RESEARCH ARTICLE

Title: Seed dispersal networks in the Galápagos and the consequences of alien plant invasions

Running Head: Galápagos seed dispersal networks

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ABSTRACT

Alien plants are a growing threat to the Galápagos unique biota. We evaluated the impact of alien plants on eight seed dispersal networks from two islands of the archipelago. Nearly ten thousand intact seeds from 58 species were recovered from the droppings of 18 bird and reptile dispersers. The most dispersed invaders were *Lantana camara*, *Rubus niveus* and *Psidium guajava*, the latter two likely benefiting from an asynchronous fruit production with most native plants, which facilitate their spread. Lava lizards dispersed the seeds of 27 species, being the most important dispersers (higher strength), followed by small ground finch, two mockingbirds, the giant tortoise and two insectivorous birds. Most animals dispersed alien seeds but these formed a relatively small proportion of the interactions. Nevertheless, the integration of aliens was higher in the island which has been invaded for longest, suggesting a time-lag between alien plant introductions and their impacts on seed dispersal networks. Alien plants become more specialized with advancing invasion, favouring more simplified plant and disperser communities. However, only habitat type significantly affected the overall network structure. Alien plants were dispersed via two pathways: dry-fruited plants were preferentially dispersed by finches, while fleshy-fruited species were mostly dispersed by other birds and reptiles.

Keywords: Exotics, Frugivory, Mutualistic interactions, Oceanic islands, Ornithochory, Saurochory

INTRODUCTION

Globally, invasive species rank among the most serious threats to native biodiversity and as such they become a major driver of global change [1]. Their ravaging effects are nowhere more powerful than on oceanic islands [2], where ecologically “naïve” species evolved under low selective pressure from higher trophic level species [3].

Even in remote archipelagos such as the Galápagos, Mauritius and Hawaii, alien plants already outnumber native species [4-6]. Many of these aliens have high invasion rates due to the long distance dispersal of their seeds [7]. Seed dispersal may be particularly decisive when frugivores include the fruit of invasive plants into their diets and consequently facilitate their establishment and spread [8].

Most oceanic islands, particularly remote ones, have low species diversity and some animal groups are more poorly represented than plants species [3], i.e. the ratio between animal and plant species tends to be lower on islands than on continents [9]. This can magnify the effect of anthropogenic shifts in the assemblage of frugivores, affecting seed dispersal and influencing overall vegetation structure and ecosystem functioning [10]. Knowledge of seed dispersal processes can thus prove crucial to understanding the dynamics of plant invasions and the planning of effective conservation strategies such as the control or eradication of fleshy-fruited weeds [11]. There are increasing efforts to collect information on the potential dispersers of invasive plant species [12] and on the plants dispersed by introduced animals [13]. However, rigorous information on the entire species assemblages of plants, seed dispersers and their interactions is still rarely available [14]. Even when such studies exist they have mainly considered birds, with reptiles and mammals receiving much less attention [15]. In order to make an unbiased community-level assessment of seed dispersal, all animals that include fruits or seeds in their diets should be considered simultaneously [16].

Much ecosystem functioning is founded on species interactions [17] and it is through the network of interactions that disturbances cascade through biological communities [18]. In recent years, this growing realization has lifted the focus of conservation efforts from species to ecosystems [1, 19]. While there is an increasing number of studies documenting different aspects of the dispersal of native and invasive plants by frugivores [10, 20], the consequences of the integration of alien plants into seed dispersal networks has been poorly explored [21]. In contrast, several studies have evaluated the impact of alien plants upon pollination networks. These have produced different results, with some studies detecting changes in the structure of pollination networks [22, 23], while others have not [24, 25]. These results suggest that the effect of alien species is system dependent. In some cases, the disruptive effects of alien plants can be detected at the network-level, whereas in others, changes are more subtle and take place at the level of individual species [25]. We focused our analysis at both, network and species levels.

We report the results of a study on the impact of alien plant species upon plant-seed disperser networks on the Galápagos Islands. The Galápagos Islands and their unique biodiversity are seriously threatened by alien invasive plants [26]. These may affect native species directly, but repercussions may also ripple off throughout the entire ecological network of an island or the archipelago without necessarily leading to the local extinction of native species [27]. We suggest that such a disturbance scenario can be better understood by a network approach; however, our knowledge on seed dispersal networks in the archipelago is still very limited [28]. In this study, we analyse a wide category of interactions, viz. the links connecting fruiting plants and their seed dispersers.

There are four objectives in our study: 1) Evaluate the synchrony in the fruiting phenology of the most abundant native and alien plants. We hypothesize that alien species maximize their benefit from seed dispersers if their fruit crop is available in periods of native fruit shortage. 2) Evaluate the extent to which alien plants infiltrate the seed dispersal network and the structural consequences of that integration at the species and network levels. We hypothesized that the linkage pattern in invaded sites would become more generalized given that alien species tend to be attractive to many frugivores [29]. 3) Assess the relative importance of different fruit-eating species as seed dispersers. 4) Evaluate the existence of preferred "invasion routes" taken by animal-dispersed fleshy- and dry-fruited alien plants into the Galápagos seed dispersal systems.

METHODS

***Study site.* –** The Galápagos lie on the equator in the Eastern Pacific, c. 960 km west of South America (Appendix A). This young volcanic archipelago, 0.5 - 4 MY, [30] is composed of 13 islands larger than 10 km^2 and numerous islets.

The archipelago has two seasons: a hot/wet season prevails from January to May, corresponding to the fruiting period of most plants, while a cold/dry season occurs from June to December [31]. During the dry season a permanent drizzle (or garúa) allows the development of a permanently humid habitat in the highest part of the tallest islands, whereas the lowland zone of all the islands is markedly dry [31].

The late establishment of permanent human settlements in the archipelago, as recent as the 19th century, delayed the onset of anthropogenic habitat degradation [32]. However, alien species rapidly took their toll and changed extensive areas of the archipelago [33, 34]. The Galápagos flora consists of 557 native vascular plant species (of which 32% are endemic), and more than 825 alien species [35]. Among the most problematic invasive plants are the fleshy-fruited *Psidium guajava* (guava) and *Rubus niveus* (blackberry) which have severely altered the composition and structure of some of the natural ecosystems, particularly in the humid zone [33].

***Experimental design.* –** Data were collected from eight sites using a hierarchical design (Appendix A) including the two most human-populated islands (Santa Cruz and San Cristóbal), the two most representative vegetation types (dry lowland and humid highland) and two levels of invasion (‘native’ and ‘invaded’). The eight sites were sampled with equal effort between March 2010 and February 2011. During the main fruiting season (February–July) each site was visited twice per month, while the same sites were visited once per month in the cold/dry season. Data from each site were pooled and used to build year-round seed dispersal networks. Quantitative seed dispersal networks were based on the analysis of faecal samples from birds, the giant tortoise and lava lizards. Interaction frequency was quantified as the number of droppings from each animal species containing at least one intact seed of each plant species. Bird faecal samples were collected during 18 ringing sessions with mist nets at each site. In each session, mist nets were opened at sunrise and remained open for six consecutive hours. Captured birds were left up to 30 minutes in ringing bags to defecate. Intact seeds in droppings were identified under a dissecting microscope by comparison with the reference collection in the Charles Darwin Foundation. Reptile droppings were collected along one fixed 50 x 2 m linear transect in each plot and seed identification was performed with the same methodology. Overall, 2,879 droppings were collected: 2,293 from 15 bird species and 586 from three reptile species.

To document fruiting phenology, the abundance of fleshy fruits was estimated for each plot by monthly counts of all ripe fruits within a swathe of vegetation of 1 m either side of a fixed 50 m linear transect.

***Species interaction patterns.* –** We explored the effects of *Level of Invasion, Plant origin*, *Island* and *Habitat*, on the following species-level parameters: linkage level (or degree), plant specialization (d'), and species strength. Linkage level is the number of disperser species per plant. Plant specialization (d') as suggested by Blüthgen et al. [36] is a measure of the selectivity of a species which takes into account surrogates of overall plant availability for their interactions partners. Species strength of plants and dispersers, suggested by Bascompte et al [37], is the sum of each species' dependencies and reflects the importance of each species to the other 'trophic' level.

***Network structure.* –** We tested whether the integration of alien plants affected six common network descriptors: connectance, weighed nestedness (WNODF), plants' niche overlap, dispersers' generality, robustness against extinction of dispersers, and weighted interaction evenness (see Dormann et al. [38] and references therein for detailed descriptions of all parameters and their implementation).

***Data analyses.* –** Species and network level parameters were calculated using the statistical package Bipartite 1.16 [38] for R [39]. Species-level descriptors did not achieve normality after transformations and were included in Generalized Linear Models with the most appropriate error distribution (normal, gamma or Poisson) and correspondent link function. Four explanatory variables were included as fixed factors in the model: *Island*, *Habitat*, *Level of invasion* and *Plant origin*. Network-level descriptors were transformed and included in General Linear Models with three fixed factors (*Island*, *Habitat* and *Level of invasion*). Network size was used as a covariate in all models as it is known to influence most network descriptors [40]. All models were fitted using SPSS v17.

The existence of 'preferred' dispersal routes was evaluated with 2-way chi-square contingency tables to test for independence between the frequency of occurrence of seeds of dry- and fleshy-fruited plants in the droppings of the following disperser groups: Galápagos finches, other birds and reptiles.

RESULTS

Intact seeds were retrieved from 498 bird (22%) and 208 reptile (36%) droppings. Only droppings from the birds *Lateralus spilonotus*, *Zenaida galapagoensis* and *Coccyzus melacoryphus* did not have any intact seed.

A total of 9,159 intact seeds from 58 plant species were retrieved from the droppings, revealing a total of 144 interactions with the 18 dispersers. The overall seed dispersal network is shown in Figure 1 and site-specific networks in Appendix B. Identified plants included 33 (57%) natives and 14 (24%) alien species. The remaining 19% could not be identified to species-level. Of all identified seeds, 8,019 (88%) were from natives and only 447 (5%) were from aliens. This result, however, is influenced by the high abundance of the very small seeds of *Miconia robinsoniana* (n = 5781 seeds; 63.1 % of all seeds found), which was mainly dispersed by the yellow warbler (*Dendroica petechia*). However, even excluding the seeds of this species, the majority (66%) were native, compared to 13% alien and 21% of undetermined origin. Nevertheless, intact alien seeds were found in droppings of 15 out of the 18 seed dispersers. Among the serious invasive species, seeds of *R. niveus* were dispersed by six bird species (mainly *Myiarchus magnirostris* and *Mimus melanotis*); *Lantana camara* was mainly dispersed by the two lizard species, and to a minor extent by *M. magnirostris* and *M. melanotis*; finally, *P. guajava* was dispersed by the bird *M. melanotis,* the lizard *Microlophus bivattatus*, and the giant tortoise *Chelonoidis nigra* (Appendix C).

Level of invasion and fruiting phenology. **–** Fruit production was highly variable among sites (Appendix D). The total number of fleshy fruits counted at each site over the whole year ranged from 480 to 34,654 (mean = 11,178). The proportion of alien fruits was nearly 100-fold higher in the invaded than the native site across all pairs (Table 1), supporting the *a priori* experimental design. Although the proportion of alien fruits at native sites was consistently small, there was much variation in *Level of invasion* among invaded sites (0.3%, 42.1%, 65.5% and 96.1%, respectively), with higher *Level of invasion* on San Cristóbal (Appendix E).

The peak of the fruiting season was reached in May and ranged from April to August for most species, although some species like *Scutia spicata* set fruit earlier (Figure 2, Appendix F). Most common native plants had sequential fruiting peaks with a large overlapped in fruit production. However, two common alien invasive species fruited mostly asynchronously with the main peak of native fruit production: *R. niveus* in February *and P. guajava* in July-August.

***Species interaction patterns.* –** On Santa Cruz, native plants tended to have more disperser species than aliens whilst the opposite was found on San Cristóbal (Fig. 3; Table 2).

On average, plants from the humid zone showed a higher degree of specialization (d'), i.e. a higher selectivity among possible dispersers, and also a higher strength than species from the dry zone (Table 2). Invaded sites had lower levels of specialization (d') for native plants but greater levels for aliens (Fig. 4), implying that natives become less selective on their dispersers as invasion progresses whereas aliens become more selective. Moreover, alien plants showed higher linkage level than natives on the most invaded San Cristóbal, whilst the opposite occurred on Santa Cruz (Fig. 3).

Reptiles, particularly the two species of lava lizards, were the most important dispersers for the plant community in terms of their strength (Fig. 5). Among birds, the small ground finch (*Geospiza fuliginosa*), followed by the two endemic mocking birds (*Mimus* spp.), showed the highest link strength.

***Network structure.* –** As suggested from the visual inspection of the networks (Appendix B), the overall network structure was quite similar between islands and between native and invaded sites (Table 1; Appendix E). Regarding habitat, however, networks in the humid zone were simpler in structure than in the dry zone and were usually dominated by two or three very common interactions (Appendix B). Thus, *Habitat* had a strong effect on network structure, affecting most network descriptors. However, when network size was included as a covariate in the model, none of the parameters was significantly affected, indicating a high correlation between network size and most descriptors. Similarly, none of the network descriptors were significantly affected by *Level of invasion* or by the interaction between this variable and either of the two other explanatory variables (Table 1).

Invasion routes. **–** Overall, 28 plant species with dry fruits and 24 species with fleshy fruits (excluding undetermined species) had their seeds dispersed by 18 animals. In our analysis, we operated with three disperser types: (*i*) 10 species of finch, (*ii*) five other bird species, and (*iii*) three species of reptiles (the giant tortoise and two lava lizards).

Different seed disperser types dispersed significantly different fruit types (fleshy vs. dry) ($\chi^2 = 18.17$, d.f. = 2, $P < 0.001$). Dry fruits were dispersed by finches more than expected by their overall proportion (Exp. 11.3, Obs. 17; $\chi^2 = 6.21$, d.f. = 1, $P = 0.013$), and fleshy fruits were dispersed by 'other birds' (Exp. 11.1, Obs. 18; $\chi^2 = 8.04$, d.f. = 1, $P = 0.005$) and reptiles (Exp. 16.2, Obs. 22; $\chi^2 = 3.93$, d.f. = 1, $P = 0.047$), more often than expected (see details in appendix I).

On average, the number of disperser types used by native plants (1.53) was slightly lower than for aliens (1.80). A high proportion of plants (*n* = 29; 56%) appeared to be consumed by only one type of disperser type whereas only four species were consumed by all three types. These four plants included two dry-fruited aliens *Portulaca oleraceae* and *Talinum paniculatum*, the fleshy-fruited invader *R. niveus* and the fleshy-fruited native *Tournefortia psilostachya* (Appendix J).

DISCUSSION

Despite the serious threats posed by alien species in the Galápagos, with c. 60% of the flora being alien and over 100 invasive species [6], the proportion of alien plants in the seed dispersal networks in the archipelago is still relatively low (24% of the species; 17% of the droppings; 5% of the seeds). Although comparable data are not available for most oceanic archipelagos, this invasion level is considerably lower than that found in the Azores c. 60% (Heleno, R., *unpublished data*), and Tahiti c. 95% [21]. Nevertheless, four of the five top invasive plants in the Galápagos have fleshy fruits and we found three of these (*R. niveus*, *L. camara* and *P. guajava*) well integrated into the seed dispersal networks.

The role of different vertebrates as seed dispersers. **–** Lava lizards (*Microlophus albermarlensis* in S. Cruz and *M. bivattatus* in S. Cristóbal) were quantitatively the most important seed dispersers of all. The seven endemic *Microlophus* species are abundant in the dry zone of all main islands (except on Darwin and Wolf), which is the most common habitat type in the archipelago [41]. Although lizards are important seed dispersers on other oceanic islands [42], their role as seed dispersers in the Galápagos had not been previously evaluated. In the present study, the two species of lava lizards dispersed 972 intact seeds of 27 plant species, especially *T. psilostachya*, *Zanthoxylum fagara*, *Chiococca alba* and *L. camara* (Fig. 1). The attractiveness of *Z. fagara* fruits is puzzling considering the sharp spines protecting fruiting branches and the almost complete absence of fruit pulp. Notwithstanding, these fruits were among the preferred food items of lizards and flycatchers, resulting in the dispersal of many (n = 246) intact seeds. We hypothesize that such consumption might be related to the antifungal properties recently identified in *Z. fagara* fruits [43].

Although giant tortoises were only present at one of our study sites, this species also played an important role as seed disperser (*i.e.* high species strength). Thus, the extirpation of tortoises must have had a negative impact upon seed dispersal in general [44]. The current reintroduction of tortoises to several islands is likely to have important consequences for the population dynamics of many species and should be monitored carefully [45].

Our results also support the findings of Carrión-Tacuri et al. [46] that ground finches act mainly as seed predators, and not so much as dispersers, of *L. camara*. Instead, we found 100 intact seeds of this species in the droppings of lava lizards (n = 38), mockingbirds (n = 5), flycatcher (n = 8) and giant tortoise (n = 1), which clearly shows that animals are actively involved in the dispersal of this invasive shrub.

Among birds, *G. fuliginosa* was the main disperser, followed by the two mocking bird species from each island (*Mimus parvulus* in S. Cruz and *M. melanotis* in S. Cristóbal). However, when considered together, these two species exceeded the importance of *G. fuliginosa*, which occurs on both islands. *Geospiza fuliginosa* dispersed a high number of intact seeds by virtue of its high abundance (c. 37% of all bird captures; Appendix H) and wide distribution in the dry and humid zones, but many seeds were physically destroyed [47]. In contrast, mockingbirds, mostly restricted to the dry zone, appeared to act more as legitimate dispersers than as seed predators.

The important contribution of insectivores for seed dispersal (particularly *M. magnirostris* and *D. petechia*) (Fig. 1) suggests that the effectiveness of the Galápagos dispersers is better described as a gradient from poor to good dispersers than by the typically assumed dichotomy between legitimate seed dispersers and non-dispersers, akin to the distribution described by Heleno et al. [48] in the Azores (and see also Nogales et al. [49]). The only introduced bird in the Galápagos, *Crotophaga ani*, has been suggested to play an important role in facilitating plant invasions [50, 51]. Even if based on a small number of droppings (n=12), we found little evidence for this effect, as 99.7% of the seeds retrieved from its droppings were from native species (*M. robinsoniana*, *T. psilostachya*, and *Z. fagara*.

Historical factors driving a delayed integration of invaders. – San Cristóbal was colonized by humans earlier than Santa Cruz, which translated into an earlier arrival of invasive plants [6, 52]. This might explain the stronger integration of alien plants in the San Cristóbal networks. Although Santa Cruz has now more naturalized species, as a consequence of its exponential human population growth [32], many of these aliens have not yet become widely spread [6], and may consequently be still poorly infiltrated into the local seed dispersal networks. It is thus likely that seed dispersal networks in Santa Cruz will develop along the same trajectory as that seen in San Cristóbal. Two of the most invasive species, *R. niveus* and *L. camara,* are especially widespread and abundant in San Cristóbal compared to Santa Cruz. This might actually lead to the higher number of dispersers of alien plants observed in the former, and supports the hypothesis of a delayed integration of alien plants in Santa Cruz.

Native and alien fruiting phenology and invasion routes. – Fruiting phenology is an important constraint of plant-disperser interactions [53], although knowledge regarding fruiting phenology of most Galápagos plants is very limited. The pattern described here of sequential ripening of native fruits in the Galápagos is compatible with an inter-specific strategy to avoid satiation of dispersers, in line with what has been suggested for asynchronous fruit ripening within conspecific plants [54]. Similarly, the asynchronous fruit production of *R. niveus* and *P. guajava* in relation to most native species is likely to offer a competitive advantage to these aliens, as the abundance of seed dispersers in periods of native fruit shortage might be an important mechanism assisting alien expansion. Although our study is a first step in the understanding of fruit-frugivore dynamics in the archipelago, such a hypothesis deserves further attention.

Exotic plant species invaded the seed dispersal networks along one of two pathways: the dry-fruited and the fleshy-fruited routes. The invasion along the dry-fruited route was facilitated by finches, whereas the invasion along the fleshy-fruited route was facilitated by other bird species, lizards and the giant tortoise (Appendix J). We found almost no exception to this pattern.

***Species interaction patterns.* –** Disperser specialization was lower in the dry than in the humid zone, which we attribute to the more diverse vegetation in the former, as it offers a higher variety of resources to frugivores. Moreover, disperser strength was, on average, higher in the humid than in the dry zone, reflecting a greater importance of each disperser species for humid communities, with less disperser species. Our findings showed that alien plants tend to disperse more seeds by means of fewer dispersers (i.e. becoming more specialized) as invasion progresses, while native plants show the opposite pattern. We attribute these results to the selective pressure that alien plants may exert on the frugivore community, starting off by being dispersed by generalists but favouring the dispersers that are most effective in consuming their fruits and displacing those that are more dependent on native resources, from highly invaded sites. The end result might thus be a simplified plant community, which would tend to promote a less diverse community of dispersers [21].

***Network structure.* –** Overall, network topology did not vary much between islands or with the level of invasion, although differences between native and invaded sites were easily perceived and quantified in the field. It is possible that seed dispersal networks behave like phase-shift systems, i.e. highly resilient to intermediate levels of disturbance and then suddenly breaking down irreversibly, as suggested for trophic [55] and pollination networks [56]. If that is the case, our data suggest that this phase-shift threshold has not yet been reached in any of the studied sites; however, the networks on San Cristóbal are at a more advanced stage of degradation.

The dry and humid zones in the Galápagos are markedly different, and differences in their seed dispersal systems were also expected. This expectation was largely confirmed as most network and species level descriptors evaluated differed significantly between dry and humid habitats (Table 1). Such differences were largely explained on the basis of network size, with much larger, diverse networks in the dry lowlands. *Miconia robinsoniana,* the characteristic tree in the humid habitats (also known as the Miconia zone), was the only species found to be dispersed into all habitats suggesting that the species distribution is not limited by seed dispersal. Hence, this species might respond well to the ongoing control of alien species in the humid zone by the Galapagos National Park.

***Concluding remarks.* –** Despite the advanced plant invasions in Galápagos, the level of integration of alien seeds into seed dispersal networks is still relatively moderate. Lava lizards were found to be the most important dispersers, at least quantitatively, moving the seeds of 27 species. The large representation of granivorous and insectivorous birds is reflected in an overall low frequency of occurrence of intact seeds in droppings. Nevertheless, two insectivorous species (*M. magnirostris* and *D. petechia*) showed an unexpected high contribution to the overall seed dispersal process.

By fruiting outside the main native fruiting season, the aliens *R. niveus* and *P. guajava* might benefit from an unsaturated disperser community to assist their spread. On average, alien plants were found to become more specialized during the invasion process, favouring more simplified plant and disperser communities. Sites on San Cristóbal were at a more advanced stage of invasion, which translated into a higher integration of alien fruits in the seed dispersal networks. This suggests a time-lag between the establishment of alien plants and their impacts on the structure and function of seed dispersal networks. We hypothesize that there is an extinction-debt in recently invaded islands such as Santa Cruz. Alien plants tend to be integrated into seed disperser networks via two preferred routes: dry-fruited species such as grasses and herbs tend to be dispersed by Galápagos finches, mostly granivorous, whereas fleshy-fruited plants are mainly dispersed by other birds and reptiles, particularly lava lizards.

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REFERENCES

1. Millennium Ecosystem Assessment. 2005 Ecosystems and human well-being: A synthesis. In *Millennium Ecosystem Assessment* (Island Press, Washington D.C.
2. Sax D. F., Gaines S. D. 2008 Species invasions and extinction: The future of native biodiversity on islands. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 11490-11497. (doi:10.1073/pnas.0802290105).
3. Whittaker R. J., Fernández-Palacios J. M. 2007 *Island biogeography: Ecology, evolution, and conservation*. Oxford, UK, Oxford University Press; 401 p.
4. Olesen J. M., Eskildsen L. I., Venkatasamy S. 2002 Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. *Diversity and Distributions* **8**(3), 181-192. (doi:10.1046/j.1472-4642.2002.00148.x).
5. Brockie R. E., Loope L. L., Usher M. B., Hamann O. 1988 Biological invasions of island nature reserves. *Biological Conservation* **44**(1-2), 9-36. (doi:10.1016/0006-3207(88)90003-1).

6. Trueman M., Atkinson R., Guezou A., Wurm P. 2010 Residence time and human-mediated propagule pressure at work in the alien flora of Galapagos. *Biological Invasions* **12**(12), 3949-3960. (doi:10.1007/s10530-010-9822-8).
7. Nathan R. 2006 Long-distance dispersal of plants. *Science* **313**, 78. (doi:10.1126/science.1124975).
8. Nathan R., Muller-Landau H. C. 2000 Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* **15**(7), 278-285. (doi:10.1016/S0169-5347(00)01874-7).
9. González-Castro A., Traveset A., Nogales M. 2012 Seed dispersal interactions in the Mediterranean Region: contrasting patterns between islands and mainland. *Journal of Biogeography*. (doi:10.1111/j.1365-2699.2012.02693.x).
10. Milton S. J., Wilson J. R. U., Richardson D. M., Seymour C. L., Dean W. R. J., Iponga D. M., Proches S. 2007 Invasive alien plants infiltrate bird-mediated shrub nucleation processes in arid savanna. *Journal of Ecology* **95**(4), 648-661. (doi:10.1111/j.1365-2745.2007.01247.x).
11. Gosper C. R., Stansbury C. D., Vivian-Smith G. 2005 Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options. *Diversity and Distributions* **11**(6), 549-558. (doi:10.1111/j.1366-9516.2005.00195.x).
12. Padrón B., Nogales M., Traveset A., Vilà M., Martinez-Abrain A., Padilla D. P., Marrero P. 2011 Integration of invasive *Opuntia* spp. by native and alien seed dispersers in the Mediterranean area and the Canary Islands. *Biological Invasions* **13**(4), 831-844. (doi:10.1007/s10530-010-9872-y).
13. Linnebjerg J. F., Hansen D. M., Bunbury N., Olesen J. M. 2010 Diet composition of the invasive red-whiskered bulbul *Pycnonotus jocosus* in Mauritius. *Journal of Tropical Ecology* **26**(03), 347-350. (doi:10.1017/S0266467409990617).

14. Buckley Y. M., Anderson S., Catterall C. P., Corlett R. T., Engel T., Gosper C. R., Nathan R., Richardson D. M., Setter M., Spiegel O., et al. 2006 Management of plant invasions mediated by frugivore interactions. *Journal of Applied Ecology* **43**(5), 848-857. (doi:10.1111/j.1365-2664.2006.01210.x).

15. Mello M., Marquitti F., Guimarães P. R., Kalko E., Jordano P., Aguiar M. d. 2011 The missing part of seed dispersal networks: structure and robustness of bat-fruit interactions. *PLoS ONE* **6**(2), e17395. (doi:10.1371/journal.pone.0017395).

16. Donatti C. I., Guimarães P. R., Galetti M., Pizo M. A., Marquitti F. M. D., Dirzo R. 2011 Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. *Ecology Letters* **14**, 773–781. (doi:10.1111/j.1461-0248.2011.01639.x).

17. Duffy J. E., Carinale B. J., France K. E., McIntyre P. B., Thébault E., Loreau M. 2007 The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* **10**(6), 522-538. (doi:10.1111/j.1461-0248.2007.01037.x).

18. Heleno R. H., Ceia R. S., Ramos J. A., Memmott J. 2009 The effect of alien plants on insect abundance and biomass: a food web approach. *Conservation Biology* **23**(2), 410-419. (doi:10.1111/j.1523-1739.2008.01129.x).

19. Tylianakis J. M., Laliberté E., Nielsen A., Bascompte J. 2010 Conservation of species interaction networks. *Biological Conservation* **143**(10), 2270-2279. (doi:10.1016/j.biocon.2009.12.004).

20. Kawakami K., Mizusawa L., Higuchi H. 2009 Re-established mutualism in a seed-dispersal system consisting of native and introduced birds and plants on the Bonin Islands, Japan. *Ecological Research* **24**(4), 741-748. (doi:10.1007/s11284-008-0543-8).

21. Spotswood E. N., Meyer J.-Y., Bartolome J. W. 2012 An invasive tree alters the structure of seed dispersal networks between birds and plants in French Polynesia. *Journal of Biogeography*. (doi:10.1111/j.1365-2699.2012.02688.x).

22. Memmott J., Waser N. M. 2002 Integration of alien plants into a native flower-pollinator visitation web. *Proceedings of the Royal Society B-Biological Sciences* **269**(1508), 2395-2399. (doi:10.1098/rspb.2002.2174).

23. Aizen M. A., Morales C. L., Morales J. M. 2008 Invasive mutualists erode native pollination webs. *PLoS Biology* **6**(2), 396-403. (doi:10.1371/journal.pbio.0060031).

24. Padrón B., Traveset A., Biedenweg T., Díaz D., Nogales M., Olesen J. M. 2009 Impact of alien plant invaders on pollination networks in two archipelagos. *PLoS ONE* **4**(7), e6275. (doi:10.1371/journal.pone.0006275).

25. Vilà M., Bartomeus I., Dietzsch A. C., Petanidou T., Steffan-Dewenter I., Stout J. C., Tscheulin T. 2009 Invasive plant integration into native plant-pollinator networks across Europe. *Proceedings of the Royal Society B-Biological Sciences* **276**(1674), 3887-3893. (doi:10.1098/rspb.2009.1076).

26. Magee J., McMullen C. K., Reaser J. K., Spitzer E., Struve S., Tufts C., Tye A., Woodruff G. 2001 Green invaders of the Galapagos islands. *Science* **294**(5545), 1279-1280. (doi:10.1126/science.294.5545.1279c).

27. Jäger H., Kowarik I., Tye A. 2009 Destruction without extinction: long-term impacts of an invasive tree species on Galapagos highland vegetation. *Journal of Ecology* **97**(6), 1252-1263. (doi:10.1111/j.1365-2745.2009.01578.x).

28. Heleno R., Blake S., Jaramillo P., Traveset A., Vargas P., Nogales M. 2011 Frugivory and seed dispersal in the Galápagos: What is the state of the art? *Integrative Zoology* **6**(2), 110-128. (doi:10.1111/j.1749-4877.2011.00236.x).

29. Renne I. J., Barrow W. C., Randall L. A. J., Bridges W. C. 2002 Generalized avian dispersal syndrome contributes to Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasiveness. *Diversity and Distributions* **8**(5), 285-295. (doi:10.1046/j.1472-4642.2002.00150.x).

30. White W. M., McBirney A. R., Duncan R. A. 1993 Petrology and geochemistry of the Galapagos islands - portrait of a pathological mantle plume. *Journal of Geophysical Research-Solid Earth* **98**(B11), 19533-19563. (doi:10.1029/93JB02018).

31. Trueman M., d'Ozouville N. 2010 Characterizing the Galapagos terrestrial climate in the face of global climate change. *Galapagos Research* **67**, 26-37.

32. Tye A. 2006 Can we infer island introduction and naturalization rates from inventory data? Evidence from introduced plants in Galápagos. *Biological Invasions* **8**, 201-215. (doi:10.1007/s10530-004-3574-2).

33. Guézou A., Trueman M., Buddenhagen C. E., Chamorro S., Guerrero A. M., Pozo P., Atkinson R. 2010 An extensive alien plant inventory from the inhabited areas of Galapagos. *PLoS ONE* **5**(4). (doi:10.1371/journal.pone.0010276).

34. Sulloway F. J. 2009 Tantalizing Tortoises and the Darwin-Galapagos Legend. *Journal of the History of Biology* **42**(1), 3-31. (doi:10.1007/s10739-008-9173-9).

35. Jaramillo P., Guézou A., Mauchamp A., Tye A. 2012 CDF checklist of Galapagos flowering plants. In *Charles Darwin Foundation Galapagos Species Checklist; http://checklistsdatazonedarwinfoundationorg/* (eds. Bungartz F., Herrera H., Jaramillo P., Tirado N., Jímenez-Uzcategui G., Ruiz D., Guézou A., Ziemmeck F.). Puerto Ayora, Galapagos, Charles Darwin Foundation.

36. Blüthgen N., Menzel F., Blüthgen N. 2006 Measuring specialization in species interaction networks. *BMC Ecology* **6**, 9. (doi:10.1186/1472-6785-6-9).

37. Bascompte J., Jordano P., Olesen J. M. 2006 Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* **312**(5772), 431-433. (doi:10.1126/science.1123412).

38. Dormann C., Gruber B., Frund J. 2008 Introducing the bipartite package: Analysing ecological networks. *R news* **8**(2), 8-11.

39. R Development Core Team. 2010 *R: A language and environment for statistical computing*. Vienna, Austria, R Foundation for Statistical Computing.

40. Dormann C. F., Fründ J., Blüthgen N., Gruber B. 2009 Indices, graphs and null models: analyzing bipartite ecological networks. *The Open Journal of Ecology* **2**, 7-24.

41. Tye A. 2006 Restoration of the vegetation of the Dry Zone in Galapagos. *Lyonia* **9**(2), 29-50.

42. Olesen J., Valido A. 2003 Lizards as pollinators and seed dispersers: an island phenomenon. *Trends in Ecology & Evolution* **18**(4), 177-181. (doi:10.1016/s0169-5347(03)00004-1).

43. Prieto J. A., Patino O. J., Delgado W. A., Moreno J. P., Cuca L. E. 2011 Chemical composition, insecticidal, and antifungal activities of fruit essential oils of three Colombian *Zanthoxylum* species. *Chilean Journal of Agricultural Research* **71**(1), 73-82.

44. Blake S., Wikelski M., Cabrera F., Guezou A., Silva M., Sadeghayobi E., Yackulic C. B., Jaramillo P. 2012 Seed dispersal by Galápagos tortoises. *Journal of Biogeography*. (doi:10.1111/j.1365-2699.2011.02672.x).

45. Hansen D. M., Donlan C. J., Griffiths C. J., Campbell K. J. 2010 Ecological history and latent conservation potential: large and giant tortoises as a model for taxon substitutions. *Ecography* **33**(2), 272-284. (doi:10.1111/j.1600-0587.2010.06305.x).

46. Carrión-Tacuri J., Berjano R., Guerrero G., Figueroa E., Tye A., Castillo J. M. 2012 Predation on seeds of invasive *Lantana camara* by Darwin's finches in the Galapagos islands. *The Wilson Journal of Ornithology* **124**(2), 338-344. (doi:10.1676/11-111.1).

47. Guerrero A. M., Tye A. 2009 Darwin's finches as seed predators and dispersers. *The Wilson Journal of Ornithology* **121**(4), 752-764. (doi:10.1676/09-035.1).

48. Heleno R. H., Ross G., Everard A., Ramos J. A., Memmott J. 2011 On the role of avian seed predators as seed dispersers. *Ibis* **153**, 199–203. (doi:10.1111/j.1474-919X.2010.01088.x).

49. Nogales M., Heleno R., Traveset A., Vargas P. 2012 Evidence for overlooked mechanisms of long-distance seed dispersal to and between oceanic islands. *New Phytologist* **194**, 313-317. (doi:10.1111/j.1469-8137.2011.04051.x/full).

50. Guerrero A. M., Tye A. 2011 Native and introduced birds of Galapagos as dispersers of native and introduced plants. *Ornitología Neotropical* **22**(2), 207-217.

51. Connett L., Guézou A., Herrera H. W., Carrión V., Parker P. G., Deem S. L. *in press* Gizzard contents of the Smooth-Billed Ani, *Crotophaga ani* (L.), in the Galapagos Islands, Ecuador. *Galapagos Research*.

52. Restrepo A., Colinvaux P., Bush M., Correa-Metrio A., Conroy J., Gardener M. R., Jaramillo P., Steinitz-Kannan M., Overpeck J. 2012 Impacts of climate variability and human colonization on the vegetation of the Galápagos Islands. *Ecology* **93**(8), 1853-1866. (doi:10.1890/11-1545.1).

53. Encinas-Viso F., Revilla T. A., Etienne R. S. 2012 Phenology drives mutualistic network structure and diversity. *Ecology Letters* **15**(3), 198-208. (doi:10.1111/j.1461-0248.2011.01726.x).

54. Thompson J. N., Willson M. F. 1979 Evolution of temperate fruit-bird interactions - phenological strategies. *Evolution* **33**(3), 973-982.

55. Duffy J. E. 2002 Biodiversity and ecosystem function: the consumer connection. *Oikos* **99**(2), 201-219. (doi:10.1034/j.1600-0706.2002.990201.x).

56. Memmott J., Waser N. M., Price M. V. 2004 Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society B-Biological Sciences* **271**(1557), 2605 - 2611. (doi:10.1098/rspb.2004.2909).

TABLE AND FIGURE CAPTIONS

Table 1. Mean values of the network descriptors for *Island*, *Habitat* and *Level of invasion*. Significant differences for α = 0.05 are marked with " * ".

Table 2. Mean parameter values for the plant species-level descriptors for *Island*, *Habitat* and *Level of invasion*. Significant differences for α = 0.05 are marked with " * ".

Figure 1. Graphic representation of the overall seed dispersal network. Native species are shaded in light grey and alien species in black.

Figure 2. Number of ripe fleshy fruits of the most abundant species counted along monthly linear transects in the eight study sites between March 2010 and February 2011. Alien species are represented in grey and native species in black. Note the different scales on the Y-axis (values indicate the scale maximum).

Figure 3. Mean number of disperser species for native and alien plants (i.e. plant linkage level or degree) at each study site.

Figure 4. Effect of invasion on the variation of the specialization index (d') proposed by Blüthgen et al. [36] for native and alien plants. Positive bars indicate an increase in d' with invasion, while negative bars represent a decrease. White columns indicate native plants; black columns indicate changes in alien plants.

Figure 5. Mean species strength of seed dispersers in native and invaded sites. The disperser strength, suggested by Bascompte et al. [37], reflects the importance of each species for the plant community.

TABLES

Table 1

	island				habitat				invasion				invasion x island		invasion x habitat	
	mean		*P*	*p*	mean		*p*	*p*	mean		*p*	*p*	*p*	*p*	*p*	*p*
	St. Cruz	S. Cristóbal		w/size	humid	dry		w/size	invaded	native		w/size		w/size		w/size
Network size	144.8	164.5	0.800		59.8	249.5	**0.003***		144.0	165.3	0.512		0.718		0.655	
% alien fruits	11.3	41.0	**0.004***	0.056	34.6	17.6	**0.012***	0.242	51.7	0.6	**0.001***	**0.030***	**0.005***	0.059	**0.009***	0.078
P - plant species	17.0	18.5	0.867	0.665	7.8	27.8	**0.002***	0.411	16.0	19.5	0.274	0.222	0.592	0.829	1.000	0.302
D - disperser species	8.3	8.3	1.000	0.787	7.5	9.0	0.070	0.649	8.3	8.3	1.000	0.675	0.814	0.466	0.178	0.247
Unique interactions (pairs)	28.0	31.8	0.768	0.738	15.3	44.5	**0.000***	0.085	28.3	31.5	0.303	0.442	0.628	0.300	0.932	0.647
Connectance	0.23	0.23	0.932	0.611	0.28	0.18	**0.033***	0.593	0.25	0.21	0.251	0.399	0.370	0.172	0.164	0.190
Weighted nestedness (WNODF)	21.22	21.14	0.992	0.611	28.15	14.21	**0.014***	0.871	23.26	19.11	0.282	0.456	1.000	0.214	0.276	0.347
Robustness dispersers exterminated	0.44	0.45	0.822	0.981	0.41	0.48	**0.003***	0.369	0.43	0.45	0.112	0.216	0.443	0.478	0.138	0.220
Plant niche (i.e. dispersers) overlap	0.30	0.40	0.349	0.305	0.40	0.31	0.498	0.959	0.35	0.35	0.996	0.938	0.232	0.646	0.917	0.976
Dispersers generality	3.95	4.30	0.815	0.960	2.46	5.80	**0.001***	0.084	3.76	4.49	0.127	0.192	0.663	0.451	0.870	0.938
Interaction evenness	0.80	0.83	0.328	0.330	0.79	0.84	0.226	0.700	0.82	0.81	0.755	0.590	0.659	0.270	0.442	0.591

Table 2

	island			**habitat**			**invasion**			**plant origin**			**island x invasion**	**island x origin**	**invasion x origin**
	mean		*p*	mean		*p*	mean		*p*	mean		*p*	*p*	*p*	*p*
	Santa Cruz	S. Cristóbal		dry	humid		native	invaded		native	alien				
Plant linkage level	1.65	1.72	0.228	1.60	1.97	**0.024***	1.62	1.77	0.223	1.83	1.72	0.105	0.760	**0.010***	0.864
Plant specialization (d')	0.26	0.29	0.212	0.26	0.31	**0.044***	0.28	0.26	0.885	0.26	0.25	0.726	0.113	0.156	**0.032***
Plant strength	0.49	0.45	**0.009***	0.32	0.97	**0.000***	0.42	0.52	0.105	0.58	0.36	**0.007***	0.222	**0.000***	0.156

Figure 1

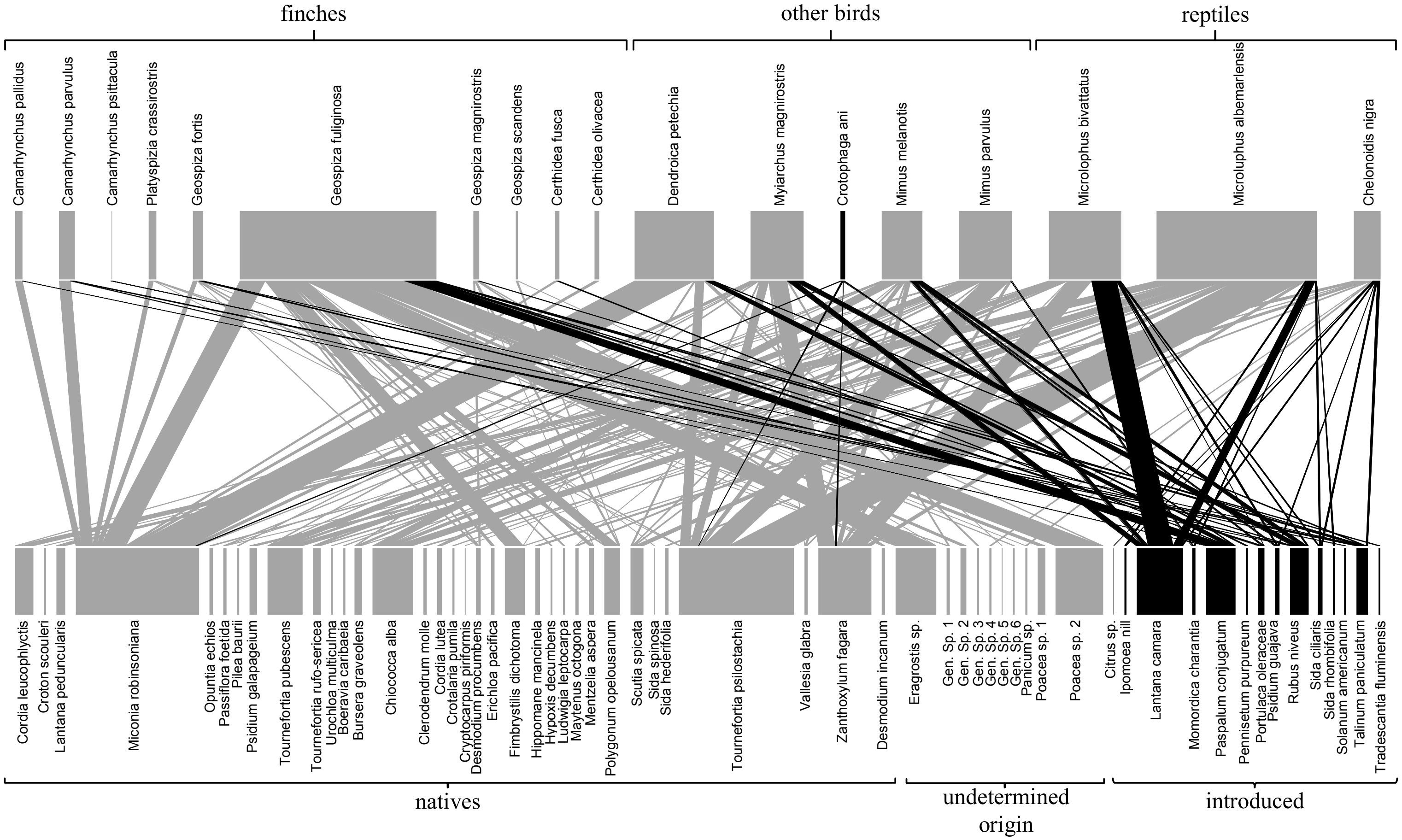

finches
other birds
reptiles
Camarhynchus pallidus
Camarhynchus parvulus
Camarhynchus psittacula
Platyspizia crassirostris
Geospiza fortis
Geospiza fuliginosa
Geospiza magnirostris
Geospiza scandens
Certhidea fusca
Certhidea olivacea
Dendroica petechia
Myiarchus magnirostris
Crotophaga ani
Mimus melanotis
Mimus parvulus
Microlophus bivattatus
Microluphus albemarlensis
Chelonoidis nigra
Cordia leucophlyctis
Croton scouleri
Lantana peduncularis
Miconia robinsoniana
Opuntia echios
Passiflora foetida
Pilea baurii
Psidium galapageium
Tournefortia pubescens
Tournefortia rufo-sericea
Urochloa multiculma
Boeravia caribaeia
Bursera graveolens
Chiococca alba
Clerodendrum molle
Cordia lutea
Crotalaria pumila
Cryptocarpus piriformis
Desmodium procumbens
Erichloa pacifica
Fimbrystilis dichotoma
Hippomane mancinela
Hypoxis decumbens
Ludwigia leptocarpa
Maytenus octogona
Mentzelia aspera
Polygonum opelousanum
Scutia spicata
Sida spinosa
Sida hederifolia
Tournefortia psilostachia
Vallesia glabra
Zanthoxylum fagara
Desmodium incanum
Eragrostis sp.
Gen. Sp. 1
Gen. Sp. 2
Gen. Sp. 3
Gen. Sp. 4
Gen. Sp. 5
Gen. Sp. 6
Panicum sp.
Poacea sp. 1
Poacea sp. 2
Citrus sp.
Ipomoea nill
Lantana camara
Momordica charantia
Paspalum conjugatum
Pennisetum purpureum
Portulaca oleraceae
Psidium guajava
Rubus niveus
Sida ciliaris
Sida rhombifolia
Solanum americanum
Talinum paniculatum
Tradescantia fluminensis
natives
undetermined origin
introduced

Figure 2

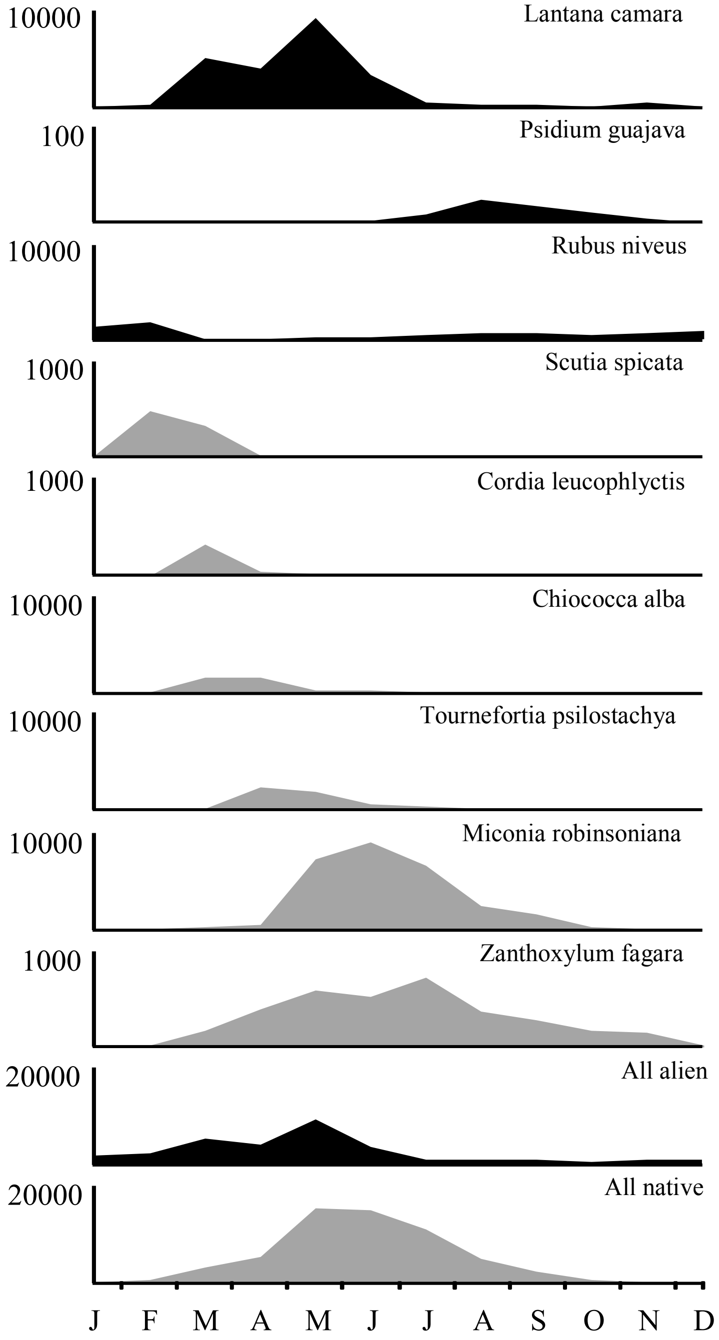
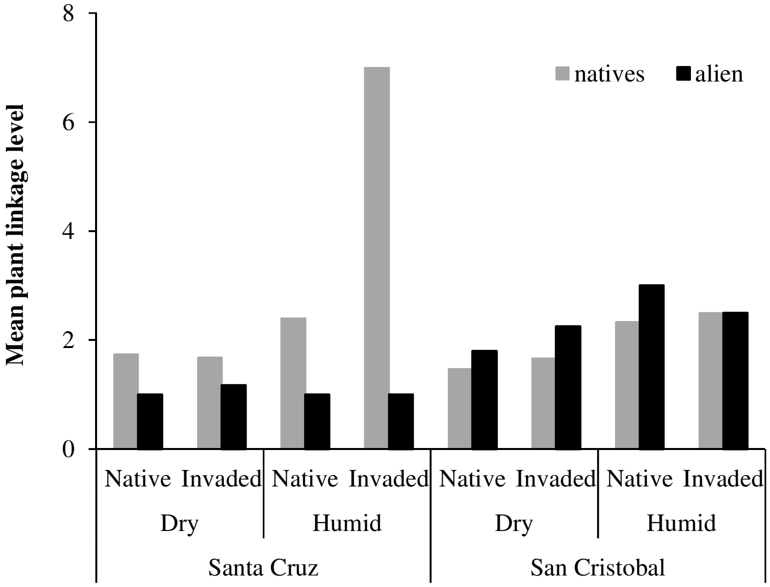

10000
Lantana camara
100
Psidium guajava
10000
Rubus niveus
1000
Scutia spicata
1000
Cordia leucophlyctis
10000
Chiococca alba
10000
Tournefortia psilostachya
10000
Miconia robinsoniana
1000
Zanthoxylum fagara
20000
All alien
20000
All native
J
F
M
A
M
J
J
A
S
O
N
D

Figure 3



Mean plant linkage level
8
6
4
2
0
natives
alien
Native
Invaded
Native
Invaded
Native
Invaded
Native
Invaded
Dry
Humid
Dry
Humid
Santa Cruz
San Cristobal

Figure 4

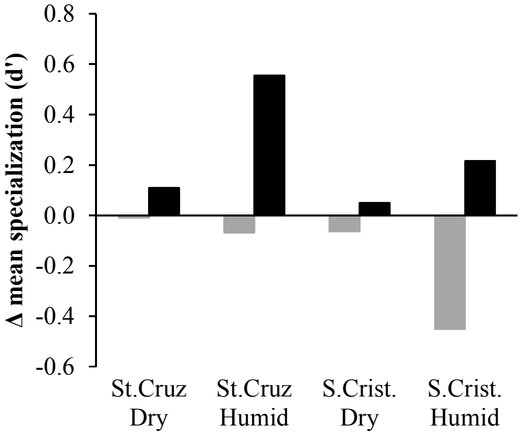
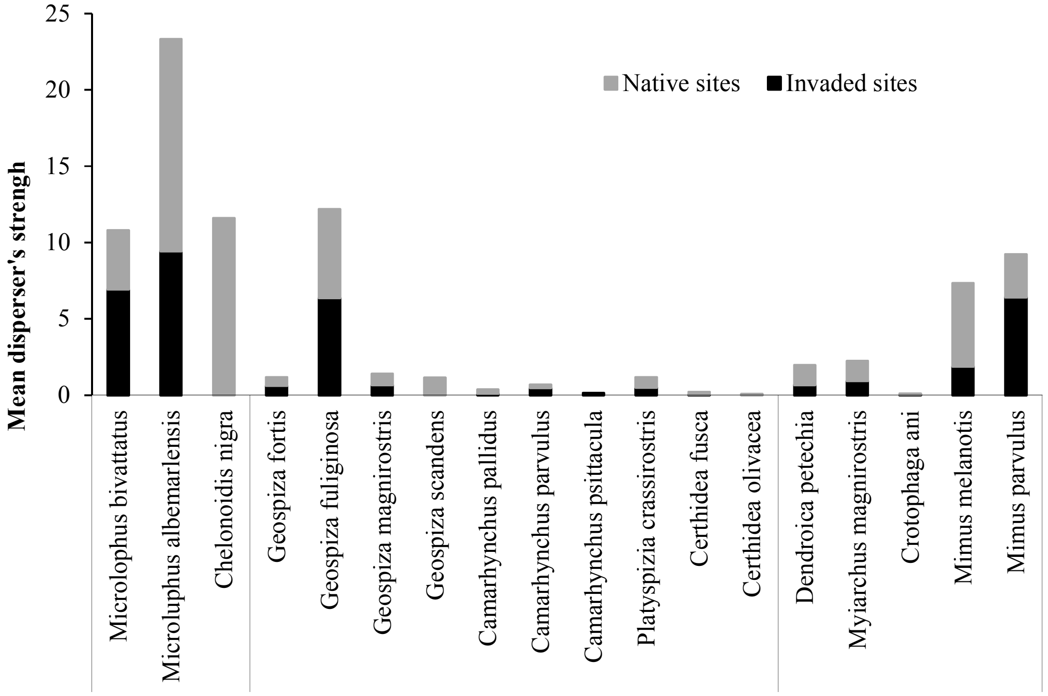

Δ mean specialization (d')
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
St.Cruz Dry
St.Cruz Humid
S.Crist. Dry
S.Crist. Humid

Figure 5


25
20
15
10
5
0
Mean disperser's strengh
Native sites
Invaded sites
Microlophus bivattatus
Microluphus albemarlensis
Chelonoidis nigra
Geospiza fortis
Geospiza fuliginosa
Geospiza magnirostris
Geospiza scandens
Camarhynchus pallidus
Camarhynchus parvulus
Camarhynchus psittacula
Platyspizia crassirostris
Certhidea fusca
Certhidea olivacea
Dendroica petechia
Myiarchus magnirostris
Crotophaga ani
Mimus melanotis
Mimus parvulus