Global Ecology and Biogeography



Macroecology of pollination networks

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ABSTRACT

Aim Interacting communities of species are organized into complex networks, and network analysis is reckoned to be a strong tool for describing their architecture. Many species assemblies show strong macroecological patterns, e.g. increasing species richness with decreasing latitude, but whether this latitudinal diversity gradient scales up to entities as complex as networks is unknown. We investigated this using a dataset of 54 community-wide pollination networks and hypothesized that pollination networks would display a latitudinal and altitudinal species richness gradient, increasing specialization towards the tropics, and that network topology would be affected by current climate.

Location Global.

Methods Each network was organized as a presence/absence matrix, consisting of *P* plant species, *A* pollinator species and their links. From these matrices, network parameters were estimated. Additionally, data about geography (latitude, elevation), climate at the network site (temperature, precipitation) and sampling effort (observation days) and extent (study-plot size) were gathered. Analyses were done using simultaneous autoregressive modelling (SAR).

Results Species richness did not vary strongly with either latitude or elevation. However, network modularity decreased significantly with latitude whereas mean number of links per plant species (L_p) and A/P ratio peaked at mid-latitude. Above 500 m a.s.l., A/P ratio decreased and mean number of links per pollinator species (L_a) increased with elevation. L_p displayed mid-ambient peaks with temperature and nestedness and modularity displayed linear relationships with precipitation.

Main conclusion Pollination networks showed macroecological patterns. No strong latitudinal or altitudinal gradient in species richness was observed. L_p and the A/P ratio peaked at mid-latitude whereas modularity decreased linearly. Both patterns are suggestive of a more specialized interaction structure towards the tropics. In particular, mean annual precipitation appeared influential on network topology as both nestedness and modularity varied significantly. Importantly, corrected regressions suggest that neither sampling effort nor extent affected the observed patterns.

Keywords

Climate change, ecological networks, geographical gradients, macroecology, pollination, sampling effort, species interactions.

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INTRODUCTION

Besides number of species, biodiversity also encompasses the interactions among species (Hooper *et al.*, 2005; Tylianakis

that has grown considerably in popularity during the last couple of decades (Ings *et al.*, 2009). In particular, it allows us to go

et al., 2010), and ecological network analysis is a powerful way to

analyse species and their interactions as an entity - an approach

beyond the sheer numbers involved in biodiversity and look into its detailed structure. In ecological networks, species are connected through various kinds of linkage, e.g. antagonistic (e.g. predation) or mutualistic (e.g. pollination) links (Memmott, 1999; Dunne et al., 2002; Woodward et al., 2005). Among mutualistic networks, pollination networks are the most intensively studied. They show distinct link patterns such as nestedness (Bascompte et al., 2003) and modularity (Olesen et al., 2007). If nested, specialist species link to a subset of species with which generalists also interact, and if modular, species are organized into modules with their linkage pattern being more dense within than between modules. Furthermore, pollination networks show strong temporal dynamics (Alarcón et al., 2008; Olesen et al., 2008; Petanidou et al., 2008; Dupont et al., 2009), small world properties (Olesen et al., 2006), link asymmetry (Bascompte et al., 2006) and a skewed distribution of links (few species have many interactions and many have few) (Jordano, 1987). Thus, several regularities characterize pollination networks and much attention has been assigned to the study of these

In the analysis of ecological networks sampling effort has received much attention (Goldwasser & Roughgarden, 1997; Martinez *et al.*, 1999; Banasek-Richter *et al.*, 2004). Numbers of species and their links are particularly sensitive to undersampling, although other network properties appear resilient (Nielsen & Bascompte, 2007; Hegland *et al.*, 2010). Thus, comparative network studies have to take variation in sampling effort into account.

As disciplines, biogeography and macroecology focus upon individual species, higher taxa and regional biota (Currie, 1991; Blackburn & Gaston, 1996; Gaston, 2000; Kreft & Jetz, 2007). Macroecological studies of entire ecological communities, however, are rare. Jordano (1987), Olesen & Jordano (2002) and Ollerton & Cranmer (2002) were among the first to place mutualistic networks in a macroecological perspective by investigating geographical trends in network properties. However, their sample sizes were modest. Recently, Sugiura (2010) studied variation in the structure of plant-ant networks among a set of Japanese islands and Dalsgaard et al. (2011) analysed large-scale patterns in the degree of specialization in plant-hummingbird networks. Species assemblies are expected to show increasing species richness with decreasing latitude and elevation, but how these patterns scale up to entities as complex as entire ecological networks is not known. We investigate 54 community-wide networks of interacting plants and pollinators in order to achieve an understanding of the macroecological variation of pollination networks and its major drivers. As network measures we use, among others, species number, mean number of interactions per plant and per pollinator species, nestedness and modularity.

Since numerous studies demonstrate a general increase in species richness with decreasing latitude and elevation (e.g. Willig *et al.*, 2003, and references therein; Hillebrand, 2004), we hypothesize that species richness, in pollination networks, increases towards the tropics and decreases with elevation (acknowledging that neither latitude nor elevation are determi-

nants per se; Hawkins & Diniz-Filho, 2004). Olesen & Jordano (2002), Ollerton & Cranmer (2002) and, more recently, Dalsgaard et al. (2011) have looked at how specialization in mutualistic networks varies with latitude. Despite using different measures, both Olesen & Jordano (2002) and Dalsgaard et al. (2011) found an increase in network specialization towards the tropics (but see Ollerton & Cranmer, 2002). Consequently, we hypothesize that specialization (given by modularity and mean number of interactions per plant and per pollinator species) increases towards the tropics. Dalsgaard et al. (2011) found a positive relationship between network specialization and precipitation in plant-hummingbird networks, arguing that a high level of precipitation constitutes an adverse condition for insects, which results in a higher degree of specialization between hummingbirds and plants. In our networks, by far the majority of the pollinators are insects. Nevertheless, as specialization of plant-hummingbird networks increases with precipitation we also expect to see a higher level of specialization among those plants and insects that live in humid environments.

Thus, we investigate how the geographical variables latitude and elevation as well as the climatic variables temperature and precipitation affect network topology. Furthermore, we investigate to what extent sampling effort (observation days) and extent (observational area) affect observed patterns. Finally, all analyses were conducted with simultaneous autoregressive (SAR) modelling in order to correct for spatial autocorrelation, since our network data were very heterogeneously distributed globally.

MATERIALS AND METHODS

Network parameters

Pollination networks consist of interacting species of plants and animals. Each network may be analysed as a matrix of P plant species and A pollinator species and each matrix cell has a nonzero element (a_{ij}) whenever pollinator species i visits plant species j. Using binary data, i.e. presence or absence of a given link, a_{ij} takes the value of either 1 or 0, respectively. Generally, several network parameters describe network topology (Table 1).

Database

Data were extracted from the literature and our own unpublished data. Only studies that, within a given area, registered all observed visitations between plants and flower visitors were used – referred to here as community-wide pollination networks. All flower visitors are here operationally defined as pollinators, acknowledging that not all act functionally as such. Additionally, we only included studies offering a high taxonomic resolution. The database encompassed 54 geographically widely scattered networks from 41 studies (Fig. 1). Most did not include quantitative data and the analysis was restricted to the use of binary information (presence–absence of links).

Parameters/variables	Symbol	Min.	Max.	Mean	Median	SD
Number of pollinator species	Α	6 ¹	840 ²	146	74	186
Number of plant species	Р	7 ³	131^{4}	40	29	33
Ratio between pollinator and plant species	A/P	0.65	14.5^{6}	3.5	2.9	2.5
Size of interaction matrix	$A \times P$	60^{1}	94,080 ²	10,526	2054	21,098
Total number of species	S = A + P	16 ¹	952 ²	186	106	213
Total number of interactions	Ι	16 ¹	2,933 ⁴	378	185	506
Connectance, i.e. proportion of realized links	$C = I/(A \times P)$	1.7^{7}	39.5 ⁸	11.2	8.9	8.2
Mean number of interactions per pollinator species	La	1.29	6.3 ⁸	2.7	2.5	1.0
Mean number of interactions per plant species	Lp	1.61	30.9 ⁶	8.6	6.9	6.0
Modularity	M	0.40^{27}	0.64^{10}	0.52	0.51	0.07
Standardized modularity	$M_{z-\text{score}}$	2.2^{29}	37.5^4	7.93	5.15	7.29
Number of modules in the network [†]	N_{M}	54,15,25,27,28	167	6.6	6.0	2.4
Nestedness	NODF	4.0^{11}	63.6 ⁸	20.9	18.8	13.4
Standardized nestedness	NODF _{z-score}	2.2^{30}	44.6^{2}	10.5	7.6	9.0
Latitude (decimal degrees)	-	-43.7^{13}	81.814,15	22.0	34.2	38.3
Longitude (decimal degrees)	_	-115.0^{16}	171.8^{17}	2.1	-16.9	87.5
Mean elevation (m)	_	1^{18}	3400 ¹⁹	721	165	961
Mean annual temperature (°C)*	_	$-20.0^{14,15}$	27.6^{20}	9.5	10.0	11.3
Mean annual precipitation (mm)*	_	62 ¹⁶	340113	1084	779	821
Study plot size (m ²)	_	10026	$300,000^4$	38,678	10,000	76,037
Observation months per season	_	1 ^{1,9,12,21-23}	$12^{4,11,24}$	4.2	3.5	3.0
Total number of observation days	_	2 ¹³	625 ⁴	53	26	92
Total number of observation hours	_	1213	5000^{4}	301	114	720
Number of seasons‡	-	1‡	4.2^{4}	1.5	1.0	0.9

Table 1 Range, mean, median and standard deviation (SD) of the network parameters as well as geographical, climatic and sampling(effort and extent) variables from the 54 pollination networks.

*Obtained from interpolations of the years 1961-90.

†Twenty-five networks were not significantly modular and therefore consisted of one single large module. Among the twenty-nine significantly modular networks, five modules was the lowest number for any network.

‡Thirty-five networks were collected during one season. ¹Philipp *et al.* (2006); ²Inoue *et al.* (1990); ³Schemske *et al.* (1978); ⁴Petanidou (1991); ⁵Percival (1974); ⁶Álvaro (2004); ⁷Kato (2000); ⁸Bundgaard (2003); ⁹McMullen (1993); ¹⁰Yamazaki & Kato (2003); ¹¹Freitas & Sazima (2006); ¹²Lundgren & Olesen (2005); ¹³Primack (1983) – Mount Cook; ¹⁴Hocking (1968); ¹⁵Kevan (1970); ¹⁶Mosquin & Martin (1967); ¹⁷Primack (1983) – Cass; ¹⁸Montero (2005) – coast; ¹⁹Arroyo *et al.* (1982) – high; ²⁰Ramirez & Brito (1992); ²¹Medan *et al.* (2002) – Laguna Diamante & Río Blanco; ²²Memmott (1999); ²³Olesen *et al.* (2002); ²⁴Herrera (1988); ²⁵Arroyo *et al.* (1982) – mid; ²⁶Montero (2005) – coast, gap and interior; ²⁷Dupont & Olesen (2009); ²⁸Bek (2006); ²⁹Vázquez & Simberloff (2003); ³⁰Barrett & Helenurm (1987).

Since we reanalysed each network using data from the original source, parameter values might deviate from values previously reported. The level of modularity was estimated by the method of functional cartography by simulated annealing (Guimerà & Amaral, 2005a,b). The output of the algorithm includes both the significance level of the modularity and the number of modules within the network. Modules consist of nodes having the majority of their links inside their own modules and therefore represent tightly connected subsections of the network (for calculation see Olesen et al., 2007). Nestedness was calculated using ANINHADO v.3.0.3 with NODF as an index of level of nestedness (Guimarães & Guimarães, 2006; Almeida-Neto et al., 2008). Significance level was tested against a null model assuming that the probability of an interaction is proportional to the generalization level of both species (Ce in ANINHADO). When nestedness was included as a parameter only significantly nested networks were used, reducing the dataset to 51 networks. The same applied to modularity, reducing the dataset to 29. Additionally, we invesitigated the behaviour of standardized measures of nestedness (NODF_{z-score})

and modularity ($M_{z-\text{score}}$), where NODF_{z-score} = (NODF – NODF_{Rand})/SD_{Rand}, with NODF being the actual nestedness of the given network and NODF_{Rand} and SD_{Rand} being average and standard deviation of the randomizations, respectively (Almeida-Neto *et al.*, 2008). Similar, $M_{z-\text{score}} = (M - M_{\text{Rand}})/\text{SD}_{\text{Rand}}$, where *M* is the actual modularity of the given network and M_{Rand} and SD_{Rand} are derived from the randomizations.

For each network, information about latitude and elevation of the study site was extracted from the publication, from personal communication with authors or from nearby locations. Information about temperature and precipitation at a study site was gathered by relating the geographical coordinates of each network with world-wide interpolations (http://www.ipccdata.org) (Mitchell & Jones, 2005). Furthermore, each network site was categorized as either mainland or island. New Zealand was categorized as 'island', because its biotic elements display insular characteristics (Trewick *et al.*, 2007; Wallis & Trewick, 2009). However, most of the Japanese study sites were categorized as mainland because of their short distance to the Asian



Figure 1 Global distribution of the community-wide pollination networks used in the current study. Some of the networks are located so close that they are indistinguishable on the map.

mainland. Seventeen networks belonged to islands, i.e. four New Zealand studies, four Canarian, two Jamaican, one Dominican, one Mauritian, three from Galápagos, one Azorean, and one from a small Japanese island.

Sampling extent and effort were described by three parameters: observational area, number of observation days and hours. In cases where the publications did not include such information, we either contacted the author or made estimates based on other pieces of information in the publications. We did not obtain information about sampling extent for five networks and information about sampling effort for four networks. Thus, when using these as either explanatory or response variables these few networks were excluded, reducing our sample to 49 and 50 networks, respectively.

Statistical analyses

Measurements from geographically close locations are expected to be more similar than measurements taken from distant locations violating the usual assumption of independency (Beale *et al.*, 2010). Thus, besides ordinary least square (OLS) models we also ran SAR and eigenvector-based spatial filter (SEVM) models, both implemented in SAM v.4.0 (Rangel *et al.*, 2010), in order to reduce the effects of spatial autocorrelation.

SAR handles spatial autocorrelation by adding an additional term to the standard linear regression model, i.e. a term that defines the neighbours of a given location and their weights (Dormann *et al.*, 2007; Kissling & Carl, 2008). Here the neighbourhoods in the SAR models were based on a Gabriel network (Legendre & Legendre, 1998), because Bini *et al.* (2009) argue for its superior performance compared with inverse-decaying distances. SEVM produces eigenvectors that describe the spatial structure at different scales, and incorporates them into the models as additional predictors (Diniz-Filho & Bini, 2005). Filter selection was based on a minimization of Moran's I in

regression residuals, and if no filter was chosen automatically by this criterion we selected filters with P < 0.05. Although both spatial models were used to analyse the dataset only results from the SAR models will be reported, since SAR and SEVM gave qualitatively similar results in most analyses. Spatial autocorrelation in the regression residuals was evaluated with Moran's *I*. In some instances, SAR models only lowered the spatial autocorrelation compared with OLS models, instead of removing the spatial autocorrelation completely. However, the SAR models were still preferred as they provided more conservative *P*-values.

Unless otherwise stated, any reported R^2 was the raw effect of the variable in question without the influence of space (Rangel *et al.*, 2010). Most variables were either log or square-root transformed in order to achieve normality and homogeneity of the variance. All significant relationships had normally distributed residuals in the OLS models. However, when working with the SAR models some models did not have completely normally distributed residuals. Nevertheless, as: (1) the corresponding OLS model always had normally distributed residuals, and (2) the SAR always displayed more conservative *P*-values than the OLS we still found it more appropriate to use the SAR.

Methodological shortcomings

Although the latitudinal (43.7° S–81.8° N) and longitudinal (115° E–171.8° W) span of the included networks was comprehensive, they were heterogeneously distributed globally (Fig. 1), e.g. there are no studies from Africa and most of Asia, and several sites are located in close proximity. Despite this, our sample of community-wide pollination networks is by far the largest to date. More network studies are needed, however, from unrepresented geographical and ecological sites, e.g. Africa and lowland rain forest.

All networks are based on observations pooled throughout the entire observation period, which may include several seasons or even years, e.g. Petanidou (1991). Therefore, the phenological overlap between some pollinators and plants may be short or non-existent. Non-overlapping phenologies are believed to account for many of the empty cell entries in network matrices (Olesen *et al.*, 2011).

One of the strongest caveats in meta-analysis is the diverse sampling methods applied, e.g. the use of transects, fixed plots or even random sampling in a poorly defined area. This probably influences network topology but it was not possible to correct the data for this variation because of a lack of information. However, we analysed how sampling extent and effort influenced the network parameters.

Taxonomic and trophic lumping of species is not a problem in our database. We only operate with two trophic levels and only networks offering a high level of taxonomic resolution were included. Unidentified species are generally sorted into morphospecies. In a few instances highly similar species might be grouped as one species and, vice versa, a highly variable species might by sorted into two or more. However, the results of the network analysis will be largely unaffected as such cases are very rare.

Phylogenetic relatedness of both plants and pollinators (Rezende *et al.*, 2007) may cause statistical problems. However, since pollinator communities in our data spanned a very wide range of genera, orders and classes and since the phylogeny of insects is poorly known we did not perform phylogenetically corrected analyses.

RESULTS

General description

The 54 pollination networks encompassed 7901 pollinator species and 2163 plant species, totalling 10,064 species (containing potential duplicate species from adjacent sites), and 20,424 interactions. An overview of the database is given in Table 1. See Appendix S1 in Supporting Information for a list of included studies and a detailed description of the range and mean of number of pollinator species per network (*A*), number of plant species per network (*P*), species ratio between pollinators and plants (*A*/*P*), number of interactions (*I*), connectance [*C* = *I*/(*AP*)], mean number of interactions per pollinator (*L*_a) and per plant (*L*_p), nestedness (NODF) and modularity (*M*).

Sampling and geography and climate

Neither sampling effort (observational days and hours) nor extent (area) changed significantly with latitude, elevation, temperature or precipitation. Thus, there was no bias with respect to sampling effort and extent on a geographical and climatic scale.

Relationships between network parameters

Almost all network parameters were significantly correlated with each other. However, only the correlations with *A* and *P* are

presented here. Correlations with *I* and *C* and the corresponding discussion are given in Appendix S2.

Log(A) and log(P) correlated positively with each other ($R^2 =$ 0.57, F = 69.1, P < 0.001), positively with $\log(I) [\log(A): R^2 =$ $0.92, F = 592, P < 0.001; \log(P): R^2 = 0.64, F = 93.2, P < 0.001],$ and negatively with $\log(C)$ [log(A): $R^2 = 0.63$, F = 89.2, P < 0.001; $log(P): R^2 = 0.83, F = 255, P < 0.001$] (Table 2). R^2 values indicated that log(A) was a better predictor of log(I) than log(P), whereas log(P) was a better predictor of log(C) (Fig. 2a and b). Additionally, $\log(A)$ ($R^2 = 0.48$, F = 49.0, P < 0.001), but not $\log(P)$, was positively correlated with $\log(A/P)$ (Fig. 2c). Mean number of interactions per pollinator species $log(L_a)$ correlated with neither log(A) nor log(P). However, mean number of interactions per plant species (L_p) was well predicted by $\log(A)$ $(R^2 =$ 0.52, F = 54.5, P < 0.001), but not by $\log(P)$. Both $\log(A)$ and log(P) were negatively correlated with $log(NODF) [log(A): R^2 =$ $0.61, F = 75.4, P < 0.001; \log(P): R^2 = 0.60, F = 72.5, P < 0.001$ but positively correlated with $log(NODF_{z-score})$ [log(A): $R^2 =$ $0.62, F = 79.4, P < 0.001; \log(P): R^2 = 0.64, F = 86.1, P < 0.001$ (see also Appendix S4). Neither log(A) nor log(P) correlated significantly with modularity (M), but both correlated positively with $\log(M_{z-score})$ [log(A): $R^2 = 0.57$, F = 35.2, P < 0.001; log(P): $R^2 = 0.41, F = 18.5, P < 0.001$ (Appendix S4) and number of modules per network, $\log(N_{\rm M}) [\log(A): R^2 = 0.17, F = 5.60, P <$ 0.025; $\log(P)$: $R^2 = 0.33$, F = 13.3, P < 0.001].

Network parameters and sampling

Observational area

Log(*A*) ($R^2 = 0.09$, F = 4.60, P < 0.037), log(*P*) ($R^2 = 0.14$, F = 7.45, P < 0.009) and log(*I*) ($R^2 = 0.13$, F = 7.03, P < 0.011) correlated positively with observational area [log(Obs. area)], whereas log(NODF) correlated negatively ($R^2 = 0.18$, F = 10.1, P < 0.003).

Observation days

Observation hours [log(Obs. hours)] and observation days [log(Obs. days)] were highly correlated ($R^2 = 0.64$, F = 85.3, P < 0.001). Thus, only correlations with log(Obs. days) will be reported. Log(A) ($R^2 = 0.25$, F = 16.3, P < 0.001), log(P) ($R^2 = 0.13$, F = 6.92, P < 0.011), log(I) ($R^2 = 0.27$, F = 17.6, P < 0.001), log(A/P) ($R^2 = 0.13$, F = 7.22, P < 0.01), log(L_p) ($R^2 = 0.18$, F = 10.7, P < 0.002) and log(NODF_{z-score}) ($R^2 = 0.17$, F = 9.01 P < 0.004) all showed a significant positive correlation with log(Obs. days), whereas log(C) ($R^2 = 0.11$, F = 5.87, P < 0.019) and log(NODF) ($R^2 = 0.10$, F = 5.01, P < 0.03) correlated negatively (Fig. 3).

Network parameters and geography and climate

Latitude

Both $\log(A/P)$ ($R^2 = 0.26$, F = 8.94, P < 0.001) and $\log(L_p)$ ($R^2 = 0.29$, F = 10.3, P < 0.001) changed quadratically with latitude

Response variable	Explanatory variable	Relationship	п	<i>R</i> ² *	F	P-value
Log(P)	Log(A)	+	54	0.57	69.1	< 0.001
Log(I)	Log(A)	+	54	0.92	592	< 0.001
Log(C)	Log(A)	_	54	0.63	89.2	< 0.001
Log(A/P)	Log(A)	+	54	0.49	49.0	< 0.001
$Log(L_p)$	Log(A)	+	54	0.52	55.5	< 0.001
$Log(M_{z-score})$	Log(A)	+	29	0.57	35.2	< 0.001
$Log(N_M)$	Log(A)	+	29	0.17	5.60	0.025
Log(NODF)	Log(A)	-	51	0.61	75.4	< 0.001
Log(NODF _{z-score})	Log(A)	+	51	0.62	79.4	< 0.001
Log(I)	Log(P)	+	54	0.64	93.2	< 0.001
Log(C)	Log(P)	-	54	0.83	256	< 0.001
$Log(M_{z-score})$	Log(P)	+	29	0.41	18.5	< 0.001
$Log(N_M)$	Log(P)	+	29	0.33	13.3	0.001
Log(NODF)	Log(P)	-	51	0.60	72.5	< 0.001
Log(NODF _{z-score})	Log(P)	+	51	0.64	86.1	< 0.001
Log(A)	Log(Obs. area)	+	49	0.09	4.59	0.037
Log(P)	Log(Obs. area)	+	49	0.14	7.45	0.009
Log(I)	Log(Obs. area)	+	49	0.13	7.03	0.011
Log(NODF)	Log(Obs. area)	-	46	0.19	10.1	0.003
Log(A)	Log(Obs. days)	+	50	0.25	16.3	< 0.001
Log(P)	Log(Obs. days)	+	50	0.13	6.92	0.011
Log(I)	Log(Obs. days)	+	50	0.27	17.6	< 0.001
Log(C)	Log(Obs. days)	-	50	0.11	5.87	0.019
Log(A/P)	Log(Obs. days)	+	50	0.13	7.22	0.01
$Log(L_p)$	Log(Obs. days)	+	50	0.18	10.7	0.002
Log(NODF)	Log(Obs. days)	-	48	0.10	5.01	0.03
Log(NODF _{z-score})	Log(Obs. days)	+	48	0.17	9.08	0.004
$Log(L_p)$	Latitude	Q	54	0.26	8.94	< 0.001
Log(A/P)	Latitude	Q	54	0.29	10.3	< 0.001
Μ	Latitude	-	29	0.19	6.31	0.018
$Log(N_M)$	Latitude	-	29	0.14	4.48	0.044
$Log(L_p)$	Temperature	Q	54	0.16	4.74	0.013
Μ	✓(Precipitation)	+	29	0.15	4.60	0.041
Log(NODF)	✓(Precipitation)	-	51	0.10	5.28	0.026
Log(A/P)	Elevation (> 500 m)	-	22†	0.33	9.80	0.005
$Log(L_p)$	Elevation (> 500 m)	+	22†	0.19	4.59	0.045

Table 2Overview of significant outputsfrom the simultaneous autoregressivemodels. The relationship columnsignifies whether the best relationshipwas positive (+), negative (-) orquadratic (Q).

Abbreviations are defined in Table 1.

 R^2 values are the raw effect of the variable in question without the influence of space.

†Twenty-two networks were sampled at an elevation above 500 m a.s.l.

(0° to 90°), whereas *M* decreased linearly ($R^2 = 0.19$, F = 6.31, P < 0.018) (Fig. 4).

Temperature and precipitation

Among the included locations, precipitation and temperature correlated positively ($R^2 = 0.26 F = 18.4, P < 0.001$). This must be a result of a lack of study locations from, for example, desert areas where high temperature and low precipitation are expected. Log(L_p) displayed a quadratic relationship with temperature ($R^2 = 0.16, F = 4.74, P < 0.013$). $M (R^2 = 0.15, F = 4.60, P < 0.041)$ increased linearly with \checkmark (precipitation), whereas log(NODF) decreased ($R^2 = 0.10, F = 5.28, P < 0.026$) (Fig. 5).

Elevation

Network parameters were highly variable within the first few hundred metres of elevation (Fig. 6c–f). Temperature (corrected for latitude) displayed a similar pattern, i.e. a strong scatter within the first 500 m of elevation, but at about that threshold an abrupt decrease in temperature occurred ($R^2 = 0.45$, F = 16.1, P < 0.001) (Fig. 6b). This cut-off value was used in the subsequent analysis of altitudinal variation in network parameters. Log(A/P) decreased ($R^2 = 0.33$, F = 9.80, P < 0.005) and log(L_a) ($R^2 = 0.19$, F = 4.59, P < 0.045) increased while the remaining parameters did not change significantly (Fig. 6). However, log(A) tended towards a decrease whereas log(P) seemed less sensitive, which might explain the significant decrease in log(A/P).



Figure 2 (a), (b) Simultaneous autoregressive (SAR) modelling estimation of $\log(I)$ (number of interactions) and $\log(C)$ (connectance), respectively, plotted against the explanatory variables $\log(A)$ (number of pollinators, black triangles and full line) and $\log(P)$ (number of plants, open circles and stippled line). Among the two, *A* was the best predictor of *I*, whereas *P* was the best predictor of *C*. Notice how the scatter of triangles and circles differs within and between the two plots (a) and (b). (c) $\log(A/P)$ (ratio between animal and plant species) against $\log(A)$ (black triangles and full line) and $\log(P)$ (open circles and stippled line). The species ratio only responded significantly to changes in *A*.



Figure 3 The three network parameters log(A) (number of pollinators, black triangles and full line), log(P) (number of plants, open circles and stippled line) and log(A/P) (ratio between pollinators and plants, black crosses and punctuated line) as a function of the sampling effort variable log(Obs. days) (total number of observation days). All three network parameters increase with sampling effort.

The importance of sampling

The influence of sampling effort and extent on correlations between network parameters and geography/climate was examined by analysing corresponding residuals (see Appendix S3). Among the five cases where a corrected regression was meaningful, none of the reported relationship was affected by sampling effort, sampling extent or sampling effort + extent. Thus, sampling was not believed to have any confounding effect on the observed patterns.

Mainland and island

Mainland networks had more pollinator species (*A*) (d.f. = 51, t = 3.5, P < 0.001), more interactions (*I*) (t = 3.2, P < 0.003), lower

C (t = 2.1, P < 0.043), higher *A*/*P* (t = 3.1, P < 0.003), higher *L*_p (t = 3.1, P < 0.003) and lower NODF-values (d.f. = 48, t = 2.3, P < 0.024) than island networks (Table 3). Furthermore, mainland networks tended towards having more plant species (*P*) (d.f. = 51, t = 1.8, P < 0.085). In all these analyses (see Table 3) the data from Kato (2000), from Amami Island, were excluded because this network was extraordinary in its high *A* and *P*, and it was a strong outlier compared with all other island networks. Furthermore, number of observation hours was higher on mainlands than on islands (d.f. = 47, t = 2.5, P < 0.017) (Table 3). This pattern was significant even after excluding the methodological outlier in Petanidou (1991), which is a mainland network with 5000 observation hours; almost four times as many as the network with the second highest number of observation hours.

DISCUSSION

Sampling and geography and climate

Sampling effort and extent were not influenced by geography and climate. Ollerton & Cranmer (2002) concluded that tropical networks suffer from undersampling (because correcting for sampling effort removed the negative correlation between specialization and latitude) but the current analysis did not suggest this (see also discussion later).

Relationships between network parameters

Network parameters covaried strongly, and in particular the number of pollinators (*A*), number of plants (*P*), total number of interactions (*I*) and connectance (*C*) were related to each other and to the remaining parameters (*A*/*P*, L_a , L_p , *M*, N_M and NODF). *A* and *P* were strongly positively correlated. Thus, observing more plants within an area generally resulted in more pollinators being recorded. *A* was a more precise predictor of *I*



Figure 4 (a) Mean number of interactions per plant species, $\log(L_p)$, (b) ratio between pollinators and plants, $\log(A/P)$, and (c) modularity, *M*, plotted as a function of latitude. (Only significantly modular networks were included, n = 29.) Both $\log(L_p)$ (a) and $\log(A/P)$ (b) display a quadratic relationship whereas *M* decreases linearly (c).



Figure 5 (a) Nestedness, log(NODF), and (b) modularity, *M*, plotted against mean annual precipitation (square root transformed). Only significantly nested or modular networks were included, *n* = 51 and *n* = 29, respectively. Nestedness decreases with precipitation whereas modularity increases.

than *P*, and the latter was a better predictor of *C* (Fig. 2, Table 2). This might be a result of the phytocentric sampling procedure and/or the pollinator fauna, in general, being richer than its co-occurring flora (Table 1). Phytocentric sampling means that each time a new pollinator species is observed, a new link is scored. This is visualized by the long 'pollinator tail' in the nested version of a network (Bosch *et al.*, 2009). Furthermore, increasing the observation period seemed to increase *A* disproportionately (Fig. 3). Thus, *A* presumably becomes a better predictor of *I*. *A/P* responded positively to an increase in *A*, but was unaffected by *P* (Fig. 2c). Thus, *A* increased faster than *P* when a richer community was investigated. The importance of a phytocentric sampling, compared to zoocentric sampling (Bosch *et al.*, 2009), needs to be further explored.

 $N_{\rm M}$ increased significantly with both *A* and *P*, suggesting that more species permit the existence of more modules, although *M* did not depend on either *A* or *P* (see also Olesen *et al.*, 2007). Almeida-Neto *et al.* (2008) showed that network nestedness (NODF) was highly dependent on connectance (*C*), which is corroborated by our results as *C* explained 73% of the variation in NODF (see Appendix S2). A standardized measure of nestedness given by the z-score (see Materials and Methods) was suggested by Almeida-Neto et al. (2008) to be independent of matrix size and shape (columns:rows) and only weakly dependent on C (depending on the null model used). Here, however, both NODF_{z-score} and $M_{z-score}$ (both measuring how far the given network structures are from random) were highly correlated with A, P, I and C (see Appendix S4). However, using artificial matrices, Almeida-Neto et al. (2008) allowed only one parameter (matrix size, shape or C) to change at a time, whereas we worked with empirical networks where several parameters varied simultaneously. In addition, NODF and NODF_{z-score} displayed opposite patterns with respect to their relationships with A, P, I and C (Appendix S4). This suggests that larger networks had smaller and more stable nestedness values, whereas values for smaller networks are larger and less stable. Similar conclusions can be drawn about modularity with species-rich networks having the most stable modularity values. Further studies are needed to clarify the relationship between nestedness/ modularity and the standardized measures, and especially to elucidate the difference between empirical and simulated networks.



Figure 6 (a) Relationship between temperature and latitude. In (b)–(f), grey and black circles refer to networks sampled below and above 500 m, respectively. (b) The *y*-axis represents the residuals from the linear correlation between temperature and latitude depicted in (a). An apparent change in latitude-corrected temperature is visible for elevations above 500 m. Noticeable responses to elevations above 500 m were observed for some parameters (e) and (f), whereas numbers of plants (c) and pollinators (d) were less affected. Only full lines were significant at *P* < 0.05. *P*, number of plant species; *A*, number of pollinators; *A*/*P*, species-ratio between pollinators and plants; L_a , mean number of interactions per pollinator species.

Network parameters and sampling

Observational area

A, P and I increased with sampling extent, in agreement with the recent observation that they vary positively with island area in networks of ants and extrafloral nectar-producing plants (Sugiura, 2010). P gave a better fit than A, suggesting that the (sedentary) plants were more spatially restricted than their (mobile) pollinators, i.e. spatial turnover might be higher for plants than for pollinators. A, P and I were related to area with correlation coefficients (SAR) of 0.075, 0.087 and 0.113, respectively. Thus, our results corroborated the findings by Sabatino et al. (2010), who demonstrated that I increased faster than number of species with increasing area. Contrary to Nielsen & Bascompte (2007), who found nestedness to be relatively independent of spatial sampling, the current study and the results by Sugiura (2010) suggest that nestedness decreases with area. However, such a decrease might be driven by the correlation between nestedness and species richness.

Observation days

Not surprisingly, more observation days resulted in more observed species and interactions (Fig. 3, Table 2) agreeing with previous studies (Goldwasser & Roughgarden, 1997; Martinez et al., 1999; Devoto et al., 2005). Additionally, A/P and L_p also increased with sampling effort, demonstrating that more pollinators and more interactions per plant species were discovered with more observation days (Fig. 3). Ollerton & Cranmer (2002) also demonstrated that L_p increased with sampling effort. Thus, especially with respect to pollinators and interactions per plant species, sampling effort really matters. The phytocentric sampling procedure might explain why only L_p and not L_a was affected by sampling effort. Others have concluded that complex properties, such as nestedness, are less sensitive to sampling effort than more basic ones such as A, P and I (Nielsen & Bascompte, 2007; Hegland et al., 2010). Here, however, both NODF and NODF_{z-score} responded significantly to sampling effort (Table 2), suggesting that a smaller and more stable estimate of nestedness was achieved with increased sampling.

		Island	Mainland	Two-tailed	
	n	average§	average§	<i>t</i> -ratio§	P-value§
Study plot size (m ²)	49	19,258	48,093	0.2	0.805
Total number of observation days	49†	23	49	1.9	0.059
Total number of observation hours	49†	97	248	2.5	0.017*
Α	53‡	52	174	3.5	< 0.001*
Р	53‡	26	44	1.8	0.085
Ι	53‡	141	461	3.2	0.003*
С	53‡	14.1	10.3	2.1	0.043*
$A \times P$	53‡	1,735	12,822	3.0	0.005*
A + P	53‡	78	219	3.3	0.002*
A/P	53‡	2.0	4.0	3.1	0.003*
L_{a}	53‡	2.8	2.7	0.5	0.612
Lp	53‡	5.2	10.0	3.1	0.003*
M	28‡ ¶	0.50	0.52	0.8	0.415
$M_{z-\text{score}}$	28‡ ¶	4.21	8.94	1.7	0.103
N_{M}	28‡ ¶	6.6	7.6	0.9	0.361
NODF	50‡ ¶	26.9	19.0	2.3	0.024*
NODF _{z-score}	50‡ ¶	6.7	11.5	1.8	0.081

Table 3 Two-tailed Student's *t*-test of the difference between mainland and island networks regarding sampling effort and extent, and network parameters.

Abbreviations are defined in Table 1.

*Significant at P < 0.05 level. When excluding all the Japanese networks (that are extraordinarily well sampled in terms of number of pollinator and plant species), all the patterns remained the same except that the difference in NODF no longer was significant.

†Excluding Petanidou (1991) (mainland network).

‡Excluding Kato (2000) (island network).

§Island and mainland averages are untransformed values whereas t-ratios and P-values are from analyses of transformed data.

¶Only networks that were significantly modular/nested were included.

Network parameters and geography and climate

Latitude

A/P and L_p changed quadratically with increasing latitude, suggesting that: (1) mid-latitudes harboured more pollinators per plant species, and (2) plants generally had fewer interaction partners towards the tropics and the Arctic. Olesen & Jordano (2002) and Ollerton & Cranmer (2002) found a positive relationship between latitude and L_p , although the latter study rejected the relationship when taking sampling effort into account. The quadratic relationship in the current data might arise because of a larger sample size and, more importantly, the relationship was not affected by sampling effort (Appendix S3). Hence, the current study suggests that tropical and Arctic plants display a higher degree of specialization in terms of interaction partners. Ollerton et al. (2006) concluded that at least tropical communities have more types of specialized pollination systems, suggesting a more specialized nature of plant species towards the tropics. Bee diversity is known to be particularly rich in warm temperate arid regions, especially around the Mediterranean Basin and California (Michener, 1979). This was corroborated by our data, as the proportion of Hymenoptera among the pollinators peaked around 30-40° of latitude (K.T. & J.M.O., unpublished). Since bees are very important flower visitors, a higher diversity of bees could explain the elevated A/P-ratio, and maybe also partly the elevated $L_{\rm p}$, around intermediate latitudes. Thus, regional patterns of pollinator diversity presumably affect the macroecological patterns of pollination networks.

Higher modularity means clearer delimited or more specialized groups of interacting plant and pollinator species (Olesen et al., 2007). Thus the stronger modular structure observed at lower latitudes argues for more specialized networks, at least at the level of functional groups identified as modules. It is here important to note that whereas a highly specialized network would (all else being equal) induce high modularity (Lewinsohn et al., 2006; Olesen et al., 2007), high modularity does not, per se, entail specialization. Nevertheless, both modularity and L_{p} point towards a presence of more specialized pollination networks near the equator, agreeing with the finding that biotic interactions are more important in the tropics (Schemske et al., 2009). Similarly, in plant-hummingbird networks an increase in specialization towards the tropics has been demonstrated (Dalsgaard et al., 2011), suggesting that mutualistic networks, in general, might be more specialized at lower latitudes. Vázquez & Stevens (2004) proposed that a latitudinal gradient in niche breadth could exist if the interactions were nested and species richness followed a latitudinal gradient. Habitat heterogeneity is a potential driver of species diversity (Kerr & Packer, 1997) and might also influence modularity and specialization in pollination network. However, further data and examination are needed to clarify this.

Temperature and precipitation

 $L_{\rm p}$ was the only parameter responding to mean annual temperature, although it ranged from -20° C to 27.6°C. Thus, network topology, in general, seemed very robust to temperature variation, although individual species might respond strongly (Høye *et al.*, 2007).

M responded positively to precipitation, whereas NODF responded negatively (Fig. 5). Nestedness and modularity are tightly correlated at low connectance levels (Fortuna *et al.*, 2010) and the measures of nestedness and modularity applied in the current study are significantly negatively correlated, which may explain their opposite relationships to precipitation. Since specialization in plant–hummingbird networks (Dalsgaard *et al.*, 2011) and modularity in the current study both increased with precipitation it suggests (1) that the topology of mutualistic networks are sensitive to precipitation level, and (2) that specialization might increase in humid environments. It has been demonstrated that species distribution and interactions pattern along rainfall gradients are complex (Devoto *et al.*, 2005; González *et al.*, 2009), but here we suggest that network structure might respond in a predictable manner.

Elevation

Although highly variable within the first few hundred metres above sea level, network topology changed more consistently from 500 m and upwards (Fig. 6), e.g. A/P decreased and L_a increased above this elevation, suggesting that with elevation there exist fewer pollinators per plant species and pollinators become more generalized. Both L_a and L_p were expected to increase with elevation as the more unpredictable environment at higher elevations (Arroyo et al., 1982; Medan et al., 2002) argues for a more generalized linkage level of both plants and pollinators. However, whereas L_a responded as predicted L_p actually decreased (although not significantly). One explanation might be the decreasing A/P, because, although the actual number of pollinators and plants did not respond above 500 m the ratio between the two (A/P) decreased significantly. Thus, the ratio was approaching unity with increasing elevation, suggesting that plants have fewer animals to interact with. Additionally, it has been demonstrated that the generalization level of plants in a semi-alpine ecosystems can be unpredictable (Lázaro et al., 2010). In conclusion, since the cut-off value basically was a temperature threshold (Fig. 6b), temperature may be the regulating parameter instead of elevation in itself.

Mainland and island

Mainland networks were observed for more hours than island ones (Table 3), probably as a result of higher species richness. However, it could also be a research artefact as most researchers have their research base on mainland and, as such, are more restricted in terms of observation time when doing surveys on islands. Island networks, in general, had fewer species, which is in agreement with the general depauperate nature of many islands (Olesen *et al.*, 2010). Fewer species translated into fewer interactions (*I*) and higher connectance (*C*) on islands. The proportionally fewer pollinators (lower A/P) might explain the lower L_p resulting in an impoverished interaction community compared with mainland (also observed in Olesen & Jordano, 2002).

CONCLUSIONS

Contrary to expectations, the number of species in communitywide pollination networks did not respond to latitude and only partially responded to elevation by demonstrating a lower ratio between pollinators and plants. The current analysis supports previous studies (Olesen & Jordano, 2002; Schemske et al., 2009; Dalsgaard et al., 2011) and argues for a more specialized interaction pattern of tropical communities as they display higher modularity and fewer interactions per plant species. However, higher modularity means a higher specialization at group level and not necessarily at species level. Additionally, precipitation but not temperature appears to be an important variable regulating network structural patterns such as nestedness and modularity, supporting previous studies (Dalsgaard et al., 2011). Finally, corrected regressions suggested that the high variability in sampling effort and extent among the networks did not influence the observed patterns between network parameters and geography/climate.

Thus pollination networks show complex macroecological patterns, and other kinds of ecological network may do the same. These patterns could hardly be deduced from studies of smaller groups or guilds of interacting species. With evergrowing databases and increasingly refined network analytical tools, we anticipate macroecological network analysis will become a venue of much future research into the integrated body of global biotic complexity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Detailed description of the range and mean of included network parameters plus a list of all the papers used in constructing the database.

Appendix S2 Network parameters correlating with *I* and *C*. **Appendix S3** Regressions corrected for methodology.

Appendix S4 NODF, NODF_{z-score} and $M_{z-score}$ against A, P, I and C.

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BIOSKETCHES

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K.T. and J.M.O. planned the project, K.T. processed and analysed the data and K.T. and J.M.O. wrote the paper.

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