



Global patterns of mainland and insular pollination networks

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ABSTRACT

Aim Interaction networks are being increasingly used to evaluate macroecological patterns. We explored a global dataset to identify differences in the structure of pollination networks from islands (of oceanic and continental origin) and mainlands. For oceanic islands, we further evaluated the effects of key island traits on network structural parameters.

Location Fifty-two quantitative plant–pollinator networks from continental islands ($n = 23$), oceanic islands ($n = 18$) and mainlands ($n = 11$) located world-wide.

Methods The effect of geographical origin upon network structure was explored by means of generalized mixed models, accounting for biogeographical region, sampling intensity, latitude and network size. For oceanic island networks, the influence of area, age, elevation and isolation was also evaluated.

Results The structure of pollination networks was fairly consistent between mainland and continental islands and only a few differences were noted. Oceanic island networks, however, were smaller and topologically simplified, showing a lower interaction diversity, and higher plant niche overlap than mainland and continental island networks. Isolation and elevational range of oceanic islands influenced the total number of species and interactions. Networks from higher-elevation oceanic islands were less nested and those located towards the equator exhibited higher interaction richness. Island area showed no significant effect on any of the network metrics studied here.

Main conclusions Pollination networks appear structurally similar regardless of their geographical origin. However, networks from continental islands are more similar to their mainland counterparts than to those from oceanic islands, probably due to the geological nature of continental islands, which are fragments of the mainland to which they were once connected. Oceanic island networks are the least species- and link-rich, and exhibit the lowest interaction diversity and the highest plant niche overlap, possibly due to lower pollinator richness. The most isolated and low-elevation islands show the simplest networks, and are thus probably the most vulnerable to pollination disruptions.

Keywords

Continental islands, ecological networks, macroecology, mutualistic networks, oceanic islands, plant–insect interactions, sampling effort.

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INTRODUCTION

In the last few years, the global ecology of natural complexity, expressed as ecological network analysis, has made important

advances (Schleuning *et al.*, 2012, 2014; Carstensen *et al.*, 2013; Dalsgaard *et al.*, 2013; Trøjelsgaard & Olesen, 2013; Trøjelsgaard *et al.*, 2013). However, insufficient data and inadequate data quality, as well as strong geographical heterogeneity, have

hampered this exciting development. Island network data are an example of the problems posed by geographical heterogeneity because these networks are very idiosyncratic in their complexity. This has been found for both pollination networks (Olesen & Jordano, 2002; Padrón *et al.*, 2009; Castro-Urgal & Traveset, 2014) and seed-dispersal networks (Kaiser-Bunbury *et al.*, 2010; González-Castro *et al.*, 2012; Heleno *et al.*, 2013; Schleuning *et al.*, 2014; Sebastián-González *et al.*, 2015).

By focusing on pollination interactions, we explore whether insular ecological networks differ in structure from their mainland counterparts. We distinguish between oceanic islands (formed over oceanic plates and never connected to continental landmasses) and continental islands (either ancient continental fragments or continental shelf islands, the latter being of more recent origin) (Whittaker & Fernández-Palacios, 2007). Our goal is to advance our understanding of how insularity may affect pollination patterns at the community level. Based on current knowledge of general island biogeography and the drivers of pollination network structure, we formulated a series of working hypotheses regarding differences between mainland and insular pollination networks (Table 1) and about the potential effect of specific oceanic island traits on network structure (Table 2).

Islands show a depauperate pollinator fauna due to the poor dispersal abilities of insects (e.g. Bernardello *et al.*, 2001; Gillespie & Roderick, 2002) and a lower immigration rate of pollinators compared with plants (Whittaker & Fernández-Palacios, 2007). For these reasons, island pollination networks usually have fewer interacting species and lower pollinator/plant ratios (e.g. Olesen & Jordano, 2002; Dupont *et al.*, 2003; Padrón *et al.*, 2009; Trøjelsgaard & Olesen, 2013) than mainland networks. Species-poor insect communities of islands also experience reduced interspecific competition compared with mainlands, which may cause density compensation in a few taxa, e.g. *Xylocopa darwinii* and *Mausoleopsis aldabraensis* (Linsley *et al.*, 1966; Woodell, 1979), and make the establishment of highly generalized species (super-generalists) easier in island than in mainland communities (Olesen *et al.*, 2002; Kaiser-Bunbury *et al.*, 2009; Padrón *et al.*, 2009; Traveset *et al.*, 2013). Therefore, characteristic imprints upon the topology of island pollination networks can be expected (see hypotheses in Table 1). The low species richness and high ('super') generalization level of some island species are likely to influence not only the diversity and asymmetry of pollination interactions but also the nested and modular patterns commonly found in networks (Bascompte *et al.*, 2006; Olesen *et al.*, 2007). Density compensation promotes highly skewed species abundances, thus lowering the evenness of interactions, particularly on small or isolated islands (Sabatino *et al.*, 2010; Trøjelsgaard & Olesen, 2013). In turn, reduced evenness might lead to high nestedness (i.e. a pattern in which specialist species link to a subset of species with which generalists also interact) if interactions are mainly driven by species abundances (Bascompte & Jordano, 2007). High nestedness might also be a result of few species-specific interactions and thus low evolutionary specialization (Hagen *et al.*, 2012). Owing to higher species generalization

levels, and to the presence of super-generalists, we might also expect island networks to show comparatively higher connectance and nestedness, but lower modularity (Fortuna *et al.*, 2010) (i.e. a pattern in which species are organized into densely linked groups with sparse connections between groups) than on mainlands.

Additionally, the structure of plant–pollinator interactions on islands is likely to be influenced by different island traits (see hypotheses in Table 2), but only a few studies have so far examined this. Trøjelsgaard *et al.* (2013) found island area and age to be important predictors of plant and pollinator species richness, interaction richness and specialization levels. Sugiura (2010) reported a significant effect of island area on the structure of networks between ants and extrafloral nectar-bearing plants; specifically, connectance, nestedness and asymmetry of interactions were found to decrease with island area. Larger, higher-elevation islands are expected to sustain more habitats and, thus, to be richer in species and interactions than smaller islands of lower elevation. Nestedness might decrease with island age, as there is more time for co-evolution to occur, and generate more interactions between specialists. Likewise, young islands are likely to support less modular communities due to the lower diversity and higher generalization favoured in the colonization of species-poor environments, becoming increasingly modular with island age (the number of modules might increase as more specific interactions evolve and new niches develop). Likewise, highly isolated islands might have different pollinator/plant ratios and thus different asymmetries or interaction specializations from islands closer to mainlands, as found for seed-dispersal networks (Schleuning *et al.*, 2014).

The predictions outlined above were tested by compiling a large dataset of quantitative pollination networks, gathered from mainland sites, continental islands and oceanic islands. To our knowledge, this represents the largest compilation of island network data so far.

METHODS

Datasets

We compiled 52 quantitative (i.e. weighted) pollination networks, from the published scientific literature, several non-published studies and open-access databases (Interaction Web Database, Web of Life: ecological networks database, DRYAD and datasets included in the R package bipartite). The datasets were widely distributed (latitude 41° S–82° N, longitude 91° W–149° E) and included 11 mainland sites, 23 continental islands and 18 oceanic islands world-wide (Fig. 1, Table S1 in the Supporting Information). For each network we obtained: (1) location (including biogeographical region, following the Takhtajan (1986) categorization, country and archipelago), (2) latitude, (3) elevation of the study site, (4) sampling method (timed focal flower observations or transect observations), (5) sampling intensity (measured as the ratio between the square-root number of observed interaction events and the geometric mean of number of plant and animal species; Schleuning *et al.*, 2014),

Table 1 Testing 12 hypotheses (H1–H12) regarding the relationship between mainland (M) and island pollination networks (OI, oceanic islands; CI, continental islands). The ‘assumption’ and ‘prediction’ columns are always outlined regarding expected traits of islands when compared with mainlands. In all models, the fixed parameters were: geographical origin (mainland, continental, oceanic); latitude (in degrees); sampling intensity (ratio between the square root of the number of observed interaction events and the square root of the geometric mean of number of plant and animal species; Schleuning *et al.*, 2014); and network size (number of plant species times number of animal species) (except for H1). Archipelago (for island networks) and country (for mainland networks), nested within biogeographical region, was included as a random factor in all models in order to account for pseudo-replication (see text). Estimates of the predictor variables for each response variable can be found in Table S4.

Hypothesis (islands compared with mainlands)		Model		Confirmation of prediction	Figure 2*
Assumption	Prediction	Response variable	Significant fixed predictors		
H1 Species poverty [1]	Smaller networks	A + P	Geographical origin, latitude	Yes (only OI)	A
H2 Species poverty [1]	Fewer interactions	I	Geographical origin, network size	Yes (only OI)	B
H3 Smaller networks and presence of generalized colonizers → condensed networks [1, 2]	Higher connectance	C	Geographical origin, network size	No	C
H4 Poor dispersal abilities of insects compared with plants [3]	Higher network symmetry	A:P ratio	Sampling intensity, network size	No	D
H5 Reduction of pollinator tail in nested networks → more symmetric networks [4, but see 5]	Higher niche overlap among plants	PNO	Geographical origin	Yes (only OI)	E
H6 Reduction of pollinator tail in nested networks → more symmetric networks [4, but see 5]	Lower niche overlap among pollinators	PONO		No	F
H7 Density compensation → more skewed abundance distribution → presence of super-generalists [6]	Higher interaction asymmetry	IA		No	G
H8 Species poverty, density compensation → more skewed abundance distribution → presence of super-generalists, fewer species and interactions [7]	Lower interaction diversity	H	Geographical origin, sampling intensity, network size	Yes (only OI)	H
H9 Species and link poverty, density compensation → more skewed abundance distribution → presence of super-generalists, fewer species and interactions [7]	Lower interaction evenness	IE	Sampling intensity	No	I
H10 Presence of generalist colonizers and super-generalists	Lower interaction specialization	H'_2		No	J
H11 Higher connectance, more skewed abundance distribution → more structured networks [H3]	Higher nestedness	WNODF		No	K
H12 Higher connectance and nestedness → less heterogeneity in networks (H3, H11) [9]	Lower modularity	M		No	L

*Indicates which panel in Figure 2 displays the results.

Response variables: A + P, number of pollinator and plant species = species richness; I, total number of interactions; C, network connectance = $I/(A \times P)$; PNO, plant niche overlap; PONO, pollinator niche overlap; IA, interaction asymmetry; H, interaction diversity; IE, interaction evenness; H'_2 , network specialization; WNODF, weighted nestedness; M, modularity.

References: [1] Whittaker & Fernández-Palacios (2007); [2] Castro-Urgal & Traveset (2014); [3] Bernardello *et al.* (2001); [4] González-Castro *et al.* (2012); [5] Schleuning *et al.* (2014); [6] Olesen *et al.* (2002); [7] Trøjelsgaard & Olesen (2013); [8] Sabatino *et al.* 2010; [9] Fortuna *et al.* (2010).

Network descriptor	Predictor trait expectations		
	Isolation	Elevational range	Latitude
Number of species	↓ [1,3] ✓	↑ [1,8–10] ✓	↓ [3,13]
Number of links	↓ [1,2] ✓	↑ [1,8–10]	↓ [3,13]
Connectance (C)	↑ [1,3]	↓ [1,8–10]	↑
Interaction diversity (H)	↓ [1,2, 6,7]	↑ [1,8–10]	↓ [3,13]
Interaction evenness (IE)	↓ [3,6,9]	?	?
Network specialization (H_2')	↑ [7]	?	↓
Interaction asymmetry (IA)	↑ [6,7]	?	?
Animal/plan ratio (A:P)	↓ [3,6,7]	?	?
Plant niche overlap (PNO)	?	?	?
Pollinator niche overlap (PONO)	?	?	?
Weighted nestedness (WNODF)	↑ [10,11]	↓ [11] ✓	↓ [13]
Modularity (M)	↑ [12]	↑ [12]	↓ [13]

[1] MacArthur & Wilson (1967); [2] Whittaker & Fernández-Palacios (2007); [3] Trøjelsgaard & Olesen (2013); [4] Bernardello *et al.* (2001); [5] Gillespie & Roderick (2002); [6] Olesen *et al.* (2002); [7] Schleuning *et al.* (2014); [8] Triantis *et al.* (2008); [9] Sabatino *et al.* (2010); [10] Sugiura (2010); [11] Hagen *et al.* (2012); [12] Fortuna *et al.* (2010), [13] Sebastián-González *et al.* 2015.

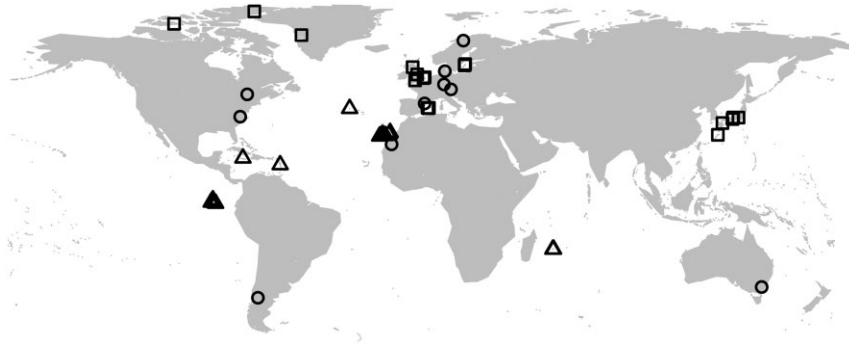


Table 2 Hypotheses about the association between oceanic island traits and descriptors of pollination network structure. Upward and downward arrows indicate, respectively, an expected increase or decrease of the network descriptor following an increase of the predictor trait. The cases where no particular expectation exist are indicated by '?'. In others (arrows with no references) we make predictions though they are not based on published information. Numbers in square brackets are the references (given below the table) on which our expectations are based, when they exist. The ✓ symbol indicates that the hypothesis has been confirmed with our data (see Fig. 3).

Figure 1 Distribution of the 52 pollination networks used in the study. A list of all networks and their characteristics is given in Table S1. Different symbols indicate the different geographical origins for each network: mainland networks (circles), continental island networks (squares) and oceanic island networks (triangles).

and (6) the type of quantitative information available (i.e. number of visits, number of visits per unit time or number of individuals captured). Additionally, each oceanic island was characterized by (1) area, (2) age, (3) altitudinal range, and (4) two estimates of isolation (distance to the mainland and distance to the nearest island) (see Table S2). Data on the number of habitats per island were not available; however, this has been shown to be highly correlated with island elevation ($r = 0.90$, $P < 0.001$, $n = 30$ island groups) and area ($r = 0.42$, $P < 0.001$, $n = 30$; Kueffer *et al.*, 2010).

The dataset was highly heterogeneous with respect to the above-mentioned characteristics (Table S1), and it was thus impossible to include all sources of heterogeneity in the analyses. For some studies encompassing different localities or sampling plots within the same landscape unit, observations were pooled in order to avoid pseudo-replication. While pooling data from nearby sites might have a slight influence on some network metrics, it did not affect the comparisons as such pooling was done for a similar number of island and mainland studies (see Results). Networks from different islands were kept as separate networks even if they belonged to the same archipelago.

When comparing ecological networks, it is crucial to consider the potential effect of different sampling efforts on the construction of each dataset (Chacoff *et al.*, 2012; Rivera-Hutinel *et al.*, 2012), as this is usually related to the number of plant and animal species, links (= interactions) and interaction frequencies in the network (Banasek-Richter *et al.*, 2004). We accounted for sampling effort using the estimate proposed by Schleuning *et al.* (2014), i.e. 'sampling intensity' defined as the ratio between the square root of the total number of visits (interaction events) and the square root of network size. This estimate reflects the number of visits per species taking into account that relatively more observations are required in species-rich than in species-poor environments. We found this estimate of sampling effort to be highly correlated ($r > 0.80$, $P < 0.01$) with the 'detection' value (percentage of asymptotic interaction richness detected estimated with the Chao2 index; Chacoff *et al.*, 2012). The number of observation hours per plant could have been used as an alternative measure of sampling effort. However, such a measure was not available for many networks and it was less correlated with the detection value than sampling intensity. Different sampling methods can also potentially affect some network

descriptors such as the proportion of singletons, although they do not seem to affect properties such as connectance or nestedness (Gibson *et al.*, 2011). The vast majority of networks in our dataset were sampled by performing timed observations at focal flowering plant individuals (i.e. plant-centred census), although some studies used the fixed transect method (Table S1). Because both methods have been applied on islands and continents we did not control for sampling method in our analyses.

Many networks included alien species. Considering only plants (as information on the origin of pollinators is largely unknown for most networks), an average of 6.9% (SD 10.2%) of the species in each network were aliens. Only in three networks did aliens comprise more than a third of the plant community, namely Kyoto City (38%), Patagonia (36%) and Ile aux Aigrettes (36%) (Table S1). The vast majority of datasets had fewer than 10% of alien plants, and there were no significant differences in the proportion of alien plants between mainland and island networks (mean mainland = 8.7% versus mean islands = 5.9%; $F_{1,50} = 0.92$, $P = 0.34$; Appendix S2). Therefore, we did not include species origin in the models.

It is important to note that despite being called ‘pollination networks’ they are all flower-visitation networks, as information regarding the effectiveness of each flower visitor is lacking. In this sense, interaction frequency is considered as a rough estimate of the importance of each pollinator species (see Schleuning *et al.* (2014) for a similar approach in the analysis of seed-dispersal networks). This assumption is supported by the direct relationship between interaction frequency and effective pollination (Vázquez *et al.*, 2005).

Network metrics and statistical analyses

We selected 12 metrics describing network structural features: *species* and *interaction richness*, *connectance* (i.e. realized proportion of possible links), *pollinator/plant ratio*, plant and animal *niche overlap* (i.e. similarity in the interaction pattern between species of the same trophic level), *interaction strength asymmetry* (i.e. difference in the dependence of animals on plants and vice versa; this metric is corrected for network asymmetry; see Appendix S1), *interaction diversity* (i.e. Shannon diversity, a measure of the complexity of associations in the entire network), *interaction evenness* (skewness in the distribution of interaction weights), *complementary specialization H_2'* (i.e. a measure of how selective the species in the network are by quantifying how the observed interactions depart from a theoretical random distribution of interactions driven by species abundances), *weighted nestedness* (i.e. specialists interact with a subset of the species interacting with generalists) and *modularity* (i.e. the existence of semi-independent groups of highly interacting species). A complete definition of all metrics is given in Appendix S1.

Network metrics were computed for all 52 networks using the package ‘bipartite’ v.2.00 (Dormann *et al.*, 2009) in R v.3.1.0 (R Development Core Team, 2014), the software *NODF* v.2.0 (Almeida-Neto & Ulrich, 2011; <http://www.keib.umk.pl/nodf/>) for the calculation of weighted nestedness based on

overlap and decreasing fill (WNODF) and the software *NETCARTO* (Guimerà & Amaral, 2005) for the computation of modularity.

We used generalized linear mixed models (GLMMs) to test for differences in the above-mentioned metrics among mainlands, continental islands and oceanic islands. The fitted models, one for each metric as a response variable, included geographical origin as the explanatory variable (a factor with three levels: mainland, continental island and oceanic island) and network size, sampling intensity and latitude as covariates. These covariates were included because different network metrics are influenced by network size (e.g. Bascompte *et al.*, 2006; Olesen *et al.*, 2007) and also by sampling intensity and latitude (Schleuning *et al.*, 2012, 2014; Trøjelsgaard & Olesen, 2013). Initial analyses showed that neither sampling intensity nor latitude differed significantly between islands and mainlands ($F_{1,2} = 0.85$, $P = 0.44$, and $t = 1.08$, $P = 0.29$, respectively), but that networks from oceanic islands tended to be sampled more from lower latitudes than continental ($t = 7.10$, $P < 0.001$) and mainland networks ($t = 4.80$, $P < 0.001$). Archipelago (for island networks) or country (for mainland networks), both nested within biogeographical region (see Table S1), were included in the models as random factors to prevent any effect of pseudo-replication. Two response variables, species and link richness, included count data, and were thus assumed to follow a Poisson distribution, approached by a log link function in the GLMMs (Zuur *et al.*, 2009). The remaining variables (all continuous) followed normal distributions and were approached by the identity link function. Data on the probability of having a significantly modular structure were also compared between islands and mainlands and were fitted to a binomial distribution (‘1’ for significant versus ‘0’ for non-significant). For those metrics in which geographical origin showed a significant effect in the model, a likelihood ratio test was performed to assess the overall effect of this predictor. Contrasts among levels of geographical origin were made by using the ‘relevel’ function.

A second set of models were performed using data from the 18 oceanic islands. Multiple model selection was conducted to determine which island traits may affect network structure. The island traits that were considered as potential predictor variables in the models were: area, age, elevational range, latitude and two complementary measures of isolation (distance to the nearest continent and distance to the nearest island) (Table S2). In these models, network size was also included as a covariate, whereas archipelago – nested within biogeographical region – was a random factor. Sampling intensity did not differ across the 18 networks ($F_{1,13} = 1.25$, $P = 0.34$), so it was not added in the models to avoid over-parameterization. A variation inflation factor (VIF) analysis showed that island age and island area should not be put together as predictors in the models due to strong collinearity. Area and elevational range were positively associated, although not significantly so ($r = 0.39$, $P = 0.11$). After removing age from the models, all VIF values were less than two, indicating low collinearity among all predictors (Zuur *et al.*, 2009). The Akaike information criterion corrected for

small sample size (AICc) was used to select the best models (those with the lowest AICc values) for each metric (Zuur *et al.*, 2009). Residuals were not overdispersed, thus refitting the data with other model families was not necessary (Bolker *et al.*, 2009). To evaluate the level of empirical support for a given model, we further assessed whether it differed from that of the null model (including only the intercept). Models differing by more than two in their AIC value compared with the best model were among the most parsimonious models (Burnham & Anderson, 2002). Moreover, Akaike weights (wAICc) were calculated to provide a standardized measure of the strength of evidence in favour of the focal model relative to the others, comparing them on a scale ranging from zero to one.

All GLMMs were performed using the package lme4 v.1.1-7, whereas model selection with the oceanic island dataset was done using the dredge function in the package MuMIn (multi-model inference) v.1.10.5 in R v.3.1.0 (R Development Core Team, 2014).

RESULTS

Overall, the dataset encompassed 19,041 plant–pollinator species interactions, with an average of 366 interactions (minimum 30, maximum 1875) per network. The pollinators were mostly insects, although a few networks also included birds and reptiles (mainly in oceanic island networks, e.g. the Galápagos). Values of all network parameters are summarized in Table S3.

Differences in network metrics between mainland and the two types of islands

Table 1 summarizes which predictors were statistically significant in each model. Figure 2 displays the average of the analysed metrics for mainland, continental and oceanic networks, respectively. More detailed results of the statistical models, including the effects of each predictor, are presented in Tables S4 & S6.

The total number of species and links was significantly lower in networks from oceanic islands compared with networks from continental islands or mainlands. There was only a marginally significant difference between mainlands and continental islands in the number of species and no difference in the number of links (Fig. 2a,b). The overall effect of geographical region on these two variables was significant in a likelihood ratio test ($\chi^2 = 8.50$ and $\chi^2 = 8.33$, respectively; $P < 0.01$). The effect of geographical origin on connectance was also significant ($\chi^2 = 6.47$, $P = 0.04$), but not in the expected direction: continental islands showed lower values than networks from either mainlands or oceanic islands, although the latter two did not differ significantly (Fig. 2c). Contrary to our expectation, the pollinator/plant (A:P) ratio showed similar values for mainland and island networks (Fig. 2d). Plant niche overlap was higher on oceanic islands than on mainlands or continental islands, although the effect of geographical origin was only marginal ($\chi^2 = 5.01$, $P = 0.08$), and the latter two did not differ (Fig. 2e).

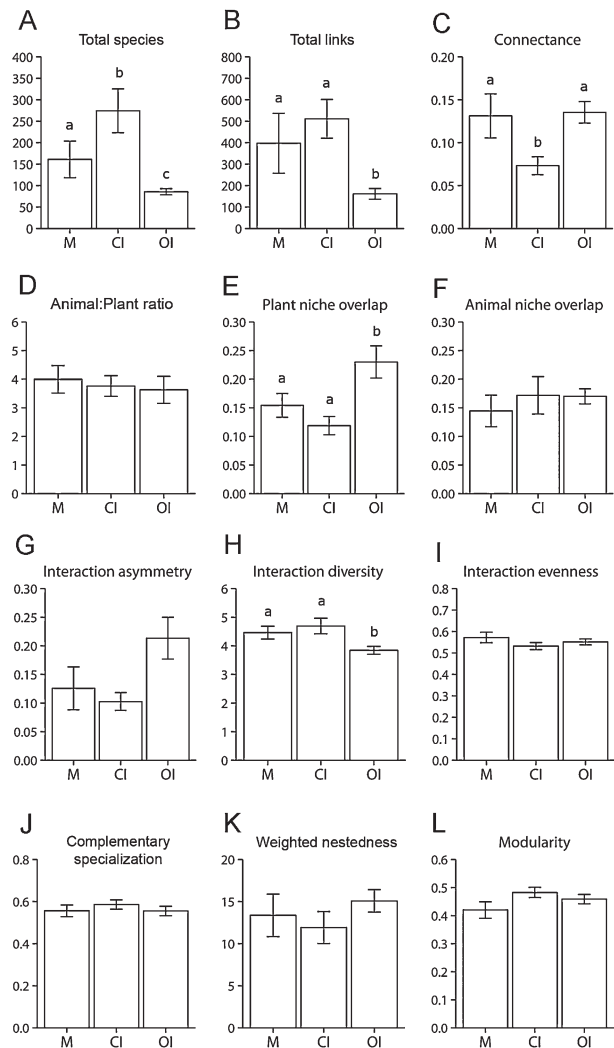


Figure 2 Differences between mainlands (M), continental islands (CI) and oceanic islands (OI) in structural network descriptors. Mean and standard error bars are given. For the metric ‘interaction asymmetry’, corrected values are shown, i.e. accounting for network asymmetry (Blüthgen *et al.*, 2007). For each metric, bars with the same letter above indicate no significant differences ($P > 0.05$). In two cases, however, differences are only marginal (see text). Model results for each parameter are given in Table S4.

Animal niche overlap, by contrast, was similar among mainland and islands (Fig. 2f). Interaction asymmetry tended to be higher on oceanic islands than on mainlands or continental islands, though differences were not significant (Fig. 2g). Values were positive in all networks except one (network *ia*, Table S1), indicating that animals are usually more dependent upon plants than vice versa.

A significant effect of geographical origin was found on interaction diversity ($\chi^2 = 6.47$, $P = 0.04$), with oceanic islands showing lower values than either continental islands or mainlands, although differences were small (Fig. 2h). On the other hand, interaction evenness, network complementary specializa-

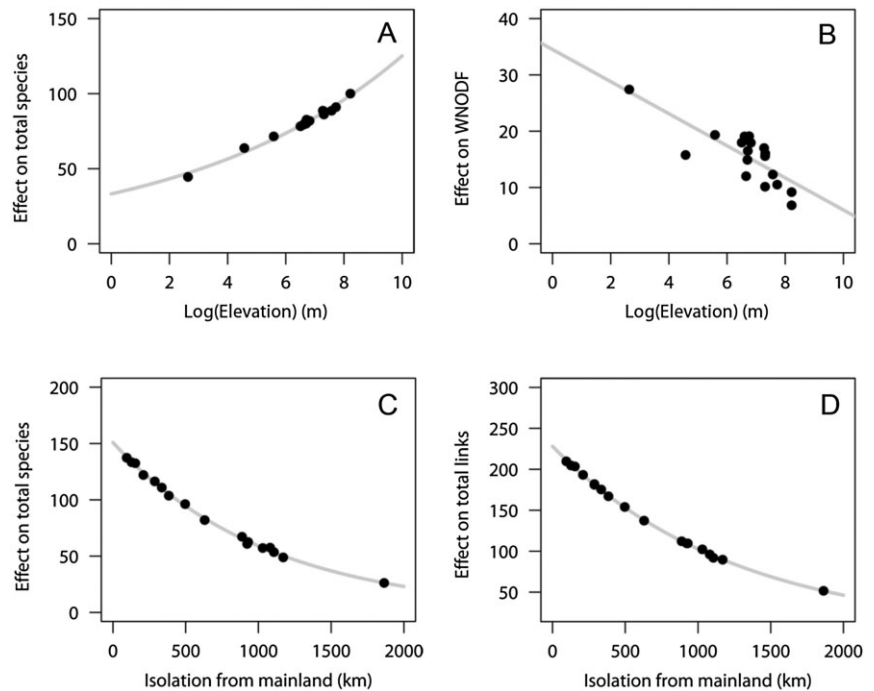


Figure 3 Relationship between oceanic island traits and pollination network metrics found in our study. The lines in each graph represent the effect of each predictor variable (X axis) on the response variable (Y axis) when holding other model predictors at constant mean values, whereas circles represent the partial residuals. See models in Table S5. Weighted nestedness based on overlap and decreasing fill (WNODF).

tion (H_2'), WNODF and modularity (M) were not significantly different among networks from different geographical origins (Fig. 2i–l); the probability that M differed significantly from that in randomized networks was also unrelated to geographical origin ($P > 0.05$; Table S4).

Oceanic island traits associated with pollination network descriptors

Only a few network descriptors (number of species, number of links and WNODF) were influenced by oceanic island traits. The most parsimonious models are listed in Table S5. Elevational range was the strongest predictor of species richness, and was negatively related to nestedness (i.e. islands with a higher elevation had larger networks with lower nestedness values (Fig. 3a,b). Isolation had a negative effect on both network size and the number of interactions, so that networks from more isolated islands had fewer species and interactions (Fig. 3c,d). Distance to the nearest island also showed a slight positive effect on species richness (Table S5); however, such an effect disappeared when two outliers (Jamaica and Mauritius, with very long distances to the nearest island compared with the other islands within archipelagos in the dataset; Table S2) were removed from the analysis. Although latitude was not selected as a predictor in the best model it was included in the second best model, and the difference in AICc between these two models was only 2.2 (i.e. they are almost similarly good models). The negative estimate ($\beta = -0.002$) indicated that the number of links decreased with latitude, i.e. tropical islands showed more links than islands in temperate and boreal regions. On the other hand, and contrary to expectations, island area had no influence on any of the network metrics studied here.

DISCUSSION

Macroecological patterns in pollination networks

Our analyses supported only some of the hypotheses listed in Table 1. Oceanic islands were poorer in species and links than continental islands and mainlands, as expected given their higher isolation from mainland masses which act as a major barrier to the arrival of many plant and animal species (e.g. Bernardello *et al.*, 2001; Gillespie & Roderick, 2002). Such lower species and interaction richness might actually translate into a reduced pollinator redundancy (see, however, Rasmussen *et al.*, 2013), potentially leading to systems that are more vulnerable to disturbances. Moreover, the probability of ‘rewiring’ – linking to new species in the case of species extinction – might also be reduced. On the other hand, plant niche overlap was greater on oceanic than on continental islands or mainlands, although this was not the case for pollinators. A wider plant niche overlap on oceanic islands might be attributed to the relatively smaller number of pollinators in the communities. However, this result does not support previous findings of more specialized plants on islands (Olesen & Jordano, 2002), and deviation might arise because Olesen & Jordano (2002) pooled data from continental and oceanic islands. Plants on oceanic islands usually have high levels of generalization, making them less susceptible to the loss of any particular pollinator species (Traveset *et al.*, 2013). Some plant species can even be super-generalists (acting as hubs in the network, i.e. interacting proportionally more with pollinators than other species). This is the case, for instance, with *Opuntia* spp. in the Galápagos (Traveset *et al.*, 2013) or the Canary Islands (Padrón *et al.*, 2009). Finally, the diversity of interactions was lowest on oceanic islands compared with continental islands

and mainland, probably reflecting their lower species and interaction richness.

Geographical origin only affected 5 out of the 12 metrics of network structure studied. Continental island networks were more similar than expected to mainland ones in species and link richness and in diversity of interactions, possibly related to the geological nature of continental islands which are fragments of the mainland to which they were once connected. Previous studies have reported higher connectance on islands than on mainlands (González-Castro *et al.*, 2012) or higher connectance on oceanic islands compared with continental islands (Castro-Urgal & Traveset, 2014; but see Padrón *et al.*, 2009, where no differences were revealed). However, our results showed no differences between mainlands and oceanic islands and a slightly lower connectance for continental islands when accounting for network size. We only found a slightly, and non-significant, lower A:P ratio on oceanic islands than on either continental islands or mainland networks. A lower A:P ratio in islands has previously been reported (Olesen & Jordano, 2002; Dupont *et al.*, 2003; Padrón *et al.*, 2009; Trøjelsgaard & Olesen, 2013) and has been attributed to the depauperate pollinator fauna due to the poor ability of insects to disperse to islands (e.g. Bernardello *et al.*, 2001; Gillespie & Roderick, 2002). Likewise, despite oceanic island networks showed a higher average interaction asymmetry than networks from mainlands and continental islands, differences were non-significant. The consistent positive values of this parameter indicate that animals are more dependent upon plants than vice versa (Blüthgen *et al.*, 2007). Moreover, the higher interaction asymmetry values of oceanic island networks suggest that their pollinators are more dependent on plants than pollinators on continental islands or mainlands (Kaiser-Bunbury *et al.*, 2010). Interaction asymmetry has been reported to increase with insularity in seed-dispersal networks (Schleuning *et al.*, 2014) due to lower species richness and niche expansion in island biota (Thornton, 2007; Kaiser-Bunbury *et al.*, 2010). However, Canarian seed-dispersal networks are more symmetric than mainland ones (González-Castro *et al.*, 2012), and consequently more data are needed to reach a consensus. Schleuning *et al.* (2014) also found negative values for this metric, indicating that island plants are more dependent on particular frugivores than vice versa. In that study, the high asymmetry in island networks – especially isolated islands – was attributed to a higher susceptibility to human-caused extinctions, especially in islands that have suffered from the loss of many frugivorous species (Schleuning *et al.*, 2014). Interaction asymmetry has been associated with functional stability of ecological networks, i.e. with their resilience to disturbances, such as species loss (Bascompte *et al.*, 2006; Blüthgen, 2010). However, strong asymmetries also imply high dependences of one interacting group on another (Schleuning *et al.*, 2014) and it is therefore difficult to generalize about the relationship between asymmetry and network resistance to species loss. Functional disruptions, due to a non-random loss of pollination interactions, have been documented in fragmented landscapes on mainland ecosystems (Aizen *et al.*, 2012) and are likely to occur in oceanic islands as well, where

super-generalist pollinators are a prevalent phenomenon (e.g. Olesen *et al.*, 2002; Traveset & Richardson 2006, Traveset *et al.*, 2013). The loss of such network hubs from pollination communities can probably have severe detrimental consequences for the reproduction of many plant species, although for most oceanic archipelagos there is still very little information available to detect those effects.

Both interaction evenness (IE) and complementary specialization showed consistent moderate values (IE \approx 0.5–0.6 and $H_2' \approx$ 0.6) in the two types of islands and mainlands. Comparable values of evenness have been reported for seed-dispersal networks (Plein *et al.*, 2013; Schleuning *et al.*, 2014); however, our H_2' values were twice as high, indicating that frugivores are less selective in their resource use (i.e. they interact with plant species that are abundant in the community) than pollinators (González-Castro *et al.*, 2012; Heleno *et al.*, 2013).

The lack of differences in WNODF between mainland and island networks suggests that the incidence of evolutionary specialization of pollination interactions is unrelated to geographical origin (Hagen *et al.*, 2012). Furthermore, contrary to our expectations, island and mainland networks were similarly modular, which is probably associated with the similar connectance across networks with different geographical origins. We did not detect any effect of latitude on the level of modularity, contradicting the findings by Trøjelsgaard & Olesen (2013) for pollination networks but in agreement with other studies (Dalsgaard *et al.*, 2013; Sebastián-González *et al.*, 2015) on seed-dispersal networks. While modularity seems to be a highly informative and promising feature in our efforts to understand community structure, much work is still needed to clarify the drivers of module formation for different ecosystems.

In short, the macroecological patterns found in this review confirm the greater simplicity of pollination networks from oceanic islands, whereas networks from continental islands share more features with mainland communities than with 'true' oceanic islands. This must be taken into account when making generalizations about the ecological complexity of islands (*sensu lato*), as this is contingent upon their history and geology. Previous network review studies have pooled data from different kinds of island systems (Olesen & Jordano, 2002; Trøjelsgaard & Olesen, 2013; Schleuning *et al.*, 2014) which may have blurred important variation. For future comparative studies we therefore recommend distinguishing between different types of islands. In addition, we should be highly selective when comparing networks for future analyses and consider only those studies with high-quality data, i.e. with a minimum sample size (number of species in the network) and a minimum sampling completeness (proportion of the interactions detected out of all those possible). Sampling methodologies should ideally be standardized, as they may influence network structure. We often found more variation within categories of geographical origin than among them, and one possible reason for this is the wide variation in sampling methods used in each of the reviewed studies. The spatial and temporal scales of the study must also be considered in such comparative studies. Usually, the networks compared are operating simultaneously at different spatial and

temporal scales, which confers heterogeneity and thus reduces the strength of the study (see Appendix S3 for further details on caveats to be considered when comparing interaction networks at a macroecological level).

Influence of oceanic island traits on the structure of pollination interactions

We confirmed that increasing isolation from mainlands leads to smaller island networks and fewer interactions, but we found no association between isolation and other network descriptors. Elevational range positively influenced the total number of species in the network. This is probably because elevation is highly associated with habitat diversity, and thus with species richness (Kueffer *et al.*, 2010). However, why elevational range was not related to the number of links requires further examination. Oceanic islands with higher elevations had lower nestedness values, consistent with results from other studies (Hagen *et al.*, 2012), indicating that their species interactions are less hierarchically organized, and might thus be less stable, than on less diverse and flat islands. High nestedness values have been positively related to network stability (Bascompte *et al.*, 2006), although there is much debate about this (e.g. James *et al.*, 2012). Our findings that altitude does not influence complementary specialization are also consistent with those reported by Benadi *et al.* (2014). Finally, the number of interactions increased towards the tropics, as also reported in other network studies (Trøjelsgaard & Olesen, 2013; Sebastián-González *et al.*, 2015).

In contrast to our expectations, island area was not included in any of the best models predicting network metrics. A negative effect of island area on connectance, nestedness and interaction asymmetry has been reported by Sugiura (2010) for ant–plant networks in the Bonin Islands. Trøjelsgaard *et al.* (2013), on the other hand, found a positive effect of island area on plant and pollinator richness in the Canary Islands. On the contrary, Schleuning *et al.* (2014) found island area to be irrelevant for the diversity and asymmetry of seed-dispersal networks at a macroecological level. Collectively, this suggests that the expected associations between area and network metrics are more difficult to document in large-scale meta-analyses.

In conclusion, the overall structure of pollination networks was not found to differ as much as expected based upon their geographical origin. However, networks from oceanic islands tend to be simpler than those from either continental islands or mainlands. Oceanic islands bear smaller networks, with relatively fewer and less diverse interactions, and show higher plant niche overlaps, possibly owing to lower pollinator richness. By contrast, the pollination networks found on continental islands are more similar to those on the mainlands from which they have originated. Elevation in oceanic islands appears to be a good predictor of species richness and nestedness, potentially providing stability to the pollinator community, i.e. islands of higher elevation might be more stable. According to our findings, isolated and low-elevation oceanic islands would tend to bear the simplest networks, which indicates that they might be the ones most influenced by pollination disruption.

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Additional references to the data sources used in this study can be found after Table S1 at [URL].

SUPPORTING INFORMATION

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

Table S1 Quantitative pollination networks used in this study, with information on sampling location and the type of data collected.

Table S2 Island traits used as predictors of metrics describing the pollination network of oceanic islands.

Table S3 Metrics describing of 52 pollination networks used in this study.

Table S4 Summary of the models predicting the effect of different factors on metrics describing pollination network structure.

Table S5 Effects of oceanic island traits on the structure of pollination networks.

Table S6 Summary of the models predicting the effect of different factors on metrics describing pollination network structure, treating Jamaica as a continental island.

Appendix 1 Definitions of the metrics used in this study to describe network structure.

Appendix 2 List of databases consulted to gather information on the percentage of alien plant species in each network.

Appendix 3 Caveats to be considered when comparing studies on mutualistic networks at the macroecological scale.

BIOSKETCHES

Anna Traveset, Ruben Heleno and Jens M. Olesen

investigate mutualistic interactions in mainland and island ecosystems in both temperate and tropical zones. They are especially interested in unravelling the mechanisms by which drivers of global change influence patterns of species interactions. **Kristian Trøjelsgaard** focuses his research on the spatial and temporal variation of ecological networks with a special emphasis on pollination networks. **Cristina Tur** and **Rocío Castro-Urgal** are working on their PhDs, studying patterns of pollination networks in island ecosystems from different perspectives.

Author contributions: A.T. and J.M.O. planned the project; A.T. and R.H. compiled the database; A.T. and C.T. analysed the data; K.T., C.T. and R.C. contributed with valuable unpublished data; A.T. led the writing, with important contributions from the rest of authors.

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