectarivore guild²⁶.

We also explored how the Galápagos bird–flower network differed from other available bird–flower networks. To do so, we compiled 24 hummingbird–flower networks, all from the mainland or continental islands (Trinidad) (Supplementary Table 6). We compared their levels of connectance, nestedness and modularity with similar values from Galápagos and New Zealand. Correcting for variation in species richness, we found that the Galápagos network had a connectance 50% higher than expected (Supplementary Fig. 6a), and the standardized level of nestedness (z -score) for the Galápagos network was 1.9 times as high as expected (Supplementary Fig. 6b). A high connectance may have a strong stabilizing role via functional redundancy, and a nested interaction pattern of interactions might also facilitate the maintenance of species coexistence²⁷, provide resistance against perturbations²⁸ and maximize total abundance²⁹. However, there is currently a strong debate about the stabilizing role of nestedness³⁰. The lack of modules in the Galápagos bird–flower network is attributed to the large bulk of interactions among generalists^{25,31}, which glues all species tightly together. The hummingbird networks were also non-modular, except for two networks (Supplementary Fig. 6c–f, Supplementary Table 6). Modularity also influences network stability against disturbances²⁸, although the precise role of modularity to network stability depends on the type of disturbance and also on the applied measure of stability (for example, species or community persistence). Thus, a low level of modularity might reduce robustness against an invasion of a parasite or an extinction of a highly connected species, but might be more robust against random secondary species extinctions³².

Bird pollination may be particularly prevalent in Galápagos because birds of the families visiting flowers in the islands were already preadapted to visit flowers in their original mainland

populations. We tested this by compiling all known bird–flower interactions involving those five bird families in South America (Supplementary Data set 1). In general, the flower-visiting Galápagos birds belonging to these five families are regarded as arthropod-eaters (for example, Yellow Warbler, the Galápagos Flycatcher) and granivores (for example, ground finches)²¹. Members of these families are also known to visit flowers in South America, but to a much lower extent: mean S. America = 16.3% of the species in the family, mean Galápagos = 82.1%; GLMM: $F_{1,4} = 8.8$, $P = 0.041$; Supplementary Table 7). A rare exception is *Dacnis cayana* (Thraupidae), which feeds frequently on the flowers of many (≥ 20) plant species. In addition, Galápagos birds visit a much higher number of plant species than their mainland counterparts (S. America = 1.7, Galápagos = 23.6; $F_{1,4} = 12.1$; $P = 0.025$, Supplementary Table 7).

Our interaction release hypothesis rests on the assumption that the islands are poor in arthropods. Such an assumption has some support^{12,33,34}, but needs validation from Galápagos. The overall insect species richness of the archipelago is well-known, but insect abundance and biomass are unknown³⁵. We did find some evidence of insect poverty in an earlier study from Galápagos¹¹, where we scored a connectance $C = 5\%$ between native insect species visiting the flowers of native plant species. This figure is lower than we should expect (8.4), if we use the regression model in ref. 9; $C = 13.83 \exp(-0.003S)$, where S is number of plant and animal species). Moreover, we suggest that birds play a relatively large role compared with insects in the pollination networks of the Galápagos. Our support for this is a tentative comparison of the bird–flower network from this study with the insect–flower network also from Galápagos¹¹. These two networks have different link currency, that is, the bird–flower links are based on pollen load and/or flower visitation, whereas the insect–flower links only are based on visitation. We pooled the bird–flower and the insect–flower networks into a total pollination network for the archipelago. The total matrix included 125 plant species, 19 bird species and 213 insect species. Birds and insects shared 40 of the 125 plant species. Nineteen plant species had only insect pollinators, and 66 had only bird pollinators. Thus, although birds only constituted 8% of the total pollinator fauna, and only made 36% of all links, they alone interacted with 53% of the flora, and together with insects with an additional 32% of the plants, thus contributing to the pollination of 85% of the flora. In addition, birds had a central position in the total network because they had a significantly higher average closeness centrality than insects, whereas their betweenness centrality was lower than that of insects. This is because a few insects, mainly in the bird-dominated module (Supplementary Note 2, Supplementary Tables 8 and 9), had high betweenness values as they connected the six insect-dominated modules with the bird–flower module. This latter module included most plants (58%) and 16 of the 19 birds, thus dominating the pollination network. However, a study of the pollen loads on insects would bring the insect- and bird-dominated modules closer together. We are confident to conclude that the small bird community compared with the large insect community plays a relatively important role to the pollination of the Galápagos plant community.

The high network generalization level facilitates the integration of alien plants into the Galápagos bird–flower network, as has also been found in other mutualistic networks^{11,36}. Galápagos birds included alien and native plants to the same levels into their diet and may thus enhance plant invasions on this increasingly human-altered archipelago. The enhancement of plant invasion by birds will obviously be higher in those species that depend on animal pollination for reproduction, and probably lower in those that are self- or wind-pollinated, such as *P. guajava*. In turn, this

alien invasive species is likely to take over and disrupt interactions between birds and native plants, with unknown ecological and evolutionary consequences³⁷. In fact, 56% of the samples included pollen of this species together with native pollen. Moreover, an average of 52% (s.d. = 34%) of the pollen grains found on those samples were from *P. guajava*, suggesting heterospecific pollen interference in ovule fertilization by deposition of alien pollen on the stigmas of native plants.

Pollination interactions had a high turnover across islands, which is also observed in other archipelagos, for example, the Canary Islands³⁸. Causes of the high turnover include sampling incompleteness, non-overlapping geographical ranges of species, rareness, phenological mismatches, strong inter-island variation in vegetation composition and specific diet preferences across islands.

Quantitative networks showed a very similar structure across Santa Cruz and San Cristóbal, lowland and highland, and hot and cold seasons (Supplementary Fig. 3, Supplementary Table 4). Thus, Galápagos birds are very opportunistic in their flower choice and search for food. The variation we did observe among islands, habitats and seasons is probably driven by differences in floral resource abundance, and consequently natural selection on bird traits might vary in a similar manner as demonstrated for the interaction between finches and their seed sources³⁹. This dynamics in community interaction structure and its evolutionary potential may become an important step in our increasing understanding and appreciation of the biodiversity puzzle of the Galápagos Islands.

Even though nobody has quantified arthropod biomass on the Galápagos, we share the impression of Darwin and many later naturalists, that these islands indeed are 'so poor a country'^{1,40}. Thus, to survive, birds widen their niche and include other food sources, such as nectar and pollen, substantiating an interaction release. This scenario is supported by two conclusions from our study: (1) all Galápagos land birds converged in their feeding niche to visit flowers and transport their pollen, and (2) connectance was considerably higher than expected for networks of this size. The first conclusion is an astonishing finding, never reported before for any ecosystem: a massive response of the bird community towards an underexploited resource. The possibility that birds primarily visited flowers to consume insects is unlikely, as the importance of flowering plant species to birds (measured as no. of bird visits) was uncorrelated with the importance of flowering plants to insects ($r_s = 0.14$, $P = 0.45$, no. of plant species = 29; data from¹¹). In addition, only very rarely, during our long observation period of flower visitors in the archipelago (>500 h), did we observe birds capturing insects in flowers. The second conclusion emerges from the core of plant and bird species that acted as super-generalists, boosting network connectance and repressing any tendency towards modularity. This result is of general importance to island biology and ecosystem stability⁴¹. Finally, we anticipate that interaction release is a widespread island phenomenon, particularly in isolated oceanic islands with simple ecological networks and disharmonic faunas.

Methods

Study sites. The Galápagos archipelago comprises 18 islands >1 km² and numerous islets. Our study focused on the 12 largest islands (excluding Baltra, ~350 m off Santa Cruz; Supplementary Fig. 1), covering the whole spectra of age, area, elevation and level of disturbance. The arid zone in the lowlands comprises ~80% of the total land cover. The flora consists of 557 native vascular species (32% endemic), and an additional 825 (~60%) aliens⁴². The archipelago has a hot/wet season (January–May) and a cold/dry season (June–December).

Observation of flower visitors. We collected data during the flowering peak (February–March) from 2010 to 2013 in all 12 islands. During three consecutive

days on each island we recorded bird visitation at all flowering species in an area of about 1 km² (see details in ref. 11). Overall, this effort resulted in ~500 h of flower-visitor observations.

Pollen transport by birds. We evaluated pollen transport on mist-netted birds in the arid zone of all islands during the flowering peak, and further sampled more intensively in Santa Cruz and San Cristóbal during 2 months of each season in the two main habitats (arid, in the lowlands and humid in the highlands). Mist nets were open from sunrise until mid afternoon under favourable weather conditions, and regularly inspected for captured birds; nets operated for ~600 h. Birds were individually sampled for pollen load by swabbing a small cube (~3 mm³) of glycerine jelly, stained with fuchsin, on their beak and peri-mandibular feathers (that is, throat and forehead). The gelatine cube was then placed on a microscope slide, which was covered and melted by a weak heat source to produce a single layer of stained pollen grains. Preparations ($n = 769$) were sealed with clear nail polish, labelled and stored. Pollen grains were later identified by means of a reference collection and counted under a light contrast Zeiss microscope.

Interaction networks. The qualitative 'archipelago network' included direct and indirect evidence of bird-flower visits from the 12 study islands. Four network metrics were obtained to describe its topology: linkage level, connectance, nestedness and modularity (Supplementary Note 1). For the more intensively sampled networks, Santa Cruz and San Cristóbal, we built quantitative matrices in which interaction weight was the number of samples in which pollen of any given plant species were identified (that is, frequency of occurrence). For these quantitative networks, we calculated the above parameters and, in addition, specialization level d' , species strength, interaction evenness, weighted nestedness $WNODF$ and H'_2 . Except for nestedness and modularity, all metrics were obtained using the *R* package *bipartite* v. 2.01 (refs 43,44). General linear models were used to compare the species-level network metrics between islands, habitats, seasons, plant origin and bird functional group. For the last comparison, we included bird abundance as a covariate in the models.

Evaluation of sampling completeness of interactions. We aimed to determine the extent to which the number of individuals sampled per bird species allowed for a sufficient description of species linkage level (L_a). Therefore, we estimated the number of interactions accumulated as sampling effort increased separately for each bird species. We first computed sampled-based rarefaction curves for each species⁴⁵ using the package *vegan* (version 2.0–6)⁴⁶ in *R* (v. 2.15.0). Following Chacoff *et al.*⁴⁷, for each of the 13 bird species from which we had obtained a minimum of 10 samples, we calculated the percentage of estimated asymptotic richness detected as, % $S_{OBS} = 100 \cdot S_{OBS} / S_E$, where S_{OBS} is the observed pollen richness in the samples (that is, birds' linkage level, L_a) and S_E is the asymptotic estimated pollen richness (that is, estimated bird L_a). To compute S_E , we used the Chao 2 non-parametric estimator, $S_E = S_{OBS} + [L^2/2M]$, where L is the number of species that occur in only one sample ('unique' species), M is the number of species that occur in exactly two samples and S_{OBS} is the observed number of species⁴⁸. Chao 2 index relies on the principle that rare species in the samples carry most information on the number of un-observed species⁴⁹ and it is one of the more robust estimators for small sample sizes⁵⁰.

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Author contributions

A.T., R.H. and J.M.O. designed the study; A.T., J.M.O. and R.H. analyzed the data; A.T., R.H., J.M.O., M.N. and P.V. collected the field data; P.J., E.A. and M.T. identified the pollen grains in the lab; A.T., J.M.O. and R.H. led the writing.

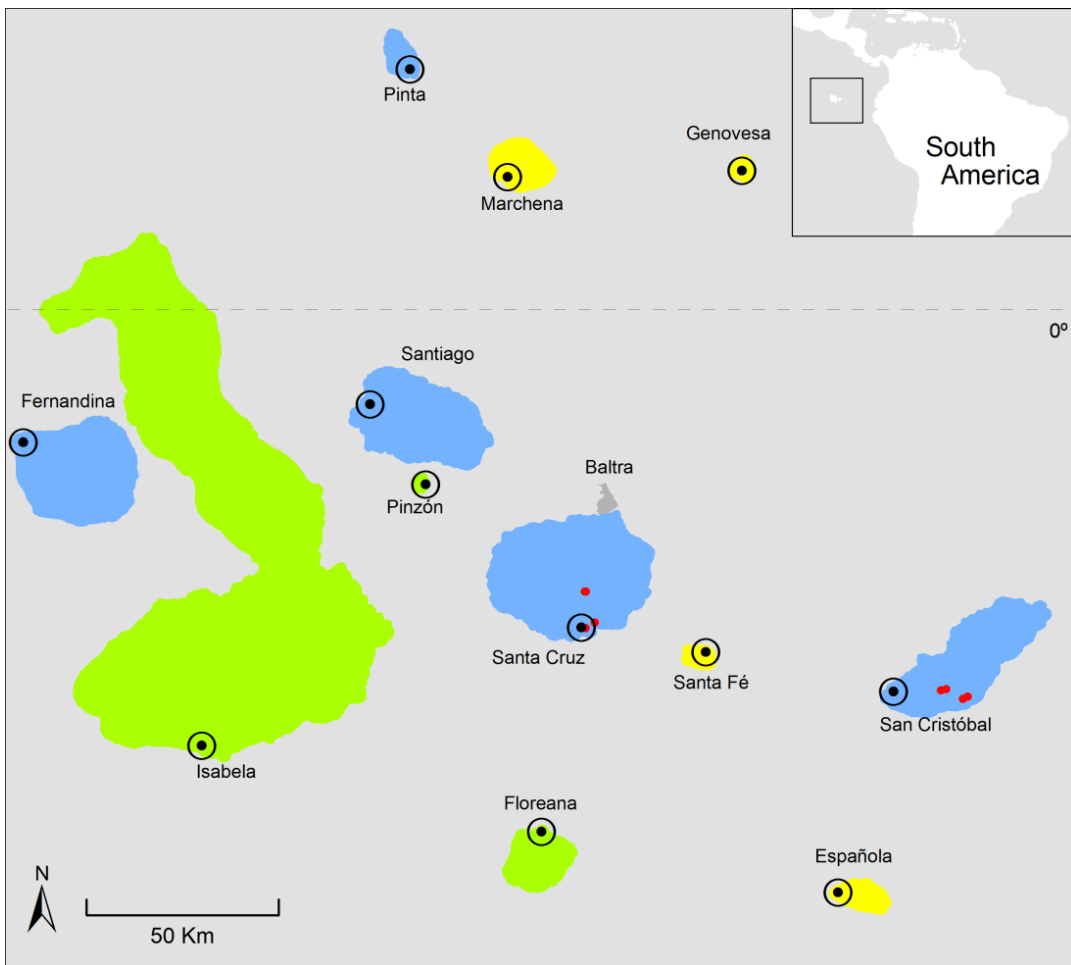
Additional information

Supplementary Information accompanies this paper at <http://www.nature.com/naturecommunications>

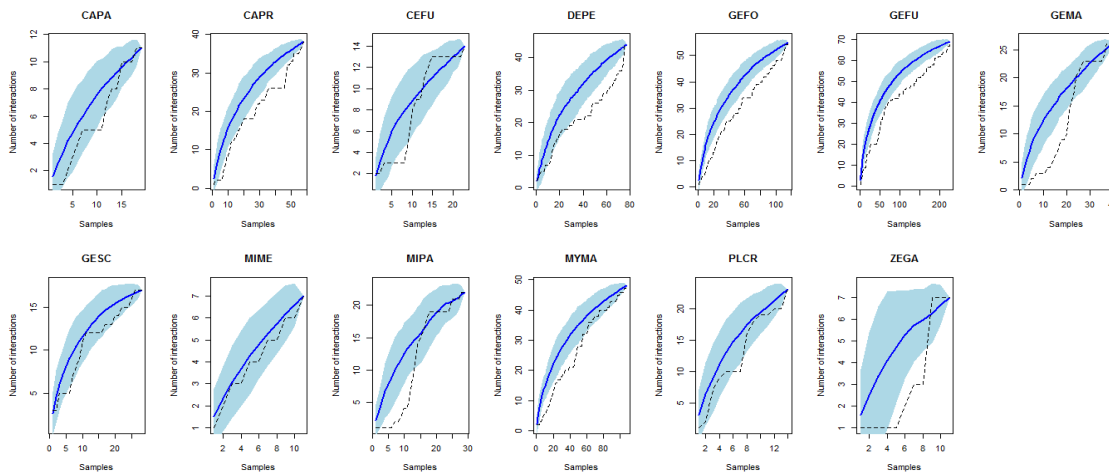
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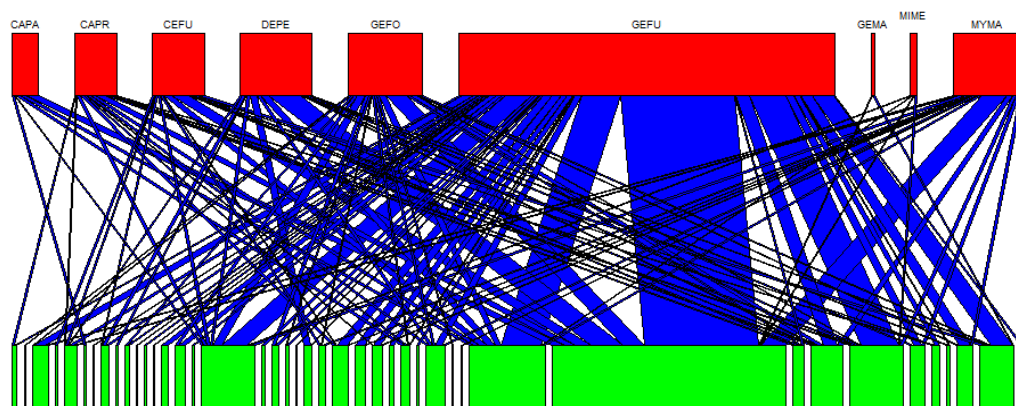
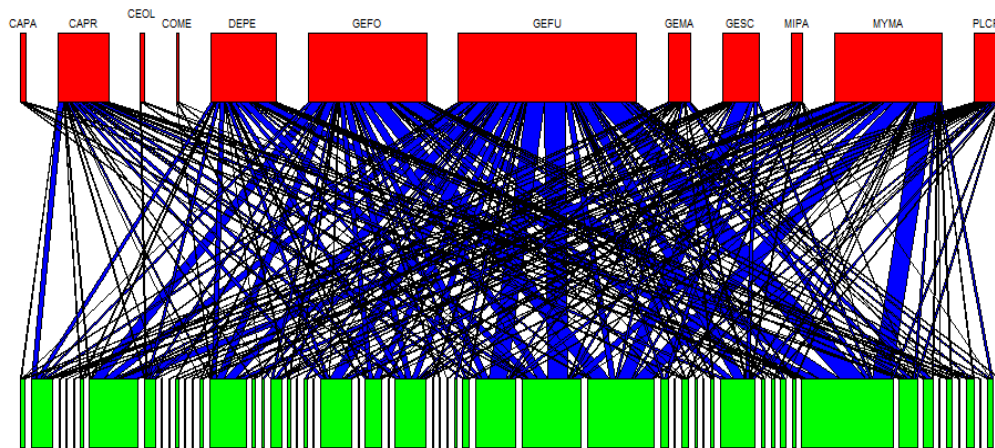


Supplementary Figure 1 | Map of the Galápagos archipelago and the locations of the field sites on the 12 islands sampled. Inset is the position of Galápagos. 'Blue' islands were sampled in 2010 and 2011; 'yellow' islands were sampled in 2012; and 'green' islands were sampled in 2013. Small red dots indicate the sites – in the dry and humid habitats – sampled during two months in each season in the two most intensively studied islands, Santa Cruz and San Cristóbal.

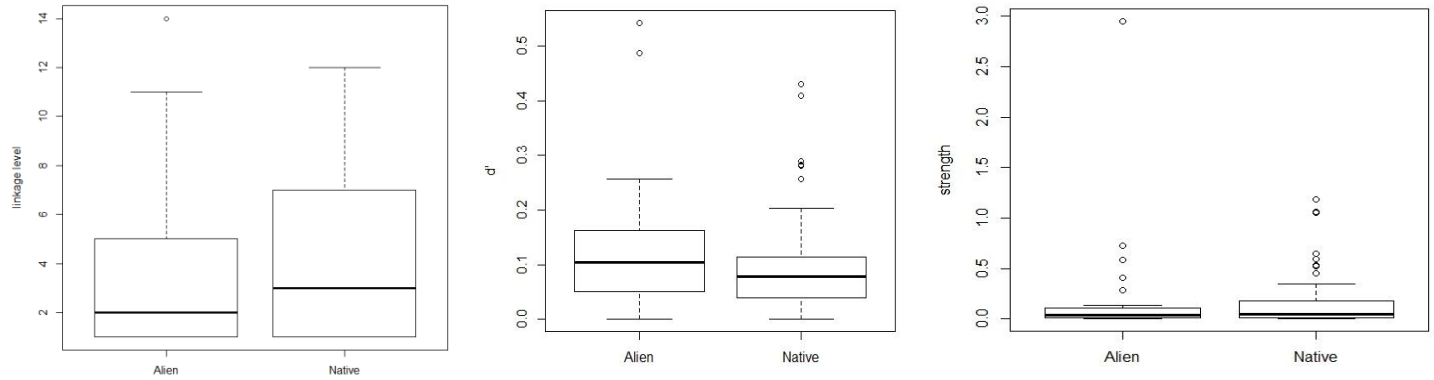


Supplementary Figure 2 | Rarefaction curves for the 13 most common bird flower-visitors, built in order to evaluate sampling completeness. Five species (CAPR, DEPE, GEFO, GEFU and MYMA) were those expected to have the highest generalization levels L (i.e. using asymptotic species richness estimator Chao2 index). With our sampling effort, we were able to detect an average of 68% of all interactions, ranging from 37% for DEPE to 91% for GESC. Although it is satisfying, it also implies that many flower-bird interactions remain to be identified in Galápagos.

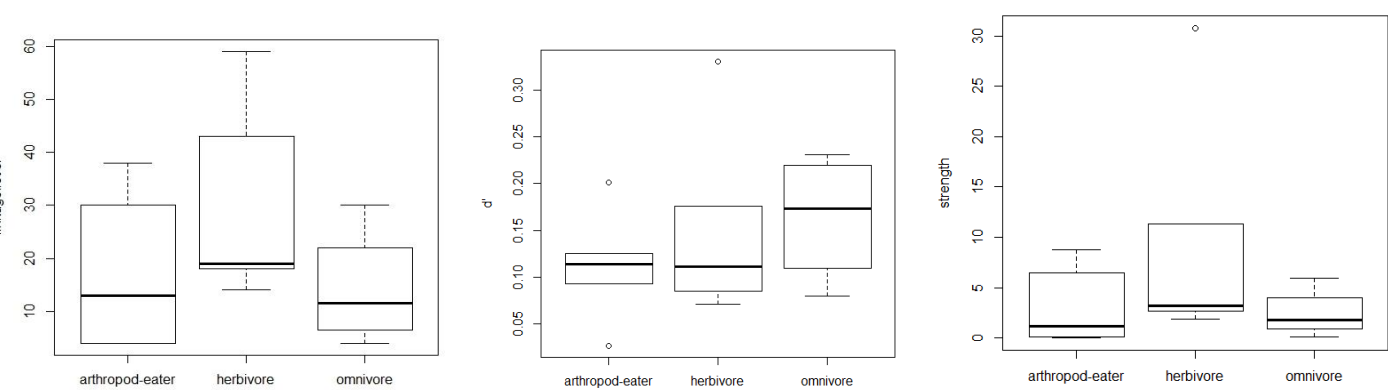
CAPA: *Camaerhynchus parvulus*, CAPR: *Camaerhynchus parvulus*, CEFU: *Certhidea fusca*, DEPE: *Setophaga (Dendroica) petechia*, GEFO: *Geospiza fortis*, GEFU: *Geospiza fuliginosa*, GEMA: *Geospiza magnirostris*, GESC: *Geospiza scandens*, MIME: *Mimus melanotis*, MIPA: *Mimus parvulus*, MYMA: *Myiarchus magnirostris*, PLCR: *Platyspiza crassirostris*, and ZEGA: *Zenaida galapagoensis*.



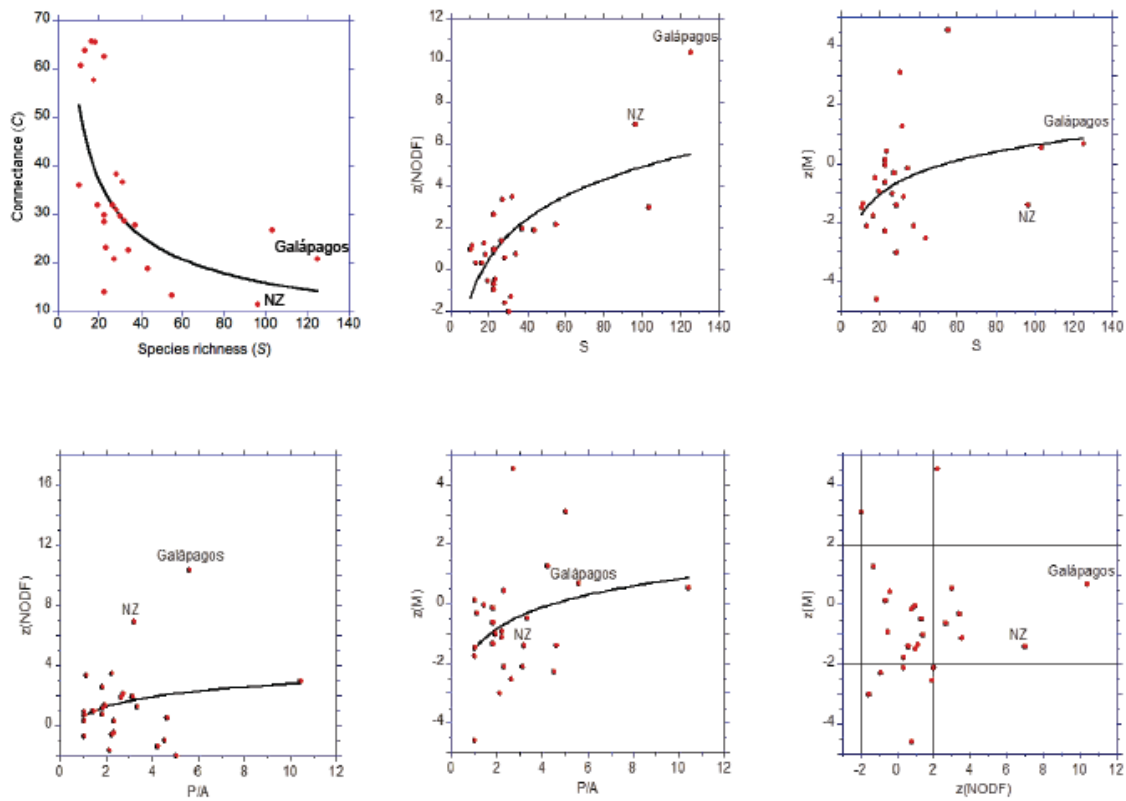
Supplementary Figure 3 | Quantitative pollen transport networks from Santa Cruz (above) and San Cristóbal (below). Red rectangles correspond to the bird species in the network whereas green rectangles correspond to the plant species being visited. The length of the rectangle is proportional to the level of generalization (number of links) of each species. Only acronyms for the bird species are given (see full scientific names in Supplementary Fig. 2). The largest green rectangle corresponds, in both cases, to the invasive alien *Psidium guajava*.



Supplementary Figure 4 | Species level network parameters, linkage level, d' and strength (Supplementary Note 1), for both alien ($n = 24$) and native ($n = 46$) plant species. Six plant species were excluded from the analysis due to unknown origin, as their pollen could only be identified to genus level. Data are from the most intensively studied islands, Santa Cruz and San Cristóbal, during 2010 and 2011. The median, 50% and 95% percentiles are shown for each parameter. The alien species *Psidium guajaba* was consistently an outlier in the three panes.



Supplementary Figure 5 | Species level parameters of the three bird functional groups. Data are from a quantitative network built by pooling data from the most intensively studied islands, Santa Cruz and San Cristóbal. The number of bird species included in each group are five herbivores, five arthropod-eaters and four omnivores (see Supplementary table S1 for details of the classification). Median, 50% and 95% percentiles of each parameter for each functional group are shown. Abundance of each bird species was used as a covariate in all analyses. The arthropod-eater, *Certhidia fusca*, and the herbivorous cactus finch, *Geospiza scandens*, are outliers in the d' pane, whereas the small ground finch *Geospiza fuliginosa* is the outlier in the strength pane.



Supplementary Figure 6 | Upper row from left: Relationship between connectance C , standardized nestedness ($NODF$) and standardized modularity (M), and number of species S . Data are 24 hummingbird-flower network, the Galápagos bird-flower network, and the New Zealand data. Lower row from left: Relationship between standardized nestedness ($NODF$) and standardized modularity (M), and plant : bird species ratio P/A and between standardized modularity (M) and standardized nestedness ($NODF$).

Species	Family	Origin	Major food (Literature)	Minor food (Literature)	Nectar (Literature)	Pollen agent in our study	Fruit (Literature)	Buds/Leaves (Literature)	English name	Our trophic classification
<i>Zenaida galapagoensis</i>	Columbidae	En	plants	arthropods	nectar	yes	fruit/seeds		Galápagos Dove	herbivore
<i>Coccyzus melacoryphus</i>	Cuculidae	Na	arthropods			yes			Dark-billed Cuckoo	arthropod-eater
<i>Nesomimus macdonaldi</i>	Mimidae	En	omnivory		nectar	yes	fruit		Española Mockingbird	omnivore
<i>Nesomimus melanotis</i>	Mimidae	En	omnivory			yes	fruit		San Cristóbal Mockingbird	omnivore
<i>Nesomimus parvulus</i>	Mimidae	En	omnivory		nectar	yes	fruit		Galapágos Mockingbird	omnivore
<i>Nesomimus trifasciatus</i> *	Mimidae	En	omnivory		nectar				Floreana Mockingbird	omnivore
<i>Setophaga petechia</i>	Parulidae	Na	arthropods	plants		yes	fruit		Yellow Warbler	arthropod-eater
<i>Camarhynchus heliobates</i> *	Thraupidae	En	arthropods	plants			fruit		Mangrove Finch	arthropod-eater
<i>Camarhynchus pallidus</i>	Thraupidae	En	arthropods			yes			Woodpecker Finch	omnivore
<i>Camarhynchus parvulus</i>	Thraupidae	En	arthropods	plants	nectar	yes	fruit/seeds	buds	Small Tree-finch	omnivore
<i>Camarhynchus pauper</i> *	Thraupidae	En	arthropods	plants	nectar			buds/leaves	Medium Tree-finch	omnivore
<i>Camarhynchus psittacula</i>	Thraupidae	En	arthropods	plants		yes	fruit		Large Tree-finch	omnivore
<i>Certhidea fusca</i>	Thraupidae	En	arthropods			yes			Grey Warbler-finch	arthropod-eater
<i>Certhidea olivacea</i>	Thraupidae	En	arthropods			yes			Green Warbler-finch	arthropod-eater
<i>Geospiza conirostris</i>	Thraupidae	En	plants	arthropods	nectar	yes	fruit		Large Cactus-finch	herbivore
<i>Geospiza difficilis</i>	Thraupidae	En	plants	arthropods	nectar	yes	fruit	leaves	Sharp-beaked Ground-finch	herbivore
<i>Geospiza fortis</i>	Thraupidae	En	plants	arthropods	nectar	yes	seeds		Medium Ground-finch	herbivore
<i>Geospiza fuliginosa</i>	Thraupidae	En	plants	arthropods	nectar	yes	seeds		Small Ground-finch	herbivore
<i>Geospiza magnirostris</i>	Thraupidae	En	plants	arthropods		yes	fruit/seeds		Large Ground-finch	herbivore
<i>Geospiza scandens</i>	Thraupidae	En	plants	arthropods	nectar	yes	fruit/seeds		Common Cactus-finch	herbivore
<i>Platyspiza crassirostris</i>	Thraupidae	En	plants		nectar	yes	fruit	buds/leaves	Vegetarian Finch	herbivore
<i>Myiarchus magnirostris</i>	Tyrannidae	En	arthropods	plants	nectar	yes			Galapágos Flycatcher	arthropod-eater
<i>Pyrocephalus rubinus</i> *	Tyrannidae	Na	arthropods						Vermilion Flycatcher	arthropod-eater

Supplementary Table 1 | Trophic characterization of the 23 native Galápagos land bird species according to literature (*Handbook of Birds of the World–Online*, <http://www.hbw.com>) and our own observations. En: endemic, Na: non-endemic native. Species with an * were not included in our study. We did not score *Camarhynchus pauper* as pollinator because its habitat, the Floreana highlands, was not included as study site, but nectar-drinking is reported in the literature (www.hbw.com). The extremely rare *Camarhynchus heliobates* has only recently been studied and no records of flower visitation are known¹. *Pyrocephalus rubinus* is known to visit bird-feeders in N America, but we did not catch any individual in our censuses. The threatened *Mimus trifasciatus* from Floreana was not sampled in our study either, but has been eventually been observed visiting the flowers of *Opuntia megasperma* (L. Ortiz, *pers. obs.*). The only alien bird, *Crotophaga ani*, was included in our study but no pollen grains were detected in any of the 11 sampled individuals.

	CAPA	CAPR	CEFU	DEPE	GEFO	GEFU	GEMA	GESC	MIME	MIPA	MYMA	PLCR	ZEGA
S_{obs}	11	38	14	44	55	69	26	17	7	22	48	23	7
Chao S	20.00	54.33	22.17	117.50	68.50	83.73	58.67	18.60	11.00	30.10	62.45	31.64	9.25
N	19	58	23	77	116	225	39	28	11	29	108	14	11
Detection	0.55	0.70	0.63	0.37	0.80	0.82	0.44	0.91	0.64	0.73	0.7	0.73	0.76

Supplementary Table 3 | Estimators of the rarefaction curves for each bird species from which more than 10 individuals were sampled. S_{obs} , number of interactions observed; Chao S, the Chao2 estimator, i.e. the number of interactions expected after considering the proportion between singletons and doubletons; N , number of individuals sampled of each species. Detection, the proportion of interactions observed out of all those that are expected. The packages “vegan” and “rich” in *R* were used to obtain these metrics. Full names of bird species are given in Supplementary Fig. 2.

Network	<i>P</i>	<i>A</i>	<i>S</i>	<i>I</i>	<i>C</i>	L_p (X±SD)	L_a (X±SD)	<i>IE</i>	H'_2	d'_p (X±SD)	d'_a (X±SD)	strength _p (X±SD)	strength _a (X±SD)	WNODF	WNODF _{rand} (X±SD)	<i>P</i>	<i>M</i>	<i>P</i>
Santa Cruz	56	12	68	228	0.34	4.07 ± 3.24	19.00 ± 11.69	0.74	0.15	0.12 ± 0.10	0.13 ± 0.06	0.21 ± 0.39	4.67 ± 5.04	43.98	42.61 ± 2.72	0.31	0.27	>0.05
San Cristóbal	43	9	52	119	0.31	2.77 ± 2.18	13.22 ± 10.15	0.68	0.18	0.10 ± 0.12	0.12 ± 0.06	0.21 ± 0.52	4.78 ± 7.29	43.27	37.31 ± 4.04	0.07	0.21	>0.05
Arid zone	71	12	83	245	0.29	3.45 ± 2.96	20.42 ± 14.69	0.72	0.18	0.11 ± 0.11	0.15 ± 0.07	0.17 ± 0.34	5.91 ± 7.42	40.96	39.00 ± 2.77	0.24	NA	NA
Humid zone	44	9	53	130	0.33	2.95 ± 2.06	14.44 ± 11.02	0.70	0.20	0.09 ± 0.10	0.14 ± 0.04	0.20 ± 0.47	4.89 ± 7.38	37.68	35.48 ± 2.97	0.23	NA	NA
Hot season	62	14	76	218	0.25	3.52 ± 2.99	15.57 ± 13.22	0.67	0.17	0.13 ± 0.13	0.16 ± 0.08	0.23 ± 0.56	4.43 ± 6.43	40.13	38.13 ± 2.91	0.25	NA	NA
Cold season	46	12	58	136	0.25	2.96 ± 2.50	11.33 ± 9.85	0.71	0.21	0.12 ± 0.15	0.16 ± 0.10	0.26 ± 0.52	3.83 ± 6.05	42.47	34.08 ± 3.07	0.003	NA	NA

Supplementary Table 4 | Network and species level parameters for the six quantitative matrices on Santa Cruz and San Cristóbal. For building the networks of each variable (island, season, habitat) the other two variables were pooled. *P*, plants; *A*, birds; $S = P + A$; *I*, number of network interactions; $C = I/(AP)$ connectance; L_p and L_a , linkage level for birds and plants, respectively; *IE*, interaction evenness; H'_2 , network specialization index; d' , species specialization index; *WNODF*, weighted nestedness (metric for the 1000 randomizations is also provided); *P*, probability that observed *WNODF* and *WNODF* obtained from 1000 randomizations differed significantly from random runs; *M*, modularity value and its *P*-value compared to 100 randomizations.

Reference	No. hummingbird spp.	Location	A	No. bird spp.
Arroyo <i>et al.</i> 1982 ³	1	Andes/High zone	25	1
Arroyo <i>et al.</i> 1982 ³	1	Andes/Mid zone	64	1
Arroyo <i>et al.</i> 1982 ³	1	Andes/Low zone	101	1
Freitas & Sazima 2006 ⁴	5	Brazil	111	5
Ingversen 2006 ⁵	2	Jamaica	45	6
Ingversen 2006 ⁵	4	Dominica	44	6
Kaiser-Bunbury <i>et al.</i> 2009 ⁶	0	Mauritius	100	1
Perceival 1974 ⁷	3	Puerto Rico	36	3
Ramírez 1989 ⁸	2	Venezuela	46	2

Supplementary Table 5 | List of pollination networks studied in a recent review² which include birds as pollinators. *A*, total number of pollinator species in the network.

Network reference	<i>A</i>	<i>P</i>	<i>P/A</i>	<i>S</i>	<i>I</i>	<i>C</i>	<i>NODF</i>	<i>NODF*</i> (Null Ce)	<i>SD</i> (<i>NODF*</i>)	<i>z</i> (<i>NODF</i>)	<i>P</i> (<i>NODF</i>)	<i>M</i>	<i>M*</i> (null)	<i>SD</i> (<i>M*</i>)	<i>z</i> (<i>M</i>)	<i>P</i> (<i>M</i>)
Hummingbird-plant networks																
Abreu et al. 2004 ⁹	8	14	1.8	22	32	28.57	42.09	24.61	6.69	2.61	0.01	0.37	0.38	0.02	-0.61	0.73
Arizmendi 1990 ¹⁰	5	23	4.6	28	44	38.26	24.68	21.54	5.38	0.58	0.28	0.32	0.34	0.02	-1.4	0.92
Brown 1979 ¹¹	4	9	2.3	13	23	63.89	34.52	30.92	10.64	0.34	0.35	0.16	0.22	0.03	-2.11	0.98
Buzato et al. 2000 ¹²	9	28	3.1	37	70	27.78	28.06	20.19	4.02	1.96	0.03	0.28	0.31	0.01	-2.11	0.98
Campos de Jordao Buzato et al. 2000 ¹² Caraguatatuba	15	40	2.7	55	80	13.33	15.83	10.69	2.36	2.18	0.02	0.52	0.46	0.01	4.56	0.00
Buzato et al. 2000 ¹² , Cunha	12	31	2.6	43	70	18.82	20.10	14.12	3.18	1.88	0.03	0.34	0.37	0.01	-2.52	0.99
Feinsinger 1976 ¹³	5	5	1.0	10	9	36.00	45.00	30.90	14.99	0.94	0.16	0.38	0.42	0.02	-1.48	0.93
Kodric-Borwn et al. 1984 ¹⁴	4	13	3.3	17	30	57.69	45.24	34.56	8.34	1.28	0.10	0.25	0.26	0.02	-0.46	0.68
Kraemer et al. 1993 ¹⁵	13	14	1.1	27	38	20.88	28.99	15.18	4.1	3.37	0.00	0.39	0.39	0.02	-0.31	0.62
Lara 2006 ¹⁶	8	8	1.0	16	42	65.63	35.89	33.41	7.78	0.32	0.38	0.18	0.21	0.02	-1.74	0.96
Leal et al. 2006 ¹⁷	4	7	1.8	11	17	60.71	51.85	38.85	11.34	1.15	0.11	0.19	0.23	0.03	-1.33	0.91
Magaard 1997 ¹⁸	11	11	1.0	22	17	14.05	5.45	7.80	3.45	-0.68	0.71	0.70	0.7	0.03	0.15	0.49
Mendonca & Anjos 2005 ¹⁹	10	22	2.2	32	63	28.64	33.71	20.31	3.85	3.48	0.00	0.32	0.34	0.02	-1.1	0.88
Snow & Snow 1980 ²⁰ , lok 1	9	13	1.4	22	35	29.91	26.61	21.53	5.21	0.98	0.17	0.34	0.34	0.02	-0.03	0.51
Snow & Snow 1980 ²⁰ , lok2	12	22	1.8	34	60	22.73	18.13	15.74	3.17	0.75	0.22	0.39	0.4	0.01	-0.13	0.55
Snow & Snow 1980 ²⁰ , lok 3	6	13	2.2	19	25	32.05	15.34	18.58	6.02	-0.54	0.69	0.39	0.42	0.03	-0.93	0.92
Snow & Snow 1986 ²¹	6	25	4.2	31	55	36.67	12.68	17.97	4.03	-1.31	0.91	0.37	0.35	0.02	1.28	0.90
Snow & Teixeira 1982 ²²	7	16	2.3	23	26	23.21	12.00	14.16	5.06	-0.43	0.65	0.51	0.5	0.02	0.45	0.33
Snow & Snow 1972 ²³	9	94	10.4	103	227	26.83	23.01	17.80	1.75	2.98	0.00	0.35	0.35	0.01	0.55	0.29
Stiles 1975 ²⁴	9	9	1.0	18	53	65.43	29.75	25.03	6.37	0.74	0.23	0.13	0.2	0.02	-4.57	0.99
Varassin & Sazima 2000 ²⁵	9	19	2.1	28	53	30.99	0.00	5.01	3.17	-1.58	0.95	0.27	0.32	0.02	-3.01	0.99
Wolf 1975 ²⁶	9	17	1.9	26	49	32.03	32.14	24.99	5.18	1.38	0.08	0.32	0.34	0.02	-1.01	0.84
Wolf 1976 ²⁷ , lok 1	4	18	4.5	22	45	62.50	20.13	26.28	6.61	-0.93	0.81	0.20	0.24	0.02	-2.28	0.99
Wolf 1976 ²⁷ , lok 2	5	25	5.0	30	37	29.60	6.86	15.84	4.52	-1.99	0.98	0.52	0.46	0.02	3.11	0.00
Non-hummingbird-plant networks																
Galápagos network	19	106	5.6	125	421	20.90	28.98	15.42	1.30	10.39	0.01	0.27	0.26	0.01	0.69	0.25
New Zealand network	22	73	3.2	95	193	11.49	22.83	11.34	1.49	6.94	0.00	0.33	0.35	0.01	-2.48	0.99

Supplementary Table 6 | Network properties of 26 pollination networks, including the study network from Galápagos. $P(NODF)$ and $P(M)$ are one-tailed probabilities. A , no. bird species; P , no. plant species; $S = A + P$; I = total number of interactions in the network; C (connectance) = $100 I / (A + P)$; $NODF$, level of nestedness; $NODF^*$ (Null Ce), mean $NODF$ of 1000 runs according to the null model Ce; $SD(NODF^*)$, standard deviation; $z(NODF)$ (z-score) = $(NODF - NODF^*) / SD(NODF^*)$; P , probability of null model; M level of modularity; M (Null), mean M of 100 runs; $SD(M^*)$, standard deviation; $z(M)$ (z-score) = $(M - M^*) / SD(M^*)$; P , probability of null model. Significant probabilities ($P < 0.05$) are highlighted.

Bird family	Mainland South America					Galápagos				
	species	Known visitor species	visited flower species	% visitor species	mean visited species	total species	Known visitor species	Visited flower species	% visitor species	Mean visited species
Thraupidae	312	64	75	20.5	1.2	14	13	98	92.9	8.2
Mimidae	10	4	13	40.0	3.3	4	3	30	100.0	10.0
Tyrannidae	369	16	18	4.3	1.1	2	1	48	50.0	48.0
Parulidae	67	3	7	4.5	2.3	1	1	45	100.0	45.0
Columbidae	49	6	3	12.2	0.5	1	1	7	100.0	7.0
Mean				16.3	1.7				88.6	23.6

Supplementary Table 7 | Proportion of bird species from each family present in Galapagos that visit flowers in mainland South America and in the Galapagos archipelago, and mean number of plant species visited by them. Significant differences between the two regions were explored by means of Generalized Linear Mixed Models, including bird families as subjects and island/mainland as a fixed factor (see main text for test results).

Reference	Mean CC	Mean BC
Plants	0.33	0.0100
Birds	0.34	0.0014
Insects	0.30	0.0044

Supplementary Table 8 | Comparison of centrality of plants, birds and insects in the total Galápagos pollination network (pooling the bird-flower network of this study and the insect-flower network of Galápagos²⁸). CC varied among the three communities (GLM: $F_{2,354} = 22.75$, $P < 0.001$). Both birds and plants had a higher CC than insects (Pairwise t comparisons: $P < 0.001$), whereas birds and plants did not differ ($P = 0.69$). BC varied among the three communities ($F_{2,354} = 18.93$, $P < 0.001$). Birds had a lower BC than plants (Pairwise t comparisons: $P < 0.03$), whereas birds and insects and insects and plants did not differ ($P = 1.00$ and $P = 0.22$, respectively). Ranking of the highest linkage level-, CC- and BC-species of each community was the same. For all three centrality measures, the highest ranked species were the tree *Croton scouleri*, the bee *Xylocopa darwini* and the ground finch *Geospiza fuliginosa*.

Module	No. plant spp.	No. insect spp.	No. bird spp.	Total no. spp.
1	1	1	0	2
2	13	42	1	56
3	6	32	0	38
4	11	73	2	86
5	7	24	0	31
6	15	34	0	49
7	72	7	16	95
Total	125	213	19	357

Supplementary Table 9 | No. species of plants, insects and birds in individual modules of the total pollination matrix (pooling the bird-flower network of this study and the insect-flower network of Galápagos²⁸). The total matrix had a modularity level M of 0.42 ($P < 0.001$). It consisted of seven modules, which differed strongly in their proportions of plants, insects and birds. Almost all birds (84%) were confined to module 7 together with 58% of the plant species.

Supplementary Note 1 | Description of network parameters used in this study

Species level parameters:

- (1) *Linkage level (L)* for plant and animal species, i.e. the number of links each plant and animal species has in the network.
- (2) *Species specialization for plants (d_p) and animals (d_a)*²⁹ gives levels of specialization of each species, accounting for the available resources provided by the interaction partners (calculated as marginal totals in the matrix). This index increases with the deviation from random selection of the available interaction partners based on their abundance. Thus, a pollinator species, for example, that visits flowering plant species proportionally to their availability in the community is considered generalized, while a species that visits rare plants disproportionately is considered specialized.
- (3) *Species strength*. The strength of an animal species (st'_a) is defined as the sum of dependencies of the plants relying on the particular pollinator, whereas the strength of a plant (st'_p) is the sum of dependencies of the pollinators relying on the particular plant species³⁰. We calculated the dependence of a bird species on a particular plant species by dividing the number of times the pollen of that plant appeared in the bird samples by the total number of samples with pollen of that plant. Conversely, the dependence of a plant species on a particular bird species is obtained by dividing the number of times the pollen of that plant appeared in the bird samples by the total number of samples from the bird species.

Network level parameters:

- (4) *Connectance (C)*, the proportion of realized interactions out of those possible in the network.
- (5) *Network specialization (H'_2)*. The degree of niche divergence among species obtained by comparing the observed value with an expected probability distribution of interaction frequencies, assuming that all species interact with their partners in proportion to their observed total frequencies³¹. It ranges from 0 (low specialization, high niche overlap) to 1 (high specialization, low niche overlap).
- (6) *Interaction evenness (IE)*³² measures the uniformity of the set of interactions between species in a network based on Shannon's evenness index. An uneven network has a high skewness in the distribution of interaction weights.

(7) *Nestedness (NODF, Nestedness metric based on the Overlap and Decreasing Fill)*. It is calculated by means of the ANHINHADO (version 3, Bangu) software³³. The significance of the *NODF* values is tested through null model analysis against 1000 random networks, using the null model Probably Rows and Columns (PRC, also named Ce), which assigns an interaction between each consumer-resource pair proportionally to the generalization of both the consumer and resource species³⁴.

(8) *Weighted nestedness (WNODF, Weighted Nestedness metric based on the Overlap and Decreasing Fill*³⁵). *WNODF* ranges from 0 for a non-nested to 100 for a perfectly nested network. To test whether *WNODF* differed significantly from a random link pattern, estimates are compared with values obtained from 1000 random networks based upon a Patefield null model, which keeps the marginal totals in the network fixed and thus allows us to test how the distribution of interactions among partners (not the distribution of species frequencies) affects network structure³⁶. Marginal totals are given by the number of flowers visited by a pollinator species across all plants species and the number of all flowers visited by all different pollinators of a particular plant species. Prior to the analysis, matrices are sorted according to row/column species richness and then sorted according to abundance totals (model 'rc' in *WNODF*, which retains the sum of the rows and columns of the original interaction matrix). This metric is obtained using the *WNODF* program³⁵.

(9) *Modularity* refers to the existence of subsets (modules) of closely interacting species with relatively few or no interactions to other subsets³⁷. We used the NETCARTO software, which runs an algorithm based on simulated annealing, to assign all nodes (plants and pollinators) to modules³⁸. When the program runs repeatedly, the affiliation of nodes to modules gets an accuracy of 90%. NETCARTO calculates a modularity index (*M*) of the matrix, which measures how clearly delimited the modules of the network are. *M* ranges from 0 to $1-1/n$, where *n* is number of modules³⁸. Modularity becomes stronger, when *M* approaches 1. The significance of modularity is tested by comparing it with *M*-values obtained from 100 randomized networks constrained by the same linkage-level ranking as the empirical one, thus retaining the same degree distribution and connectivity as the focal network. If the empirical *M*-value lies above the 95% confidence interval for *M* in the randomized networks, the empirical network is significantly modular.

Supplementary Note 2 | Comparison of the centrality of birds and insects in the total Galápagos pollination network (pooling the bird-flower network of this study and the insect-flower network of Galápagos²⁸, and their modularity.

Using the software Pajek³⁹, we calculated closeness centrality (CC) and betweenness centrality (BC) of birds, insects and plants, after transforming the bipartite networks into unipartite ones. CC measures how close a focal species is to all other species in the network³⁹⁻⁴¹. Thus, species with high CC values rapidly affect other species and *vice versa*. BC measures to what extent a species links different parts of the network together⁴¹. CC and BC vary between 0 and 1. As a third measure of centrality, we included linkage level L of species, i.e. the number of links from a species to all other species.

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