

Invaders of pollination networks in the Galápagos Islands: emergence of novel communities

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Running head: Galápagos invaded pollination networks

1 The unique biodiversity of most oceanic archipelagos is currently threatened by the
2 introduction of alien species which can displace native biota, disrupt native ecological
3 interactions, and profoundly affect community structure and stability. We investigated
4 the threat of aliens on pollination networks in the species-rich lowlands of five
5 Galápagos islands. Twenty percent of all species (60 plants and 220 pollinators) in the
6 pooled network were aliens, being involved in 38% of the interactions. Most aliens were
7 insects, especially dipterans (36%), hymenopterans (30%) and lepidopterans (14%).
8 These alien insects had more links than either endemics or non-endemic natives, some
9 even acting as island hubs. Aliens linked mostly to generalized species, increasing
10 nestedness and thus network stability. Moreover, they infiltrated all seven connected
11 modules (determined by geographic and phylogenetic constraints) of the overall
12 network, representing c. 30% of species in two of them. An astonishingly high fraction
13 (38%) of connectors, which enhance network cohesiveness, was also alien. Results
14 indicate that the structure of these emergent novel communities might become more
15 resistant to certain type of disturbances (e.g. species loss) while being more vulnerable
16 to others (e.g. spread of a disease). Such notable changes in network structure as
17 invasions progress are expected to have important consequences for native biodiversity
18 maintenance.

19 **Keywords:** biological invasions; insect and vertebrate pollination; modularity;
20 mutualistic interactions; nestedness; oceanic islands

21

22 1. INTRODUCTION

23 Islands house a large proportion of global biodiversity. However, much of it is
 24 threatened by habitat degradation and loss, exploitation of natural resources and
 25 introduction of alien species [1,2,3]. The impact of alien species is especially severe on
 26 islands rich in endemic species [2,4]. As island species are being lost, so are their
 27 interactions with other species, initiating cascading effects through entire communities
 28 [5,6,7]. Nevertheless, most conservation and restoration projects on islands fail to
 29 incorporate interactions as indicators of ecosystem functions, particularly plant-animal
 30 mutualisms like pollination and seed dispersal [8,9,10].

31 Animal pollination is essential to the reproductive success of most plant species
 32 and as such is crucial to the maintenance of diversity and functioning of terrestrial
 33 ecosystems [5,11]. There are a few general patterns of pollination networks on oceanic
 34 islands, which include: 1) small network size; 2) strong dominance of one or a few taxa
 35 and a scarcity or absence of certain groups (e.g. insect pollinators with long proboscis,
 36 bees); 3) low ratio between species richness of pollinators and plants; 4) dominance of
 37 plants with open and easily-accessible flowers, pollinated by either insects or
 38 vertebrates, especially birds and lizards; and 5) higher generalization level than
 39 mainland networks, with some species even operating as *super-generalists* or density
 40 compensators [12,13,14]. Small network size together with super-generalists result in
 41 highly connected networks, i.e. many potential interactions are also realized. Some of
 42 these network properties actually facilitate integration of alien species [15,16].

43

44

45 **(a) *Vulnerability of network structure to alien species***

46 The arrival of new species to islands may notably alter the structure and dynamics of
47 their networks [17,9,16,18,19]. However, the generality of this is still under debate, and
48 our knowledge of the mechanisms underlying the integration of alien species into native
49 networks and their subsequent impact is still limited. Network analysis is a highly
50 valuable tool in our effort to understand this process of integration and to plan robust
51 conservation and restoration strategies [[10,18,20]. A number of network metrics can
52 inform us on the ability of communities to respond to various kinds of environmental
53 perturbations, and may easily be incorporated into conservation monitoring [20]. For
54 example, higher interaction diversity may increase the rates of ecosystem processes; in
55 pollination networks, it may lead to larger seed set because of increased functional
56 complementarity [21]. Generally, integration of aliens into pollinator networks does not
57 seem to affect overall connectance [but see 22], although the number of interactions
58 among natives may decline [23,16]. Likewise, interaction evenness, which measures the
59 uniformity in the distribution of interaction frequencies and is inversely related to
60 network stability [24], may decrease with higher invasion intensity [18]. Level of
61 invasion may also reduce species specialization (d') of native species [19], implying that
62 they become less selective in their choice of mutualists by being compelled to interact
63 with the most abundant aliens as invasion progresses. Invaders can also induce changes
64 in levels of network nestedness [16,25] and modularity [25]; both link patterns are also
65 diagnostic signs of network stability [26,27]. Hence, invaded networks could be more
66 stable, because of a lower interaction evenness and specific changes in nestedness and
67 modularity, making restoration more difficult [28,22].

68

69 **(b) *The threatened Galápagos ecosystems***

70 Since the last century, the unique Galápagos ecosystems are being jeopardized by the
71 effects of globalization. Humans have increasingly settled on the islands, mediating the
72 establishment of many aliens [29]. The number of alien plants has raised exponentially,
73 currently forming 60% of the vascular flora [30]. Likewise, c. 500 insect species
74 (representing 25% of all Galápagos insect species) are introduced, a number
75 continuously growing [31]. However, little is known on the mechanisms by which such
76 aliens become integrated into the native Galápagos ecosystems and how they affect
77 mutualistic networks.

78 In this study, we investigated the pollination patterns in the arid zone of the
79 Galápagos. Firstly, we assessed the diversity of interactions within and across islands,
80 identifying the main network hubs and comparing interaction patterns of native and
81 alien species. Secondly, we evaluated level of link structure with respect to nestedness
82 and modularity, especially in relation to alien links. In particular, we examined the
83 importance of geography, phylogeny and aliens as drivers of a modular structure of the
84 pollination network of the archipelago.

85

86 **2. METHODS**

87 **(a) *Study sites***

88 The Galápagos Islands lie on the Equator in the Eastern Pacific, 960 km to the west of
89 the South American continent. This young volcanic archipelago (0.035 – 4.0 my; [32])
90 comprises 18 islands larger than 1 km² and numerous islets. Arid zones dominate the
91 lowland on all islands (c. 60% of total land area); they show the highest plant diversity

and endemism, and a relatively low fraction of alien plant species compared to the transition and humid zones [29]. The Galápagos flora consists of 557 native vascular species, of which 32% are endemic, and an additional 825 (c. 60%) aliens [30].

A recent study has reviewed all known plant-pollinator interactions in the archipelago [33]. Only one of them, performed at Isabela Island, involved a network analysis of pollination interactions [34]. These authors found high connectance, nestedness (“asymmetrical pattern of number of interactions per species”), higher pollinator than plant linkage level, and high dependence of seed production on insect visits. However, the ratio between pollinator and plant species was only 0.5, which is very low, indicating that the study site was very poor in insects, even for an insular environment [14].

We built a lowland pollination network for each of five islands (figure 1), differing in age and degree of disturbance, from youngest/pristine to oldest/disturbed: Fernandina (0.035-0.07 my), Pinta (>0.7 my, undetermined maximum), Santiago (0.8-1.4 my), Santa Cruz (1.1-2.3 my) and San Cristóbal (2.4-4.0 my) [32].

(b) *Observation of pollinators*

In February 2010 and 2011, during the peak of the flowering season, we collected data on visitation interactions to flowering plants in the arid zone of each island. Upon arrival to each island, we explored an area of about 1 km² around the disembark point (mainly for logistic reasons), and recorded all plants in flower to be subsequently censused for pollinators. During three consecutive days on each island and year, five people made pollinator observations at all those flowering plant species in a random way, always trying to maximize the number of individuals of each species. A total of 518 hours [446 diurnal (8:00–18:00) and 72 nocturnal (18:30–21:00)]; we did not have

117 permits to overnight on the islands] were invested in pollinator censuses. On average,
118 each flowering plant species was observed for c. 8 h, depending on the number of
119 islands on which it occurred and on whether or not it flowered both years. Overall
120 sampling effort was similar in all islands. All flower-visiting animals touching
121 reproductive parts of flowers were recorded and classified as pollinators, irrespective of
122 their effectiveness. Pollinators were collected when field identification was not possible.
123 A total of 4,513 flower visits were recorded. Insect specimens ($n = 710$) were identified
124 and deposited at the Charles Darwin Research Station. If identification to species level
125 could not be achieved, insects were sorted into morphotypes. Finally, flower abundance
126 of all plant species at each study site, using 500 x 6 m transects, was estimated.

127

128 **(c) *Network analysis***

129 We built a quantitative plant-pollinator interaction matrix for each island and a pooled
130 matrix for all five islands ('archipelago network', hereafter). As interaction weight we
131 used visitation frequency, expressed as the number of flowers contacted by each
132 pollinator species during a census, standardized by number of flowers observed, number
133 of census per plant species, and specific flower abundance [35].

134 We calculated eight parameters that describe network topology: two at species
135 level (linkage level and specialization level d') and six at network level (connectance,
136 interaction diversity, interaction evenness, network specialization H_2' , weighted
137 nestedness, and modularity) (for a description of these, see appendix S1 in electronic
138 supplementary material). All parameters were estimated for each study site/island,
139 except modularity, which only was calculated for the archipelago network. Most metrics
140 were calculated using the *R* package bipartite v. 2.15.1 [36]. Weighted estimates of

141 nestedness was obtained using the *WNODF* program [37] whereas modularity (M) was
142 estimated using NETCARTO [38]. The role of each species as network hub, module
143 hub, connector or peripheral was assigned following [39; see appendix S1 for details].
144 The significance level of *WNODF* estimates was assessed against 1000 randomizations
145 using a fixed row and column totals constrained null model, while that of M was
146 assessed against 100 randomizations constrained by the same linkage-level ranking as
147 the empirical one. General linear models were used to compare network metrics across
148 islands and across species of different origins, using *R 2.11*. The *multcomp* package
149 (Tukey's test) was used to test for variation between categories.

150

151 **3. RESULTS**

152 **(a) *Diversity of interactions within and across islands***

153 The archipelago network consisted of 280 species, i.e. 60 plants and 220 pollinators
154 (table 1), c. 35% of which were nocturnal. We observed a total of 758 links, resulting in
155 a connectance of 5.7 %. Mean plant linkage level was more than threefold that of the
156 pollinators ($L_p = 12.6$, $L_a = 3.5$; $t = 10.44$, $p < 0.001$; table 1), reflecting the ratio
157 between species number of pollinators and plants. Visualizations of the network from
158 each island and the combined archipelago network can be found in figure S1 in the
159 electronic supplementary material.

160 Island network size varied from 78 species on the youngest, most pristine
161 Fernandina to 114 on the oldest and most disturbed San Cristóbal. Despite the known
162 effect of network size on connectance, this parameter stayed constant across islands,
163 except for Pinta (table 1). Plants and animals had higher linkage levels on the oldest
164 islands, San Cristóbal and Santa Cruz (table 1).

165 Twenty percent of all species in the archipelago network were aliens and most of
 166 these were insects, especially dipterans (36%), hymenopterans (30%) and lepidopterans
 167 (14%). Alien pollinators visited significantly more plant species than non-endemic
 168 native pollinators (natives, hereafter) ($z = 5.53, p < 0.001$) and marginally more than
 169 endemic pollinators ($z = 2.21, p = 0.07$); endemics also visited more plant species than
 170 natives ($z = 4.15, p < 0.001$) (table 2). In total, alien pollinators, constituting 21% of all
 171 pollinator species, were involved in a disproportionately large fraction (38%) of all
 172 network links. They entered the network most often (80% of cases) by linking to highly
 173 generalist plants, i.e. those visited by ≥ 10 pollinator species. Regarding plants, 48% of
 174 the 60 species were endemic to Galápagos, and only three species were aliens:
 175 *Tamarindus indica* and *Cleome viscosa* on Santiago and *Momordica charantia* on Santa
 176 Cruz. These alien plants showed lower linkage levels ($L_p = 7$ for *Tamarindus indica*,
 177 four for *Cleome viscosa*, and three for *Momordica charantia*) than an average plant
 178 species ($L_p = 12.6$). Alien plants were visited by the super-generalist bee *Xylocopa*
 179 *darwini* and by other endemic insects as well, but five cases of alien-alien interactions
 180 were also observed, viz. *T. indica* was visited by the *Hemiargus ramon* (Lepidoptera:
 181 Lycaenidae), *Polistes versicolor* (Hymenoptera: Vespidae), and *Monomorium*
 182 *destructor* (Hymenoptera: Formicidae), whereas *M. charantia* was visited by
 183 *Monomorium floricola* and *Tapinoma melanocephalum* (Hymenoptera: Formicidae).

184 Four plant species were super-generalists, being involved in 28% of all links in
 185 the archipelago network. These were the three endemic shrubs: *Croton scouleri* (73
 186 links), *Cordia leucophlyctis s.l.* (59), and *Lantana peduncularis* (45), and the doubtfully
 187 native herb *Tribulus cistoides* (36). *Cordia leucophlyctis s.l.* and *L. peduncularis* are
 188 present on all five islands whereas the other two are on at least three. The network had
 189 also five super-generalist pollinators, with ≥ 20 links each, representing 16% of all

190 network links. Two were endemic, the bee *X. darwini* and the lycaenid *Leptotes*
 191 *parrhasioides*, but the other three were introduced: *H. ramon* (morphologically similar
 192 to *L. parrhasioides*), *P. versicolor* (Hymenoptera: Vespidae), and *Pseudodoros clavatus*
 193 (Diptera: Syrphidae). The latter was present on all five islands, *X. darwini* and *P.*
 194 *versicolor* on all islands except Pinta, whereas the two butterflies occurred on Santiago,
 195 Santa Cruz and San Cristóbal.

196 Each island network had its own hubs, which most often were not shared with
 197 networks on the other islands (table 3). Moreover, some hubs in island networks (e.g.
 198 the plants *C. scouleri*, *C. leucophlyctis s.l.*, *L. peduncularis*, and the carpenter bee *X.*
 199 *darwini*) were also hubs in the archipelago network. In island networks, the main
 200 pollinator hubs were hymenopterans, dipterans, and lepidopterans, though their relative
 201 importance varied across islands (table 3). At least one pollinator hub in each island
 202 network was an alien. Santa Cruz and San Cristóbal even had more alien than native
 203 pollinator hubs (table 3).

204 Regarding quantitative network metrics, we found that mean plant generality (i.e.
 205 the effective number of pollinator individuals visiting each plant; see appendix S1) was
 206 three times lower than pollinator generality, despite the number of links being higher for
 207 plants than for pollinators (table 1). Comparing across islands, Fernandina and Pinta
 208 showed the lowest values of plant generality whilst the highest of pollinator generality
 209 (plant and pollinator generality was not significantly correlated). Moreover, the
 210 archipelago network and all island networks were uneven in their interaction
 211 frequencies (table 1).

212 Fernandina had the highest network specialization (H'_2) (table 1). However, at
 213 the species level, specialization (d') did not vary significantly among islands either for

214 plants or for pollinators (table 1). Moreover, no significant differences in d' were
 215 detected among alien, native and endemic pollinators (all $p \geq 0.80$) (table 2).

216

217 **(b) *Nestedness***

218 Both the archipelago network and the five island networks were significantly nested
 219 (table 1). Nestedness values ranged from 9.21 for Fernandina to 17.84 for San Cristóbal.
 220 Alien plants and pollinators boosted nestedness by linking mostly to generalists. In
 221 addition, interactions between specialists were rare (figure S1).

222

223 **(c) *Modularity of the archipelago network***

224 The archipelago network was significantly modular, with a modularity level $M = 0.41$
 225 (mean \pm sd of 100 randomizations of this network = 0.37 ± 0.005 ; $p < 0.001$). It
 226 consisted of seven connected modules (i.e. subgroups of plants and pollinators more
 227 strongly linked to each other than to plants and pollinators in other modules), plus a
 228 single pair of species disconnected from the main network (table 4 and figure 2). Fifty-
 229 nine percent of all links in the network were within modules (table 4).

230 We identified six network hubs, i.e. species that had many links both within their
 231 own module and also to other modules, and consequently, become important to overall
 232 network coherence (figure 2). These were all plants: the endemics *C. scouleri*, *L.*
 233 *leucophlyctis s.l.* and *L. peduncularis*, the natives *Tournefortia psilostachya* and
 234 *Clerodendrum molle*, and the doubtfully native *T. cistoides*. All these species were
 235 present on more than three islands, except *C. molle* which was found only on Santa

236 Cruz. Three other plant species were classified as module hubs: the natives *Bursera*
237 *graveolens* and *Heliotropium angiospermum*, and the endemic *Opuntia galapageia*;
238 these plants were mainly visited by many pollinators from their own modules.

239 A total of 48 species (17%) were network connectors, which included native and
240 endemic plants but mainly (77%) insects, specifically hymenopterans, lepidopterans and
241 dipterans. Of all insect connectors (37 spp.), at least 18 species were aliens. Most
242 network connectors were found on a minimum of three islands, although a few occurred
243 on a single island. Insect connectors pollinated plants belonging to different modules
244 whereas plant connectors were visited by pollinators belonging to different modules.
245 Connectors bind modules together and are thus important to the coherence of the entire
246 network.

247 Finally, most nodes were peripheral species, i.e. poorly connected species. Here,
248 223 species (c. 80% of all species) played this role, with an average of 2.8 links each.

249 Modules had a strong geographical component, most being composed of species
250 present from the same island, although they also contained a few species from other
251 islands (table S1). A phylogenetic component was also evident, because some modules
252 were dominated by particular taxonomical groups of pollinators. The species
253 composition of each module is listed in table S1, and summarized below:

254 Module 1 was an outlier, composed of a single pair of species from Pinta, not
255 linked to any other species in the network. Module 2 had many species from San
256 Cristóbal and the highest fraction of alien species (33%), including several ant species
257 and one wasp. Module 3 had also a high fraction of alien species (29%), it was mostly
258 from Santiago and included the three bees known to the archipelago. Both modules 2

259 and 3 contained potential invasional complexes (alien plants and pollinators strongly
260 interacting with each other) and the highest number of network connectors. Module 4
261 was dominated by vertebrate pollinators and nocturnal moths, most of which were
262 recorded on Pinta. Module 5 consisted mainly of dipterans and their plants, and almost
263 half of the species were found on either Pinta, Fernandina, or both. Module 6 was the
264 largest module, it was dominated by lepidopterans, and most interactions were observed
265 on San Cristóbal, Pinta and Fernandina. Module 7 was the second smallest, with species
266 from Fernandina and Santiago. Finally, module 8 was dominated by nocturnal
267 lepidopterans from Santa Cruz.

268

269 4. DISCUSSION

270

271 (a) *Emerging pollination patterns in the Galápagos Islands*

272 In qualitative networks, connectance C is a measure, albeit crude, of network
273 generalization level. A previous study [40] analysed 29 pollination networks originating
274 from both mainland and islands, finding that $C = 13.83 \exp(-0.003(A + P))$, where A and
275 P are number of pollinator and plant species, respectively. C did not differ between
276 mainland and islands. In Galápagos, island network C had a mean of 10.8% and did not
277 vary among islands. This figure was quite similar to the expected mean $C = 10.4\%$ for
278 the island networks using the model by [40]. The C -values found in [33] for the
279 Galápagos island of Isabela was much higher (27% for the observation matrix and 33%
280 for the matrix combining observation and pollen load on insect bodies). This is
281 attributable to its much smaller network ($A + P = 16$ species). Thus, C -values of the
282 Galápagos island networks were in accordance with global patterns and did not seem to

283 depend upon the level of invasion. Nonetheless, with the continuing invasion by
284 particular species in this archipelago, the number of species interactions among natives
285 might well decline, as reported in some communities [16,23], although in some cases
286 aliens increase connectance [22].

287 Despite being one of the best preserved archipelagos in the world, as much as c.
288 40% of pollination interactions on Galápagos already involve aliens. These are mainly
289 human-mediated insect introductions, and we found that at least in the arid zone they
290 are mostly dipterans, ants and lepidopterans. A total of 58 alien species were detected,
291 although the final number will probably be higher once all cryptogenic species are
292 identified.

293 As often reported for pollination networks [16,40], plants were more generalized
294 than pollinators. This is partly attributable to the phytocentric approach of the study
295 (censusing pollinators that arrive to plants rather than following the pollinator's
296 movements among plants), although other studies on pollen transport (zoocentric)
297 matrices also find higher plant than animal linkage levels [41,42; but see 33]. Alien
298 plants in our networks were not highly generalized, thus not supporting previous
299 findings [16,23]. However, they linked to generalized pollinators, as found in these
300 studies, which increased nestedness (see below). These pollinators were either endemic
301 or alien. In the first case, those novel interactions might pose a threat to native plants if
302 these compete with alien plants for pollinators. Such competition may reduce pollinator
303 visitation rate and/or reproductive success of natives in different systems [43, but see
304 18]. For instance, the abundant and nectar-rich flowers of the alien *T. indica* attract
305 many endemic carpenter bees, which as a consequence, may visit fewer co-occurring
306 native flowers. In the second case, the novel interactions might result in invasional

307 meltdowns, as the invasion of plants may enhance that of alien pollinators and vice
308 versa. In our study sites, we did indeed detect five potential cases of “invader
309 complexes”, which need further study to assess their importance at the population and
310 community levels.

311 The generalized alien pollinators increased nestedness, which may improve
312 network stability [26,27]. Nestedness tended to be higher in the older, more invaded
313 islands of San Cristóbal and Santa Cruz, suggesting they contain more stable
314 communities. This raises the question on the relationship between network stability and
315 network degradation. A greater stability can be a signature of pristine communities, but
316 also of already eroded communities [44].

317 The three most generalized plant species are widespread endemic shrubs with a
318 large floral display. Regarding pollinators, all hubs were insects and *X. darwini* was the
319 most generalized pollinator when pooling data from the five islands, supporting findings
320 from a recent review [33]. Apart from another endemic hub, the lycaenid *L.*
321 *parrhasioides*, the most generalized pollinators were three alien insects: another
322 lycaenid, a wasp and a hoverfly. These are likely to have the strongest impact on
323 network structure and reproductive success of native/endemic plants, although a deeper
324 study should confirm so. The wasp (*P. versicolor*), in particular, was present and
325 abundant on all islands but Pinta; however, its effectiveness as pollinator is still
326 doubtful, and it is also unknown if it has any negative effects on native pollinators due
327 to competition for floral rewards. The hoverfly, *P. clavatus*, was also present on all five
328 islands and, given the importance of Syrphidae as legitimate pollinators, it might well
329 enhance pollination of native plants while being detrimental to native insects if they
330 compete for resources. On San Cristóbal and Pinta, the most important pollinators –

331 regarding linkage level - were actually alien species, perhaps after having displaced
332 some native ones, as has happened elsewhere [23].

333 The higher generality of pollinators compared to plants resulted from the greater
334 diversity in interaction frequency of the former. This has also been found in other
335 mutualistic networks [18, but see 35] and might be due to the phytocentric methodology
336 as well as the higher frequency of pollinator singletons. Mutualistic networks are always
337 uneven in their distribution of interaction frequencies and our networks are no
338 exception. On a gradient of invasion intensity, a decrease in interaction evenness was
339 observed, being attributed to shifts in the proportion of strong and weak interactions in
340 the networks [18]. The comparison of invaded vs. uninvaded areas will allow assessing
341 a change in this parameter with invasion level. Regarding network specialization (H'_2),
342 Fernandina showed the highest value, reflecting that species tend to interact with
343 partners that are not necessarily abundant. As with connectance, H'_2 values fell within
344 the range found for dispersal networks in these islands [19] and also for other island
345 networks [35]. For both plant and pollinator species, a wide variation in specialization
346 was found within each island, and that might blur any differences across islands.
347 Although alien pollinators on average visited more plant species than native and
348 endemic pollinators, they were similarly specialized. As far as we know, no data are
349 available from other studies comparing this property between alien and native insects.

350

351 ***(b) The role of aliens in the structure of novel communities***

352 Aliens entered the pollination network by interacting with generalized natives, as
353 reported in [16,23]. This usually results in increased complexity in network structure,

354 especially in nestedness, a property that buffers secondary extinctions [26,27]. In
355 addition, aliens integrated into all connected modules, representing as much as c. 30%
356 of the species in two modules, one composed mostly by species from San Cristóbal and
357 the other by species from Santiago. The potential invader complexes were also located
358 in these two modules in which mostly alien ants, bees and wasps were involved. These
359 hymenopterans might thus constitute the highest risk to plant reproduction if they are
360 less effective than native pollinators [7]. Alien dipterans were also common in the
361 archipelago network, but their interactions were spread across different modules, and
362 thus their effect on plant reproduction might be less important.

363 So far, none of the aliens are network or module hubs, but as invasion progresses
364 such species might well take over these roles from natives as described in other systems
365 [23,25], with potential cascading effects on the overall network structure [but see 18].
366 Alien insects, however, played an important role as network connectors, representing
367 38% of all connector species and taking part in 34% of all inter-module links. The
368 proportion of network connectors was slightly higher than in other pollination networks
369 [9,39]. Alien connectors may enhance module fusion, i.e. their higher generalization
370 levels lead to stronger connections among modules. This may be detrimental to overall
371 network stability as cascading processes after a disturbance (e.g. the spread of a disease)
372 are more likely to ripple through the entire network [20]. However, a more cohesive
373 network may also be more robust to cumulative extinctions of species, as lost
374 interactions can be more easily backed-up [but see 25]. On the other hand, alien
375 connectors might be replacing native network connectors, and then it might be difficult
376 to predict the consequences to stability without knowing how redundant they are with
377 respect to their pollination function. If alien insects acted as legitimate pollinators, they
378 could actually enhance plant reproductive success and replace, to some extent, lost

379 native pollinator species [7]. If, however, most alien insects are ineffective pollinators,
380 the network might seem cohesive from a topological viewpoint but in fact might be
381 weak from an ecosystem service's perspective [see also 25].

382 Modularity is a topological metric that may also be informative from an
383 evolutionary viewpoint [39]. We might predict that species belonging to the same
384 module – in our case, being also found in the same island -, are more likely to be
385 coadapted to each other than with species from other modules [45]. The discovery of
386 such modules can indeed be the platform for more detailed studies on the evolutionary
387 interactions between pollinators and their nectar plants. We further predict that the alien
388 intruders into these modules will probably affect such coadaptations, with unknown
389 consequences to the success of native species.

390

391 **5. CONCLUSIONS**

392 We identified a surprisingly high proportion of alien insects visiting the flowers of
393 plants in the dry zone of five Galápagos islands. Overall, alien species took part in c.
394 40% of the 758 interactions recorded. The flowers of alien plants were visited by
395 endemic and alien pollinators and we detected five cases of potential invasional
396 meltdown. The most generalized plants and pollinators were endemic but, on average,
397 alien pollinators visited more plants than native and endemic counterparts. Moreover,
398 alien species tended to interact with the most generalized counterparts; by doing so,
399 they increase network nestedness and, hence, stability against perturbations involving
400 species losses. Alien insects have infiltrated seven of the eight modules identified,
401 representing up to 30% of the species in two of them and undertaking structurally

402 important roles as module connectors. Specifically, a high fraction of them connected
403 the different modules, contributing to network cohesiveness. This might decrease
404 network robustness if the probability of cascade losses after a perturbation (e.g. entrance
405 of a parasite) is lower in highly modular networks. On the contrary, alien connectors
406 might enhance network robustness against specific perturbations affecting particular
407 modules (e.g., a vertebrate pollination module) if they counteract the wipe out of such
408 module and/or contribute to maintain its functioning. A recent study stresses the
409 importance of improving biological forecasting by detecting early ‘warning signals’ of
410 critical transitions, both at a global and local scale [46]. We believe that a critical
411 threshold to maintain community functioning may have already been reached in
412 Galápagos, one of the best preserved archipelagos in the World.

413

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425

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552

553 **Table captions**

554

555 **Table 1.** Topology descriptors of the pollination networks in five Galápagos islands. P
 556 and A : number of plant and animal species, respectively; S : network size ($P+A$); I :
 557 number of realized interactions; C : connectance (I/AP); IE : interaction evenness; H'_2 :
 558 index of network specialization; WNODF: weighted nestedness metric. For each plant
 559 (p) and animal (a) species, the number of links (L), generality (G), and index of species
 560 specialization (d') are also given. Interaction weight in the quantitative networks is the
 561 number of visited flowers by each pollinator species standardized by census time and
 562 flower abundance in the community. For each L and d' column, values sharing the
 563 same letter are not significantly different ($p < 0.05$). All WNODF values are significant
 564 ($p < 0.001$).

565 **Table 2.** Animal species richness, linkage level (L_a) and specialization index (d'_a) of
 566 pollinators classified according to their distribution status ($n = 148$). Data were pooled
 567 from the five study islands. For each column, values sharing the same letter are not
 568 significantly different ($p < 0.001$). Only species of known origin were used for the
 569 analyses.

570 **Table 3.** Plant and pollinator hubs in the five Galápagos islands. The taxonomic order
 571 of the pollinator species is given abbreviated before its scientific name (Hy:
 572 Hymenoptera; Di: Diptera; Le: Lepidoptera). Number of links of each species is given in
 573 parentheses. Alien species to Galápagos are indicated by *.

574 **Table 4.** Number of species and links of the modules of the pooled pollination network.
 575 Module connectance is the proportion of realized links in the module. Modules are
 576 named according to their species composition and to the geographical origin of most of
 577 their species. Species identities in each module are given in Appendix S3.

578

Table 1

Island	<i>P</i>	<i>A</i>	<i>S</i>	<i>I</i>	<i>C</i>	<i>L_p</i> (X±SD)	<i>L_a</i> (X±SD)	<i>G_p</i>	<i>G_a</i>	<i>IE</i>	<i>H'₂</i>	<i>d'_p</i> (X±SD)	<i>d'_a</i> (X±SD)	WNODF
Fernandina	18	60	78	125	0.12	6.94 ± 5.43 ^a	2.08 ± 1.60 ^{ac}	1.60	8.06	0.69	0.70	0.62 ± 0.18 ^a	0.44 ± 0.25 ^a	9.21
Pinta	21	76	97	133	0.08	6.33 ± 7.04 ^a	1.75 ± 1.65 ^a	1.68	12.38	0.76	0.52	0.65 ± 0.21 ^a	0.44 ± 0.23 ^a	10.41
Santiago	24	69	93	168	0.10	7.00 ± 5.26 ^a	2.43 ± 3.13 ^{ab}	2.20	3.84	0.51	0.49	0.52 ± 0.25 ^a	0.49 ± 0.22 ^a	13.25
Santa Cruz	23	76	99	215	0.12	9.35 ± 6.53 ^b	2.83 ± 3.40 ^b	2.13	6.36	0.60	0.60	0.49 ± 0.16 ^a	0.47 ± 0.20 ^a	16.04
San Cristóbal	21	93	114	234	0.12	11.14 ± 8.63 ^b	2.52 ± 2.68 ^{cb}	2.93	4.77	0.66	0.59	0.46 ± 0.23 ^a	0.39 ± 0.18 ^a	17.84
All islands	60	220	280	758	0.06	12.63 ± 13.51	3.45 ± 4.61	3.28	9.69	0.67	0.57	0.52 ± 0.19	0.42 ± 0.22	11.87

Table 2

Pollinator origin	N of species	L_a ($\bar{X} \pm \text{SE}$)	d'_a ($\bar{X} \pm \text{SE}$)
Endemic	64	4.17 ± 0.68^a	0.39 ± 0.03^a
Native (non-endemic)	26	2.38 ± 1.06^b	0.41 ± 0.04^a
Alien	58	4.97 ± 0.70^c	0.40 ± 0.03^a

Table 3

FERNANDINA	PINTA	SANTIAGO	SANTA CRUZ	SAN CRISTOBAL
Plant hubs (n pollinator species)				
Bursera graveolens (22)	Croton scouleri (31)	Tribulus cistoides (22)	Cordia leucophlyctis s.l.(25)	Croton scouleri (36)
Tribulus cistoides (15)	Opuntia galapageia (15)	Lantana peduncularis (19)	Clerodendrum molle (22)	Cordia leucophlyctis s.l. (29)
Cordia leucophlyctis s.l.(11)	Lantana peduncularis (13)	Blainvillea dichotoma (12)	Croton scouleri (21)	Vallesia glabra (21)
Pectis tenuifolia (10)	Bursera graveolens (11)	Heliotropium angiospermum (11)	Tournefortia psilostachya (16)	Cordia lutea (15)
	Cryptocarpus pyriformis (10)	Commicarpus tuberosus (10)	Lantana peduncularis (14)	Waltheria ovata (14)
	Prosopis juliflora (10)	Cordia leucophlyctis s.l. (10)	Cordia lutea (13)	
		Macraea laricifolia (10)		
Pollinator hubs (n plants visited)				
Hy-Camponotus planus (10)	Di-Lepidanthrax tinctus (11)*	Hy-Xylocopa darwini (15)	Hy-Xylocopa darwini (16)	Le-Hemiargus ramon (15)*
Di-Pseudodoros clavatus (6) *	Di-Chrysanthrax primitiva (9)	Le-Agraulis vanillae (14)	Hy-Polistes versicolor (14)*	Hy-Camponotus conspicuus zonatus (11)*
Di-Chrysanthrax primitiva (5)	Hy-Oxybelus schusteri (7)	Le-Hemiargus ramon (14) *	Le-Leptotes parrhasioides (13)	Hy-Xylocopa darwini (11)
		Di-Pseudodoros clavatus (9) *	Hy-Tapinoma melanocephalum (12)*	Le-Urbanus dorantes (9)
		Le-Leptotes parrhasioides (9)	Hy-Paratrechina longicornis (11)*	Hy-Anthidium
		Le-Urbanus dorantes (8)	Hy-Brachygastra lecheguana (9)*	vigintiduopunctatum (8)*

Table 4

Module	No. plant spp.	No. pollinator spp.	No. within- module links	No. between- module links	Module connectance
1 -Pinta	1	1	1	0	1.00
2 –San Cristobal (alien ants & wasps)	11	29	80	124	0.25
3- Santiago (bees)	13	22	67	105	0.23
4-Pinta (vertebrates & nocturnal lepidopterans)	6	31	40	52	0.22
5- all islands (dipterans)	13	25	64	102	0.20
6-Pinta, Fernandina, San Cristóbal (lepidopterans)	7	59	111	125	0.27
7-Fernandina, Santiago	3	21	28	54	0.44
8-Santa Cruz (nocturnal lepidopterans)	6	32	47	78	0.24
Total	60	220	448	620 ^a	

^a The number of between-module links corresponds to twice the number of actual links, as links are counted in the both modules they connect.

Figure captions

Figure 1. Map of the Galápagos Islands showing the study sites.

Figure 2. Modules (in different colours) in the network of 60 plants and their 220 pollinators. Size of a node (species) depicts the different network roles, from peripherals (smallest) to network hubs (largest, indicated in grey circles). Plant species are represented by circles and animals by squares (species identities given in appendix S3). Links of alien species are indicated in red whereas those of the remaining species are in black (native, endemic or of unknown origin). Alien links represent 34% of all links among modules. Numbers in squares refer to the module number given in the text.

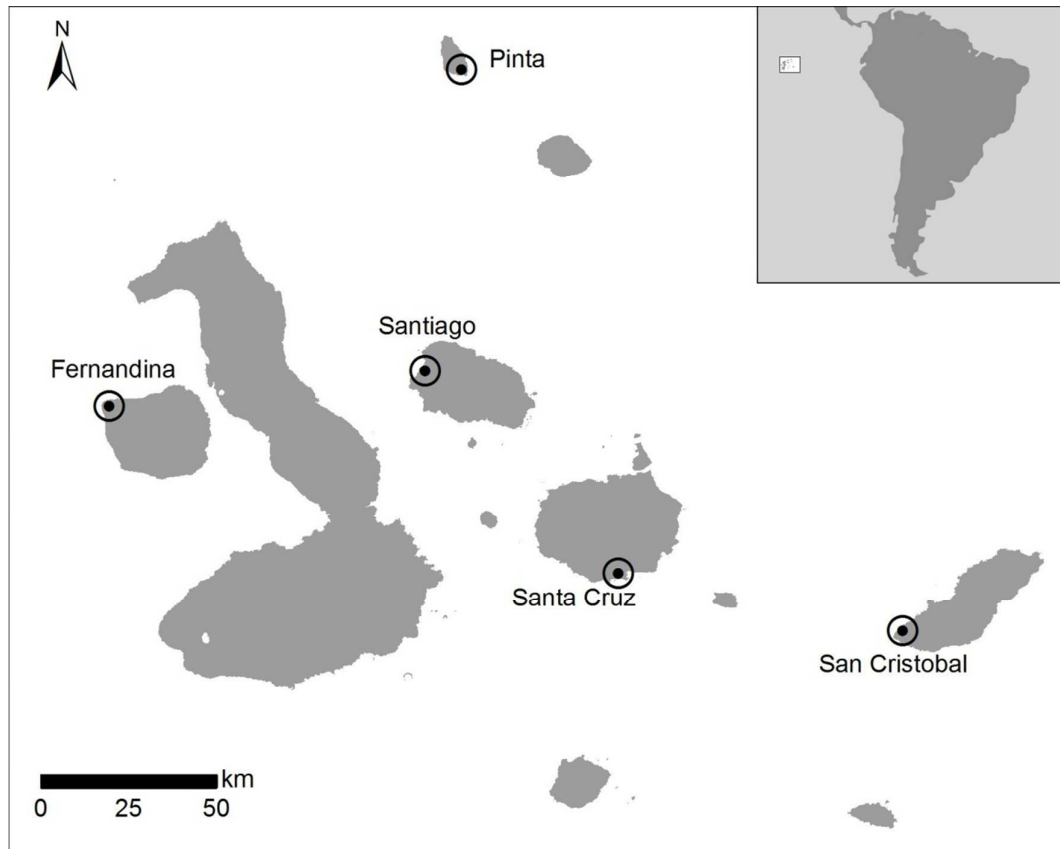
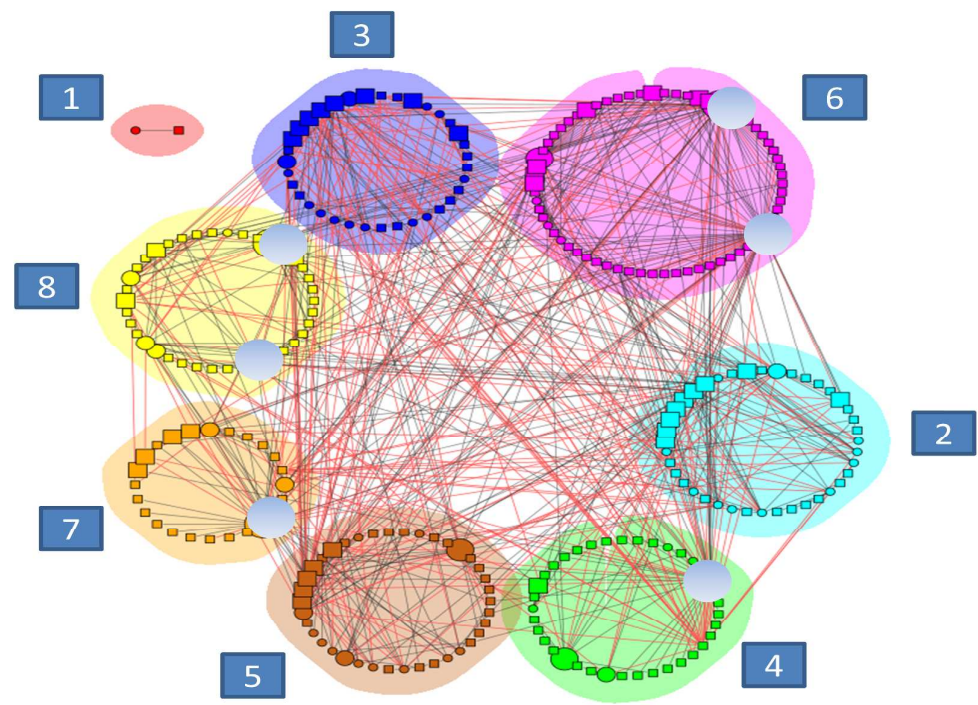
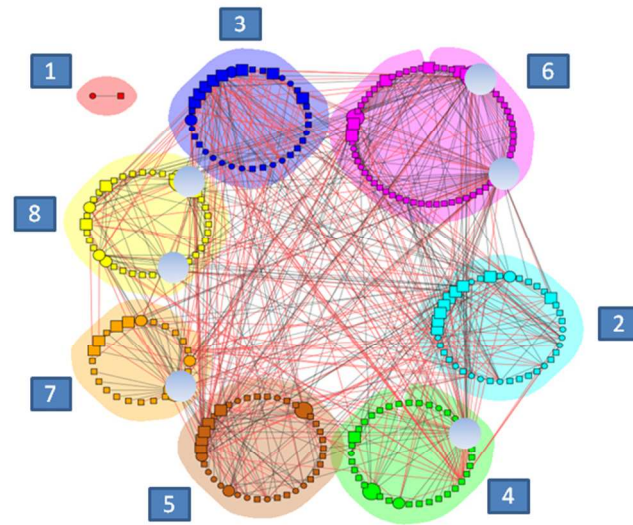
Figure 1

Figure 2





254x190mm (96 x 96 DPI)