



Seed-dispersal networks on the Canaries and the Galápagos archipelagos: interaction modules as biogeographical entities

M. Nogales^{1*}, R. Heleno², B. Rumeu^{1,3}, A. González-Castro^{1,4}, A. Traveset⁵, P. Vargas³ and J. M. Olesen⁶

¹Island Ecology and Evolution Research Group (CSIC-IPNA), La Laguna, Spain, ²Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, Coimbra, Portugal, ³Real Jardín Botánico (CSIC-RJB), Madrid, Spain, ⁴Departamento de Ciencias de la Tierra, Universidad Estatal Amazónica, Puyo, Ecuador, ⁵Institut Mediterrani d'Estudis Avançats (CSIC-UIB), Palma de Mallorca, Spain, ⁶Department of Bioscience, Aarhus University, Aarhus, Denmark

ABSTRACT

Aim Mutualistic network parameters, such as modularity and nestedness, show non-random linkage patterns. Both increase network stability in different ways. Modularity hampers extinction cascades, whereas nestedness resists network disassembly. We explore these parameters in seed-dispersal networks in two archipelagos and the significance of life history, habitat, geography and phylogeny as drivers of linkage patterns and the applicability of modules as biogeographical entities.

Location Canaries (Atlantic Ocean) and Galápagos (Pacific Ocean).

Methods We compiled data on plant–seed disperser interactions from own observations and the literature, estimated network parameters describing interaction patterns (connectance, nestedness and modularity) and constructed a backbone phylogeny for the analyses.

Results The Canarian network was highly nested but weakly modular, whereas the Galápagos network showed the opposite characteristics. Most key network species are native and have a favourable conservation status. Modularity in the Canaries is correlated with habitats (indirectly affected by altitude and orientation), whereas in the Galápagos it mainly reflects the functional roles of species.

Main conclusions The divergent link patterns for the archipelagos imply that the highly nested Canarian network is stable against disassembly, whereas the modular Galápagos network may show strong resistance against extinction cascades. This difference may be driven by the specific evolutionary dynamics on the archipelagos.

Keywords

Animal–plant interaction, fleshy fruit, food web, frugivory, insular network, modularity.

*Correspondence: M. Nogales, Island Ecology and Evolution Research Group (IPNA-CSIC), C/Astrofísico Fco. Sánchez no. 3, 38206 La Laguna, Tenerife, Canary Islands, Spain.
E-mail: mnogales@ipna.csic.es

INTRODUCTION

Biodiversity is much more than mere species lists, particularly as it also includes the myriad of ways in which species interact (Pocock *et al.*, 2012) and form spatio-temporally dynamic networks (e.g. Rasmussen *et al.*, 2013). During the last two decades, this upscaling in focus from species to networks has contributed significantly to our comprehension of the complexity of biodiversity (Bascompte & Jordano, 2013). There are plenty of important milestones along this route, especially the concepts of nestedness (Bascompte *et al.*, 2003)

and modularity (Olesen *et al.*, 2007). Their applicability in the context of biogeography and system stability is the focus of this paper.

If a network has a highly heterogeneous structure of species and their interactions, it is most often both nested and modular. In a nested link pattern, a core of generalist species interact with each other and with specialists (Bascompte *et al.*, 2003). In a modular link pattern, each module is a group of highly interconnected species, often sparsely linked together into a larger network (Olesen *et al.*, 2007). In ecology, modules are extremely useful for our understanding of mutualistic systems such as

Table 1 General characteristics of the Canarian and Galápagos archipelagos and potential consequences for biodiversity.

Characteristics	Canaries	Galápagos	Biodiversity consequences
Abiotic characteristics			
Land area (km ²)	c. 7900	c. 7500	Large area for immigration
Number of islands (> 10 km ²)	9	13	Large area for allopatric speciation
Highest peak (m asl)	3718	1707	Large topographic area for immigration and speciation
Maximum age of current islands (Ma)	21	4–6	Wide span of geological age
Current minimum distance between archipelago and mainland (km)	c. 98	c. 1000	Very different level of isolation
Volcanic activity in the last centuries	High	High	Recurrent extinction events
Climate	Subtropical Mediterranean	Equatorial	Hotspots of diversity
Biotic characteristics			
Main biomes	5	3	High habitat diversity
Biodiversity (no. of species)	High	Medium	High interaction potentiality
No. of seed-plant endemic species (%) with respect to natives	537 (40.3%)	168 (38%)	Strong signal for unique interactions
No. of fleshy fruited species (%) with respect to natives	76 (5.7%)	34 (7.6%)	Important plant component for ecological networks
No. of vertebrate disperser species (%) with respect to native land vertebrates	30 (35.7%)	28 (65%)	Important animal component for ecological networks

plant–pollinator (Traveset *et al.*, 2013) and plant–seed-disperser networks (Donatti *et al.*, 2011), but also in antagonistic systems such as food webs (Dunne *et al.*, 2002) and host–parasite networks (Anderson & Sukhdeo, 2011). Within a module, species operate in dynamic ecological–evolutionary synchrony because of their high interconnectivity. Thus if modularity is strong, a more relevant scale of analysis might be the module and not the individual species or the whole network. A module may be seen as a coevolving niche (Gómez *et al.*, 2015), a concept with wide implications for the study of coevolution, ecological convergence, local co-occurrence, system stability, invasion/extinction, migration/dispersal, geography and phenological uncoupling/climate change (Thébaud & Fontaine, 2010; Stouffer & Bascompte, 2011; Aizen *et al.*, 2012; Høye *et al.*, 2013; for a review of modularity, see Bascompte & Olesen, in press). Thus, insight into the link structure allows a deeper understanding of biodiversity, for example with respect to regional/geographical patterns (e.g. Carstensen & Olesen, 2009; Dalsgaard *et al.*, 2013), the impact of alien species (Valdovinos *et al.*, 2009; Rodríguez-Cabal *et al.*, 2013; Traveset *et al.*, 2013) and system stability (Stouffer & Bascompte, 2011; Bascompte & Jordano, 2013; Rodríguez-Cabal *et al.*, 2013).

Seed dispersal is an essential phase in the process of regeneration of plant communities and a strong driver of local biodiversity (Bascompte & Jordano, 2007). At the network level, most studies of seed dispersal have been carried out in mainland communities (Jordano *et al.*, 2003), and only a few on oceanic islands (Heleno *et al.*, 2011a, 2013; González-Castro *et al.*, 2012). This retards rigorous island–mainland comparisons (Schleuning *et al.*, 2014), although as a general pattern we know birds and mammals are major mainland biotic dispersers (Herrera, 1995) whereas birds and reptiles often play this role on oceanic islands (Nogales *et al.*, 2005).

Here we integrate network theory and biogeography in a study of seed-dispersal networks on two oceanic archipelagos, the Canaries (Atlantic Ocean) and the Galápagos (Pacific Ocean). These archipelagos differ in geographical position and isolation, age, elevation and mainland species source, but have quite a similar land surface area and high interaction potentiality (Table 1). We focused upon seed-dispersal modules in order to show their value as functional entities in biogeographical analyses.

The aims of our study were to: (1) estimate levels of nestedness and modularity, identify modules and quantify intermodule distances; (2) compare species and link composition of modules from the two archipelagos; and (3) identify local and regional drivers of modularity. Finally, we discuss the results in relation to system stability and the applicability of the module concept as a biogeographical entity in studies of the ecology and evolution of island interactions.

METHODS

Study sites

The archipelagos of the Canaries and the Galápagos (Appendices S1 & S2 in Supporting Information) differ in several respects, but also show important similarities (Table 1), for example in total land surface (7900 vs. 7500 km², respectively) and number of islands (9 vs. 13 islands > 10 km²) and palaeoislands (6 vs. 7); however, the Canaries are older and richer in plant species and main biomes (see Heleno *et al.*, 2011b; Padilla *et al.*, 2012) (Appendix S3).

Interaction matrices and network parameters

We compiled data about interactions from own field observation of frugivory (over a time span of 10 years in the Canaries

and 6 years in Galápagos) and also included all records from an exhaustive literature review (Helena *et al.*, 2011b and references therein). We also included all interactions involving non-native species, with the exception of captive/cultivated species. A seed-dispersal interaction was recorded if fruit was swallowed or removed from a plant by an animal, if undamaged seeds were found in droppings or pellets or if gut samples with intact seeds were obtained. In the Canaries, predatory birds such as the kestrel and the meridional shrike indirectly disperse more than 60 species by their predation of frugivorous lizards (Padilla *et al.*, 2012). Such records of seeds in regurgitation pellets were also included in the network. On both archipelagos, interactions were gathered all year round with a greater effort during the main fruiting seasons.

Interactions were compiled into two-mode binary adjacency matrices of *A* animal species (matrix columns) interacting with *P* fleshy fruited plant species (matrix rows) (Tables S1 & S2). If an interaction *I* between a plant and an animal species is recorded, its presence in the matrix cell is scored as '1', if not as '0'.

We estimated three network parameters: connectance, nestedness and modularity. Connectance $C = 100I/AP$ is the percentage of realized interactions out of the total possible interactions in the network. Level of nestedness was measured with the NODF algorithm (Almeida-Neto *et al.*, 2008), and the NODF value belongs to the interval [0 (not-nested); 1 (perfectly nested)]. Empirical NODF values were compared with distributions of NODF values from 1000 random networks of similar size (Almeida-Neto *et al.*, 2008). To test for modularity we used the software NETCARTO (Guimerà & Amaral, 2005), which assigns all plants and seed dispersers to modules. The level of modularity *M* of a network expresses how strongly the network is partitioned into modules. As *M* approaches 0 or 1, the level of modularity becomes weaker or stronger, respectively. Empirical *M*-values were compared with distributions of *M*-values from 100 random networks of similar size (Olesen *et al.*, 2007). The null model assumes that the ranking of the species linkage levels *L* (i.e. the number of links of each species) is like that of the empirical network. We also recorded the size and composition of each module and the number of links between and within modules. We calculated the distance between each pair of modules (intermodule distance), defined as the number of shared links between a pair of modules divided by the sum of all their links. If a module, on average, has a short distance to all other modules, it has a high module centrality.

In addition, NETCARTO also assigns topological network roles to all species based on their pattern of intra- and intermodule links (Guimerà & Amaral, 2005). The assignment of a role to a species is determined by *relative within-module degree or hubability* (*z*), quantifying how well connected a species is to other species in its module, and *among-module connectivity* (*c*), which quantifies how well distributed the links of a species are among modules. We sorted all species into four categories: (1) peripherals ($z < 2.5$, $c < 0.62$) have few links inside their own module and rarely any to other modules; (2) connectors ($z < 2.5$, $c \geq 0.62$) have a few links both to species in their own module and to species in other modules, i.e. they are important

for network cohesion by gluing modules together; (3) module hubs ($z \geq 2.5$, $c < 0.62$) have many links to other species in their own module, and are important for module cohesion, and (4) network hubs or super-generalists ($z \geq 2.5$, $c \geq 0.62$) are both connectors and module hubs (Olesen *et al.*, 2007).

Networks were visualized using the software PAJEK v.2.05 (Batagelj & Mrvar, 1998). The basic principle behind PAJEK visualization is that distance between species expresses their number of links to other species.

Testing for phylogenetic signal in network composition

The phylogenetic signal of a trait in a sample of species expresses the extent to which the phylogenetic structure of the community accounts for morphological characters of the species. In order to estimate the importance of the phylogeny in explaining the variation of trait values of our four communities (plants and dispersers in the Canaries and in the Galápagos), we constructed a backbone phylogeny for each community. Plant phylogenies were based on the supertree from APG III (Angiosperm Phylogeny Group, III, 2009), bird phylogenies from <http://birdtree.org/> and *Gallotia* lizard phylogenies from Cox *et al.* (2010). As information on branch length was not available for all taxa and phylogenies, we used a taxonomic proxy, equalizing branch lengths between species, genera and families. In order to run the R scripts, a few polytomies were resolved taxonomically into dichotomies using branch lengths $\ll 1$.

We used two measures of phylogenetic signal, *K* and λ . Blomberg's *K* compares the observed trait signal with a signal under a Brownian motion (BM) evolutionary model (Blomberg *et al.*, 2003). If $K \approx 1$, the trait is phylogenetically clustered in the sample of species. $K \approx 0$ indicates a convergent or random pattern, whereas $K > 1$ indicates a strong phylogenetic signal. The significance of *K* is tested by comparing the observed signal with the mean of the signal from randomizations based on a null model, which shuffles species randomly across the phylogeny. *K* was calculated using the package *picante* in R (Kembel *et al.*, 2010).

Pagel's λ measures how much trait correlations among species tell us about their shared evolutionary history. The value of λ ranges between 0 and 1; if $\lambda \approx 0$, the trait structure is not influenced by phylogeny, whereas $\lambda \approx 1$ implies that the trait follows a BM model. The lower and upper bounds of *K* and λ (Table S3) indicate which of the two scenarios is the most likely. This analysis was performed using the packages *picante* and *geiger* in R (Harmon *et al.*, 2008).

We tested for phylogenetic signal in each of the four communities with respect to the distribution of a set of five network traits (module affinity, module centrality, linkage level *L*, connectivity *c* and relative within-module degree or hubability *z*) and five species traits [body weight, fruit size, preferred habitat, origin (i.e. native or alien) and geographic distribution (i.e. number of islands on which the species was present); see Table S3]. Species of the same module show module affinity, whereas species of different modules do not. A phylogenetic

Table 2 Descriptive parameters of seed-dispersal networks in the Canaries and Galápagos.

	Canary Islands	Galápagos Islands
Number of seed-disperser species, <i>A</i>	30	28
Number of fleshy fruited plant species, <i>P</i>	65	34
Animals to plants ratio (<i>A/P</i>)	0.46	0.82
Network size (<i>S = AP</i>)	1950	952
Number of recorded interactions, <i>I</i>	325	153
Modularity, <i>M</i>	0.31**	0.39**
Number of modules, <i>N_M</i>	6	6
Connectance, <i>c</i> ($100I/AP$)	16.7	16.1
Nestedness NODF	27.8**	12.6**

Modularity (based on 100 randomizations) and nestedness (1000 randomizations); significance indicated by ** $P < 0.01$ (Almeida-Neto *et al.*, 2008).

signal with respect to module affinity tells us that taxonomically related species tend to be in the same module.

As a measure of the phylogenetic signal for plant origin, we used Fritz and Purvis' *D* (Fritz & Purvis, 2010), which was calculated using the R package *caper* (Orme, 2013): $D = (d_{\text{obs}} - \text{mean } d_{\text{b}}) / (\text{mean } d_{\text{r}} - \text{mean } d_{\text{b}})$, where d_{obs} is the number of character state changes needed to get the observed character state distribution in our phylogeny, d_{b} is the expected distribution of *d* under a BM model (1000 runs) and d_{r} is the expected distribution of *d* if character states are randomly distributed among species. We scaled d_{obs} by d_{r} and d_{b} in order make comparisons possible across communities and archipelagos. $D = 1$ if the distribution of a trait in a community is independent of the phylogeny of the species; $D > 1$ if the trait is phylogenetically overdispersed; $D = 0$ if the trait is distributed according to a BM model; and $D < 0$, if the trait is more phylogenetically clustered than expected according to a BM model (Nunn, 2011).

We also tested for any correlations between traits using phylogenetically independent contrasts (PIC), by means of the *ape* package in R (Paradis *et al.*, 2004).

RESULTS

The Canarian and Galápagos networks had similar connectance (Table 2). However, species richness and nestedness were higher in the Canaries, whereas modularity and intermodule distance were higher in the Galápagos (Tables 2 & 3; see also Appendix S4). In other words, the different modules operated more independently in the Galápagos. We also confirm the value of the seed-dispersal modules as study entities in biogeographical analyses.

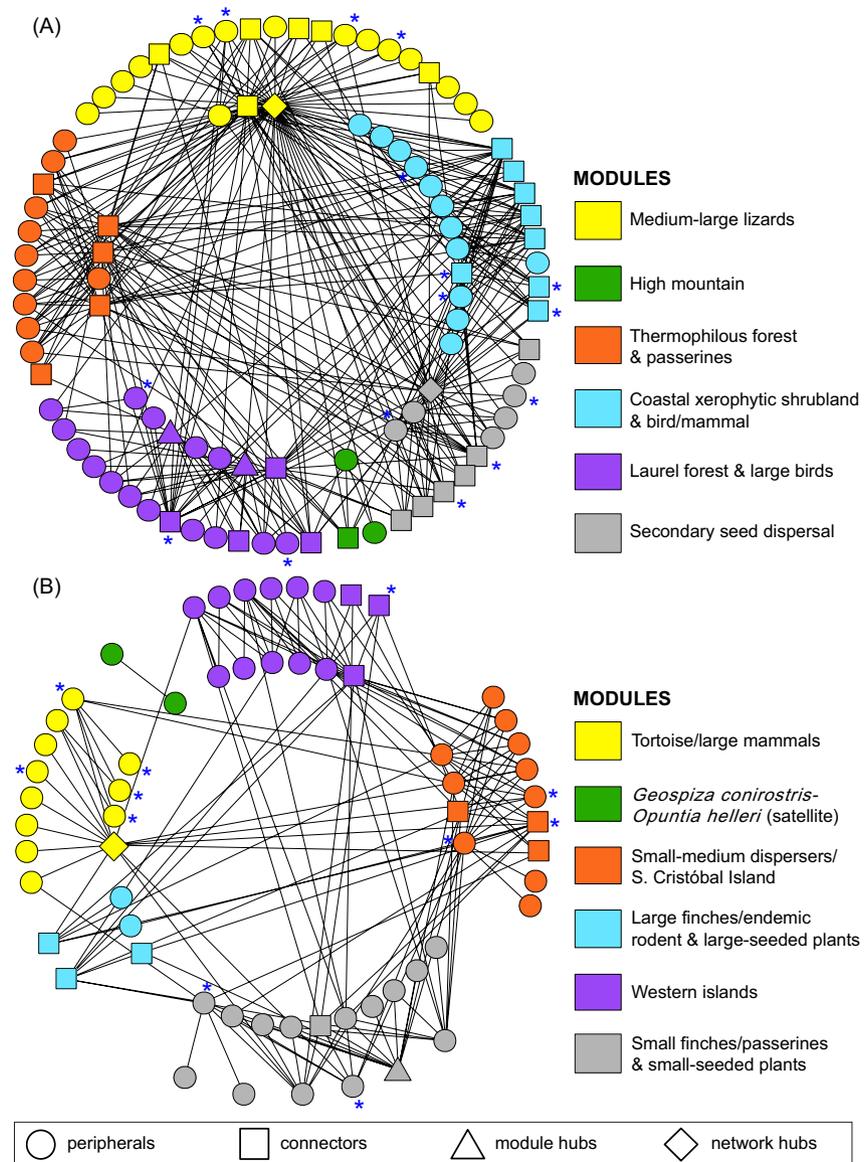
The Canarian network consisted of six interconnected modules (Fig. 1a; see Table S4 for information about modules and Appendix S5 for information about species included in Fig. 1a). The 'medium-large-sized lizards' and 'thermophilous forest and passerines' modules were closely connected, while the

Table 3 Intermodule distance. Distance between modules *i* and *j* calculated as their shared number of links $\times 100 / (\text{their total number of links})$. The module "*Geospiza conirostris-Opuntia helleri*" is an unconnected satellite module to the main network and therefore is not possible to calculate "intermodule distance" with the rest of modules.

Canarian modules		1	2	3	4	5	6
1	Laurel forest and large birds		6.3	5.2	5.5	1.1	7.0
2	Medium-large lizards			8.8	9.7	1.7	12
3	Coastal shrubland				9.5	1.0	6.5
4	Secondary seed dispersal					1.1	8.9
5	High mountain						1.7
6	Thermophilous forest						
Average distance							5.7
Galápagos modules		1	2	3	4	5	6
1	<i>Geospiza conirostris-Opuntia helleri</i>		-	-	-	-	-
2	Small-medium dispersers/San Cristóbal			21	14	13	23
3	Western islands				3.0	12	15
4	Tortoise-large mammals					5.0	7.8
5	Large finches/endemic rodent						8.6
6	Small finches/passserines						
Average distance							12.24

'laurel forest and large birds' module was the most isolated. A high proportion (49%) of all links were between modules (Table 4), i.e. intermodule distance was low. The network was formed by two network hubs or super-generalists (the lizard *Gallotia galloti* and the kestrel *Falco tinnunculus*), two module hubs (the pigeons *Columba bollii* and *Columba junoniae*) and 30 connectors (six seed dispersers and 24 fleshy fruited plants) (Figs 1a & 2, Appendix S5). Besides, four of the six modules were habitat-specific, namely high mountain, laurel forest, thermophilous forest and coastal shrubland. Thus, an extensive elevational habitat zonation enforced modularity (Appendix S3). The other two modules were dominated by lizards and secondary seed dispersers (shrikes and kestrels; Appendix S5).

The Galápagos network also consisted of six modules (Fig. 1b; see Table S5 for information about modules and Appendix S6 for information about species included in Fig. 1b). Only the modules 'small-medium dispersers/San Cristóbal Island' and 'western islands' and 'small-medium dispersers/San Cristóbal' and 'small finches/passserines' were strongly connected to each other. By contrast, the modules 'western islands' and 'tortoise/large mammals', and the 'tortoise/large mammals' and 'large finches/endemic rodent and large-seeded plants' modules were poorly connected. The cactus *Opuntia helleri* and the finch *Geospiza conirostris* made an independent small satellite module, unconnected to the main network. Only 37% of all links were between modules (Table 4). The giant tortoise *Chelonoidis nigra* was the only network hub, the plant *Miconia robinsoniana* was the only module hub, and 10 species were connectors (four dispersers and



six plants) (Figs 1b & 2, Appendix S6). One module was dominated by the giant tortoise, together with cattle, pigs and goats, while the other modules were characterized by bird and reptile seed dispersers. Thus, in contrast to the Canaries, functional group affinity in the Galápagos disperser guild was a stronger driver than habitat specificity.

With regard to the drivers of modularity, K and λ gave qualitatively similar results; network traits only showed some significant phylogenetic signals (Table S3). Canarian plants showed phylogenetic clustering with respect to their ability to link different modules (related plant taxa were important connectors), and related taxa (e.g. species of finches) in Galápagos had a high linkage level. Body weight was a trait that was affected by phylogeny among both Canarian and Galápagos dispersers; the 'tortoise/large mammals' module from Galápagos strongly contributed to this. Habitat specificity ('main habitat') was influenced by phylogeny in the Canarian disperser community and both the plant and the disperser communities on the Galápagos.

Other traits showed phylogenetic signals, e.g. fruit size ('fruit dm³'). Phylogeny also influenced geographic distribution ('no. of islands') of Canarian seed dispersers and Galápagos fruiting plants.

In the phylogenies of Canarian plants and dispersers, and Galápagos dispersers, the trait 'native versus alien' was distributed according to a Brownian motion model of evolution ($D \leq 0$), indicating a phylogenetic signal. However, native and alien Galápagos plant species were distributed independently of their phylogeny (D was closer to 1 than to 0).

Several traits were correlated after correcting for phylogenetic dependency (Table 5), but the pattern differed strongly between communities and between archipelagos. In the Galápagos, disperser species sharing a module ('module affinity') had a more similar extent of geographical distribution ('no. of islands') than a random species set; by contrast, the other communities (Galápagos plants and Canarian plants and dispersers) did not show this correlation. The Canarian modules were more associated

Table 4 Number of species and links in modules of seed-dispersal networks of the Canary Islands and the Galápagos. Module connectance C_M is the proportion of realized links inside the module (i.e. number of observed links/number of possible links in the module, excluding links to other modules).

Module	No. of plant species	No. of disperser species	No. of within-module links	No. of between-module links	C_M
Canary Islands					
Medium-large lizard	20	3	34	76	0.57
High-mountain	2	1	2	7	1.00
Thermophilous forest and passerines	11	4	37	70	0.84
Coastal xerophytic shrubland and bird/mammals	8	12	36	58	0.38
Laurel forest and large birds	14	7	35	44	0.36
Secondary seed dispersal	10	3	22	63	0.73
Total	65	30	166	318*	–
Galápagos Islands					
Tortoise–large mammal dispersers	8	4	13	11	0.41
<i>Geospiza conirostris</i> – <i>Opuntia helleri</i>	1	1	1	0	1.00
Small–medium dispersers/San Cristóbal Island	9	4	27	36	0.75
Large finches/endemic rodent and large-seeded plants	2	3	4	13	0.67
Especially two passerines (<i>Geospiza scandens</i> and <i>Mimus parvulus</i>), one dove (<i>Zenaida galapagoensis</i>), the iguana <i>Conolophus subcristatus</i> and rich flora	8	6	26	25	0.54
Especially five small passerines (<i>Certhidea olivacea</i> , <i>Certhidea fusca</i> , <i>Camarhynchus parvulus</i> , <i>Geospiza fuliginosa</i> , <i>Dendroica petechia</i>) and endemic tree-like <i>Miconia robinsoniana</i>	6	10	26	27	0.43
Total	34	28	97	112*	–

*Number of between-module links is equal to the half of these values, because each between-module link is counted twice, i.e. from modules A to B, and from B to A.

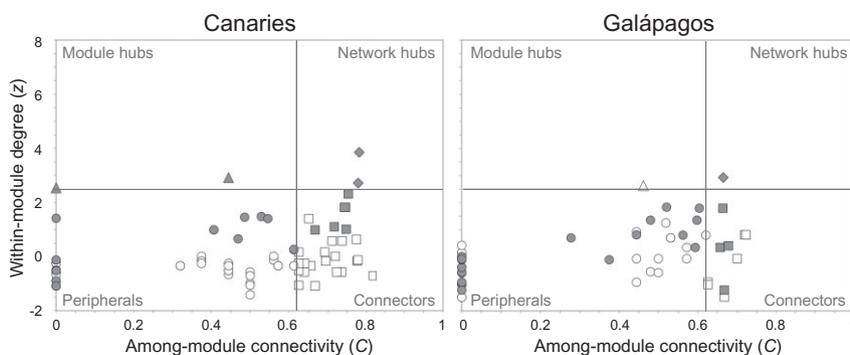


Figure 2 Distribution of seed dispersers and fleshy fruited plants according to their network role (symbols as in Fig. 1) in the Canary and Galápagos archipelagos. Cut-off values (2.5 for z and 0.62 for c , see Material and Methods); each dot represents a species; white dots are fleshy fruited plants and grey dots are frugivores.

with habitats within islands. Large Canarian dispersers ('body weight') had a central position in their modules (high z), whereas those specific large Galápagos dispersers had a high habitat preference ('main habitat') and were dominated by invasive alien mammals. The three main network parameters (l , c and z) were positively correlated in all communities except c and z for the Galápagos plants. The most widespread Canarian fruiting plants ('no. of islands') had more links (L) and showed more connectivity (c). Thus we see relationships between modular structure and body weight, habitat preference and native/alien status, and also between network characteristics and geographical distribution.

DISCUSSION

Although both oceanic archipelagos harbour rich communities with similar diversity of dispersers, connectance level, and the same number of modules, they differed considerably on overall plant diversity and on network topology. The robustness against disturbances of a network is influenced by levels of nestedness, modularity and connectance. High nestedness (Thébaud & Fontaine, 2010), and also high modularity, may add stability to a mutualistic network, but they do it in different ways (Sebastián-González *et al.*, 2015). The Canarian network was highly nested and thus strongly coherent, resisting community

Table 5 Coefficient of determination between traits (continuous/categorical) in communities of seed dispersers and their fruiting plants in the Canary Islands and the Galápagos after correcting for the influence of phylogeny (including introduced species).

	Module centrality	log(body weight)	Main habitat	Native/invasive	log(linkage level, <i>L</i>)	Connectivity, <i>c</i>	Hubability, <i>z</i>	No. of islands
Canary Islands								
Seed dispersers								
Module affinity	–	n.s.	n.s.	n.s.	0.16*	0.27**	n.s.	n.s.
Module centrality		n.s.	(–)0.46***	n.s.	0.14*	0.20**	n.s.	n.s.
log(body weight)			n.s.	n.s.	n.s.	n.s.	0.19*	n.s.
Main habitat				n.s.	n.s.	(–)0.11*	n.s.	n.s.
Native/invasive					n.s.	n.s.	n.s.	n.s.
log(linkage level, <i>L</i>)						0.87***	0.75***	n.s.
Connectivity, <i>c</i>							0.48***	n.s.
Hubability, <i>z</i>								n.s.
Galápagos Islands								
Seed dispersers								
Module affinity	–	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.30**
Module centrality		(–)0.40***	n.s.	(–)0.18*	0.14*	0.21**	n.s.	0.14*
log(body weight)			0.34***	0.31**	n.s.	n.s.	n.s.	n.s.
Main habitat				0.36***	n.s.	n.s.	n.s.	n.s.
Native/invasive					(–)0.34***	(–)0.37***	(–)0.17*	n.s.
log(linkage level, <i>L</i>)						0.82***	0.82***	n.s.
Connectivity, <i>c</i>							0.63***	n.s.
Hubability, <i>z</i>								n.s.
Canary Islands								
Fruiting plants								
Module affinity	–	(–)0.07*	n.s.	n.s.	0.16***	0.17***	n.s.	n.s.
Module centrality		n.s.	(–)0.12**	n.s.	(–)0.28***	(–)0.21***	n.s.	(–)0.05*
Fruit dm			n.s.	0.12**	n.s.	n.s.	n.s.	n.s.
Main habitat				n.s.	n.s.	n.s.	(–)0.10**	n.s.
Native/invasive					n.s.	(–)0.08*	n.s.	n.s.
log(linkage level, <i>L</i>)						0.80***	0.22***	0.30***
Connectivity, <i>c</i>							n.s.	0.15**
Hubability, <i>z</i>								n.s.
Galápagos Islands								
Fruiting plants								
Module affinity	–	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Module centrality		(–)0.11*	n.s.	n.s.	0.16*	n.s.	n.s.	n.s.
Fruit dm			n.s.	0.13*	n.s.	(–)0.13*	n.s.	(–)0.48***
Main habitat				0.14*	n.s.	n.s.	n.s.	n.s.
Native/invasive					n.s.	n.s.	n.s.	n.s.
log(linkage level, <i>L</i>)						0.64***	0.45***	n.s.
Connectivity, <i>c</i>							n.s.	n.s.
Hubability, <i>z</i>								(–)0.09*

Significance level: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s., not significant. Module affinity is a binary variable, indicating if a species is member of the same module or not; module centrality is the number of between links of a module/(total number of links in a module), i.e. links from a given module to all other modules, divided by the total number of links of the module (no. links to other modules + no. links within the module). Minus signs in bracket indicate the direction of the correlation.

disassembly, especially the extinction of rare species (Bascompte *et al.*, 2003; Rodríguez-Cabal *et al.*, 2013), whereas the Galápagos network consisted of well-separated modules (intermodule distance was twice as large as the Canarian and the proportion of between-module links was considerably lower). According to that, the different modules operate more independently in the Galápagos. This pattern reduces the risk of coextinction cascades (Rodríguez-Cabal *et al.*, 2013; Bascompte & Olesen, in

press). The strong coherence of the Canarian network is due to its many connectors (three times as many as in the Galápagos); these are animals moving between habitats, and plants with a wide elevational range. In general, the Galápagos network is functionally structured (assemblages of birds, lizards, tortoises and their plants, and one introduced mammal module), whereas the Canarian network mainly reflects the underlying habitat diversity (elevational zones: mountains, forests, coastland). Both

are geographically well structured, and each module was often located on one or a few islands.

Seed-dispersal networks and modules

The general trend that more diverse networks have more modules (Olesen *et al.*, 2007) was not observed in our study, even though the Canarian network had twice as many plant species as the Galápagos one. The reasons for this are: (1) the large intermodule distance and thus high modularity level of the Galápagos network; and (2) the higher topological rank (connectors, module and network hubs) of Canarian species in particular – Canarian connectors were more frequent. Both features tend to reduce the number of modules. If we regard a module as a kind of niche shared by a set of strongly interacting species (Gómez *et al.*, 2015), then our results demonstrate that the Galápagos have a more clearly delimited and fine-grained niche structure than the Canaries. Finally, the stronger Galápagos modularity was further enhanced by invasive alien mammals, which formed their own module.

In the Canaries, the kestrel and the lizard *G. galloti* were network hubs. The wide foraging range of the kestrel and the wide elevational range of the lizard (Padilla *et al.*, 2012) circumvent the habitat specificity of their modules, in contrast to the other four modules. A key role was also played by the two endemic laurel forest pigeons, both being hubs in the 'laurel forest and large birds' module. Their central role (10–15 fruit plants) emphasizes the importance of these birds to this unique forest. Furthermore, the pigeons were responsible for two-thirds of all dispersal links in the forest and such a modular structure could perhaps be said to have the signature of both the considerable age of the forest and the strong elevational zonation of the islands. Fortunately, both species of pigeon have healthy populations and no immediate threats are known.

In the Galápagos, the tortoise *C. nigra* constituted the sole network hub, while the plant *Miconia robinsoniana* was the only module hub, and both are endemic. The role played as seed disperser by *C. nigra* (see Blake *et al.*, 2013) is due to its large body size, home range and capacity to disperse both small seeds and the largest fleshy fruited plants such as *Hippomane mancinella* (Euphorbiaceae) (Blake *et al.*, 2012; Heleno *et al.*, 2013). Populations of this tortoise are, in general, recovering their former size with the eradication of competing feral mammals occupying the same module. Modularity would certainly increase further if the populations of tortoise were treated taxonomically as distinct species (Jiménez-Uzcátegui *et al.*, 2014). Following the recent release of tortoises to new islands, for example Pinta and Santa Fe, we can expect strong network changes, particularly with the reintroduction of an 'extinct function' within these communities. *Miconia robinsoniana* is the dominant plant throughout the highland *Miconia* zone. Here, it is one of the few species producing fleshy fruits (Heleno *et al.*, 2013) and is a key resource for most dispersers in its module (Table S5).

Although human-induced extinction is relatively common on oceanic islands, the frugivore assemblage of both archipelagos is

fortunately still mostly intact, with the exception of local extinctions of giant tortoises on Galápagos. However, a closer look at the influence of differences in network structure, as observed on the Canaries and the Galápagos, upon extinction dynamics, might be a fruitful future research programme that may expose different colonization–extinction dynamics.

The drivers of modularity

The drivers of modularity appear to be quite different on the two archipelagos. Habitat diversity and number of biomes are higher on the Canaries, perhaps due to a considerably higher elevation coupled with a much wider geological age span. Fleshy fruited plants were well represented in all habitats, except in the pine forest. Birds were more important in forest environments, while lizards were more so in the open habitat modules, in both coastal and high-mountain habitats (Valido *et al.*, 2003; Rumeu *et al.*, 2011). The two modules differed because they were organized around lizards and secondary seed dispersers, confirming the role of these animals in mutualistic insular systems (Olesen & Valido, 2003; Nogales *et al.*, 2007; Padilla *et al.*, 2012).

In the Galápagos, each module was formed by species with somewhat similar traits, selecting similar functional groups of species, especially birds and lizards (but see the 'tortoise/large mammals' module). Most modules included sauropsid representatives and the importance of seed dispersal by birds, lizards and tortoises is well known from islands (e.g. Guerrero & Tye, 2009; Heleno *et al.*, 2011b, 2013; Blake *et al.*, 2012).

In general, the paucity of well-resolved studies of seed dispersal modularity (two exceptions from mainland environments being Donatti *et al.*, 2011; and Schleuning *et al.*, 2011) still hampers comparisons of island and mainland networks. However, we hypothesize that modularity could be higher in continents, where rich species assemblages tend to have been interacting for longer evolutionary periods, forcing species to specialize and occupy smaller realized niches. In contrast, the poorer biodiversity of oceanic islands allows some species to become very common (density compensation), broadening their trophic niche (interaction release; Traveset *et al.*, 2015) to become super-generalists, and thus to make the network more coherent. In spite of this reasoning, the number of modules was rather similar between our two oceanic archipelagos and the two mainland sites (Donatti *et al.*, 2011; Schleuning *et al.*, 2011), though the island networks were smaller. Detailed studies are needed in order to delve deeper into the interpretation of modularity between insular and continental environments.

Irrespective of the two main causes of modularity in the Canaries (environmental heterogeneity) and Galápagos (species functional roles), the six modules detected on each archipelago may produce strong isolation over time. On the other hand, it is possible that islands have high modularity due to the important habitat diversity in the different archipelagos and the strong temporal dynamics (e.g. vulcanism). These two factors are probably the basic drivers of fast speciation occurring within remote territories isolated in the middle of the two largest oceans.

Indeed, we suggest that island studies focusing upon the importance of modularity for speciation rate could be a most promising research avenue.

CONCLUDING REMARKS

This is the first detailed study of the modularity of seed–dispersal networks on oceanic islands. We demonstrate that insular seed–dispersal networks may differ profoundly in their linkage structure among oceanic archipelagos. In this sense, modules form promising biogeographical entities for exploring the interplay between ecology and evolution on islands and elsewhere. Thus the evolutionary history of insular networks might also differ with important consequences for our general understanding of island biogeography, colonization/extinction dynamics and speciation patterns.

ACKNOWLEDGEMENTS

Many colleagues in the Canaries shared with us their observations on interactions between dispersers and fruiting plants, but especially Alfredo Valido, Félix M. Medina, Juan D. Delgado, David P. Padilla, Patricia Marrero, Airam Rodríguez and Marta López. In the Canaries, we also express our gratitude to public institutions at national (Parques Nacionales) and autonomic level (Gobierno de Canarias and Cabildos insulares). In the Galápagos, we thank the Charles Darwin Foundation and the Parque Nacional de Galápagos for offering us much information and logistic support. The editors and two anonymous referees provided useful comments and suggestions to improve this manuscript. R.H. was funded by FCT grant IF/00441/2013 and the Marie-Curie CIG-321794. This study is framed within a biodiversity project in the Galápagos Islands, financed by BBVA Foundation (Spain) and by projects CGL2012-C02-01 and CGL2013-44386-P financed by Ministerio de Economía y Competitividad (Spain).

REFERENCES

Aizen, M.A., Sabatino, M. & Tylianakis, J.M. (2012) Specialization and rarity predict nonrandom loss of interactions from mutualist networks. *Science*, **335**, 1486–1489.

Almeida-Neto, M., Guimarães, P., Guimarães, P.R., Loyola, R.D. & Ulrich, W. (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, **117**, 1227–1239.

Anderson, T.K. & Sukhdeo, M.V.K. (2011) Host centrality in food web networks determines parasite diversity. *PLoS ONE*, **6**, e0026798.

Angiosperm Phylogeny Group, III (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society*, **161**, 105–121.

Bascompte, J. & Jordano, P. (2007) Plant–animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution and Systematics*, **38**, 567–593.

Bascompte, J. & Jordano, P. (2013) *Mutualistic networks*. Princeton University Press, Princeton.

Bascompte, J. & Olesen, J.M. (in press) Mutualistic networks. *Mutualism* (ed. by J.L. Bronstein). Oxford University Press, Oxford.

Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003) The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences USA*, **100**, 9383–9387.

Batagelj, V. & Mrvar, A. (1998) Pajek: a program for large network analysis. *Connections*, **21**, 47–57.

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*, **39**, 1961–1972.

Blake, S., Yackulic, C.B., Cabrera, F., Tapia, W., Gibbs, J.P., Kümme, F. & Wikelski, M. (2013) Vegetation dynamics drive segregation by body size in Galapagos tortoises migrating across altitudinal gradients. *Journal of Animal Ecology*, **82**, 310–321.

Blomberg, S.P., Garland, T. & Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, **57**, 717–745.

Carstensen, D.W. & Olesen, J.M. (2009) Wallacea and its nectarivorous birds: nestedness and modules. *Journal of Biogeography*, **36**, 1540–1550.

Cox, S.C., Carranza, S. & Brown, R.P. (2010) Divergence times and colonization of the Canary Islands by *Gallotia* lizards. *Molecular Phylogenetics and Evolution*, **56**, 747–757.

Dalsgaard, B., Trøjelsgaard, K., Martín González, A.M., Nogués-Bravo, D., Ollerton, J., Petanidou, T., Sandel, B., Schleuning, M., Wang, Z., Rahbek, C., Sutherland, W.J., Svenning, J.C. & Olesen, J. (2013) Historical climate-change influences modularity and nestedness of pollination networks. *Ecography*, **36**, 1331–1340.

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.

Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002) Food-web structure and network theory: the role of connectance and size. *Proceedings of the National Academy of Sciences USA*, **99**, 12917–12922.

Fritz, S.A. & Purvis, A. (2010) Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. *Conservation Biology*, **24**, 1042–1051.

Gómez, J.M., Perfectti, F., Abdelaziz, M., Lorite, J., Muñoz-Pajares, A.J. & Valverde, J. (2015) Evolution of pollination niches in a generalist plant clade. *New Phytologist*, **205**, 440–453.

González-Castro, A., Traveset, A. & Nogales, M. (2012) Seed dispersal interactions in the Mediterranean region: contrasting patterns between islands and mainland. *Journal of Biogeography*, **39**, 1938–1947.

- Guerrero, A.M. & Tye, A. (2009) Darwin's finches as seed predators and dispersers. *The Wilson Journal of Ornithology*, **121**, 752–764.
- Guimerà, R. & Amaral, L.A.N. (2005) Functional cartography of complex metabolic networks. *Nature*, **433**, 895–900.
- Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E. & Challenger, W. (2008) Geiger: investigating evolutionary radiations. *Bioinformatics*, **24**, 129–131.
- Heleno, R., Ross, G., Everard, A.M.Y., Memmott, J. & Ramos, J.A. (2011a) The role of avian 'seed predators' as seed dispersers. *Ibis*, **153**, 199–203.
- Heleno, R., Blake, S., Jaramillo, P., Traveset, A., Vargas, P. & Nogales, M. (2011b) Frugivory and seed dispersal in the Galápagos: what is the state of the art? *Integrative Zoology*, **6**, 110–129.
- Heleno, R., Olesen, J.M., Nogales, M., Vargas, P. & Traveset, A. (2013) Seed dispersal networks in the Galápagos and the consequences of alien plant invasions. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20122112.
- Herrera, C.M. (1995) Plant–vertebrate seed dispersal systems in the Mediterranean: ecological, evolutionary and historical determinants. *Annual Review of Ecology and Systematics*, **26**, 705–727.
- Høye, T.T., Post, E., Schmidt, N.M., Trøjelsgaard, K. & Forchhammer, M.C. (2013) Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. *Nature Climate Change*, **3**, 759–763.
- Jiménez-Uzcátegui, G., Márquez, C. & Snell, H.L. (2014) CDF checklist of Galapagos reptiles – FCD lista de especies de reptiles de Galápagos. *Charles Darwin Foundation Galapagos species checklist* (ed. by F. Bungartz, H. Herrera, P. Jaramillo, N. Tirado, G. Jiménez-Uzcátegui, D. Ruiz, A. Guézou and F. Ziemmeck). Charles Darwin Foundation, Puerto Ayora, Galapagos. Available at: <http://www.darwinfoundation.org/datazone/checklists/vertebrates/reptilia/> (last updated 23 January 2014).
- Jordano, P., Bascompte, J. & Olesen, J.M. (2003) Invariant properties in coevolutionary networks of plant–animal interactions. *Ecology Letters*, **6**, 69–81.
- Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P. & Webb, C.O. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, **26**, 1463–1464.
- Nogales, M., Nieves, C., Illera, J.C., Padilla, D.P. & Traveset, A. (2005) Effect of native and alien vertebrate frugivores on seed viability and germination patterns of *Rubia fruticosa* (Rubiaceae) in the eastern Canary Islands. *Functional Ecology*, **19**, 429–436.
- Nogales, M., Padilla, D.P., Nieves, C., Illera, J.C. & Traveset, A. (2007) Secondary seed dispersal systems, frugivorous lizards and predatory birds in insular volcanic badlands. *Journal of Ecology*, **95**, 1394–1403.
- Nunn, C.L. (2011) *The comparative method in evolutionary anthropology and biology*. University of Chicago Press, Chicago.
- Olesen, J.M. & Valido, A. (2003) Lizards as pollinators and seed dispersers: an island phenomenon. *Trends in Ecology and Evolution*, **18**, 177–181.
- Olesen, J.M., Bascompte, J., Dupont, Y.L. & Jordano, P. (2007) The modularity of pollination networks. *Proceedings of the National Academy of Sciences USA*, **104**, 19891–19896.
- Orme, D. (2013) The caper package: comparative analysis of phylogenetics and evolution in R. Available at: <http://cran.r-project.org/web/packages/caper/vignettes/caper.pdf> (accessed 25 April 2015).
- Padilla, D.P., González-Castro, A. & Nogales, M. (2012) Significance and extent of secondary seed dispersal by predatory birds on oceanic islands: the case of the Canary archipelago. *Journal of Ecology*, **100**, 416–427.
- Paradis, E., Claude, J. & Strimmer, K. (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289–290.
- Pocock, M.J.O., Evans, D.M. & Memmott, J. (2012) The robustness and restoration of a network of ecological networks. *Science*, **335**, 973–977.
- Rasmussen, C., Dupont, Y.L., Mosbacher, J.B., Trøjelsgaard, K. & Olesen, J.M. (2013) Strong impact of temporal resolution on the structure of an ecological network. *PLoS ONE*, **8**, e81694.
- Rodríguez-Cabal, M.A., Barrios-García, M.N., Amico, G.C., Aizen, M.A. & Sanders, N.J. (2013) Node-by-node disassembly of a mutualistic interaction web driven by species interactions. *Proceedings of the National Academy of Sciences USA*, **110**, 16503–16507.
- Rumeu, B., Elias, R.B., Padilla, D.P., Melo, C. & Nogales, M. (2011) Differential seed dispersal systems of endemic junipers in two oceanic Macaronesian archipelagos: the influence of biogeographic and biological characteristics. *Plant Ecology*, **212**, 911–921.
- Schleuning, M., Blüthgen, N., Flörchinger, M., Braun, J., Schaefer, H.M. & Böhning-Gaese, K. (2011) Specialization and interaction strength in a tropical plant–frugivore network differ among forest strata. *Ecology*, **92**, 26–36.
- Schleuning, M., Böhning-Gaese, K., Dehling, D.M. & Burns, K.C. (2014) At a loss for birds: insularity increases asymmetry in seed-dispersal networks. *Global Ecology and Biogeography*, **23**, 385–394.
- Sebastián-González, E., Sandel, B., Dalsgaard, B. & Guimarães, P. (2015) Macroecological trends in nestedness and modularity of seed-dispersal networks. *Global Ecology and Biogeography*, **24**, 293–303.
- Stouffer, D.B. & Bascompte, J. (2011) Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences USA*, **108**, 3648–3652.
- Thébault, E. & Fontaine, C. (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, **329**, 853–856.
- Traveset, A., Heleno, R., Chamorro, S., Vargas, P., McMullen, C.K., Castro-Urgal, R., Nogales, M., Herrera, H.W. & Olesen, J.M. (2013) Invaders of pollination networks in the Galápagos Islands: emergence of novel communities. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20123040.

- Traveset, A., Olesen, J., Nogales, M., Vargas, P., Jaramillo, P., Antolin, E., Trigo, M. & Heleno, R. (2015) Bird–flower visitation networks in the Galápagos unveil a widespread interaction release. *Nature Communication*, **6**, 6376, doi: 10.1038/ncomms7376
- Valdovinos, F.S., Ramos-Jiliberto, R., Flores, J.D., Espinoza, C. & López, G. (2009) Structure and dynamics of pollination networks: the role of alien plants. *Oikos*, **118**, 1190–1200.
- Valido, A., Nogales, M. & Medina, F.M. (2003) Fleshy fruits in the diet of Canarian lizards *Gallotia galloti* (Lacertidae) in a xeric habitat of the island of Tenerife. *Journal of Herpetology*, **37**, 741–747.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Map of the Canarian archipelago.

Appendix S2 Map of the Galápagos archipelago.

Appendix S3 Main habitats along the elevation gradient represented in Canary Islands and the Galápagos.

Appendix S4 Modular seed–dispersal networks in the archipelagos of the Canaries and Galápagos.

Appendix S5 Detailed interaction network of the Canary Islands.

Appendix S6 Detailed interaction network of the Galápagos.

Table S1 Seed–dispersal interactions recorded in the Canary Islands.

Table S2 Seed–dispersal interactions recorded in the Galápagos archipelago.

Table S3 Phylogenetic signal for a set of traits in seed–dispersal communities in the Canary Islands and the Galápagos.

Table S4 Modular structure of the seed–dispersal network of the Canary Islands

Table S5 Modular structure of the seed–dispersal network of the Galápagos.

BIOSKETCH

Manuel Nogales works on the evolutionary ecology of island organisms, with a special interest in animal–plant mutualistic interactions. All the team has a wide experience in the ecology, evolution and biogeography of oceanic islands.

Author contributions: M.N., R.H., B.R. and J.O. conceived the ideas; All authors contributed to the network database; B.R. and J.O. analysed the data; M.N. and J.O. led the writing but all authors contributed to interpretation and writing.

Editor: Richard Field