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Macroecological trends in nestedness and modularity of seed-dispersal networks: human impact matters

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ABSTRACT

Aim We aim to characterize the macroecological patterns in the structure of mutualistic seed-dispersal networks. Tropical areas hold more species than temperate ones. This difference in species number may favour ecological processes that minimize interspecific competition in species-rich areas. There is theoretical evidence that both modularity (i.e. the presence of semi-independent groups of highly interacting species) and nestedness (i.e. specialists interact with a subset of the species interacting with generalists) reduce the effects of competition. Thus, we expect high degrees of modularity or nestedness at low latitudes in seed-dispersal networks. Moreover, we test whether climate, topography and human impact influence network structure.

Location Thirty-four qualitative and 21 weighted seed-dispersal interaction networks located world-wide.

Methods We related the degree of modularity and nestedness of seed-dispersal interaction networks with latitude. To disentangle the macroecological drivers of network structure, we also associated modularity/nestedness with species richness, altitudinal range, human impact and an array of climate predictors: precipitation, temperature, precipitation/temperature seasonality and historical climate-change velocity and anomaly.

Results Binary networks showed stronger macroecological patterns than weighted networks. Latitude was unrelated to the structure of seed-dispersal networks, but more nested assemblages were species rich and were located in areas with a high degree of human impact, high temperature seasonality, low precipitation, and, especially on the mainland, high stability in precipitation. Modular networks were species rich and found in areas with low human impact. For both nestedness and modularity, the effects of species richness and human impact were especially strong and consistent.

Main conclusions As for previous macroecological studies of mutualistic networks, we found that the structure of seed-dispersal assemblages was related to current and historical climate. The largest influences on nestedness and modularity, however, were the number of competing species and the degree of human impact. This suggests that human disturbance, not just climate, is an important factor determining the structure of a seed-dispersal network.

Keywords

Climate, conservation, ecological networks, frugivory, human impact, latitude, mutualism, species interactions.

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INTRODUCTION

During the last decades, several studies have revealed the network structure of mutualistic interactions (Olesen & Jordano, 2002; Bascompte *et al.*, 2003; Vázquez *et al.*, 2009). The network organization of mutualisms may have implications for the conservation of the species involved because it affects the persistence of species within communities (Bascompte & Jordano, 2007; Thébault & Fountaine, 2010; Passmore *et al.*, 2012) and the co-evolutionary dynamics of interacting species (Guimarães *et al.*, 2011). A next step in the analysis of mutualistic networks is to identify the extrinsic factors that affect the patterns of interaction of component species. In this sense, the identification of macroecological patterns in mutualistic interaction networks, and the factors driving these patterns, may be useful both for conservation biology and for better understanding the co-evolution of interacting species (e.g. Dalsgaard *et al.*, 2011, 2013; Schleuning *et al.*, 2012, 2014a; Dáttilo *et al.*, 2014).

Network structure has been described using various metrics such as modularity (i.e. the presence of semi-independent groups of highly interacting species) and nestedness (i.e. specialists interacting with a subset of the species interacting with generalists). For pollination networks, Olesen & Jordano (2002) and more recently Dalsgaard *et al.* (2011, 2013), Schleuning *et al.* (2012), and Trøjelsgaard & Olesen (2013) have already identified macroecological patterns in specialization, modularity and nestedness. Most studies found a more specialized and modular structure in the interaction pattern towards the tropics (but see Schleuning *et al.*, 2012), and an effect of current precipitation on the structure of pollinator networks (Dalsgaard *et al.*, 2013; Trøjelsgaard & Olesen, 2013). Moreover, Dalsgaard *et al.* (2011, 2013) found Quaternary climate-change velocity to decrease specialization and modularity, but increase nestedness of pollination networks.

Several studies have detected latitudinal trends in communities of fruit-producing plants and their frugivorous animals (Fleming & Kress, 2013). For example, Moles *et al.*, (2007) found an increasing gradient in the proportion of plant species dispersed by animals from high to low latitudes, and Kissling *et al.* (2009) found that avian frugivory is more common in tropical than temperate areas. However, few studies have examined the macroecological patterns of seed-dispersal networks. Focusing on avian seed-dispersal networks, Schleuning *et al.* (2012, 2014a) found specialization and modularity to be higher in temperate regions, possibly because of higher temperature seasonality and higher seasonal partitioning of fruits and birds in temperate regions than in the tropics. As both mammals and birds disperse fruits (e.g. Mello *et al.*, 2011) and nestedness is a pervasive pattern of these networks (Bascompte *et al.*, 2003), further community-wide research is needed to completely understand the latitudinal patterns and underlying factors determining the structure of seed-dispersal networks.

Furthermore, human disturbance is known to affect species interactions in general (Tylianakis *et al.*, 2007, 2008) and mutualisms in particular (e.g. Kearns *et al.*, 1998). For seed dispersal, hunting and selective logging may reduce the number of

seeds removed by animals (Markl *et al.*, 2012) or change the patterns of seed dispersal (Galetti *et al.*, 2013). The removal of smaller numbers of seeds may be related to a reduction in the number of interactions and the number of seed dispersers, which in turn may affect species interaction patterns and processes. Also, Menke *et al.* (2012) found that plant–frugivore networks were more connected, more nested and more robust against species extinctions at forest–farmland edges than in the forest interior. This could perhaps be caused by the most fragile and specialized species going locally extinct in areas of high human impact. Despite this documented effect of human impact on seed dispersal, previous macroecological studies have focused on the effects of climate and overlooked the possible importance of human impacts on network structure.

The study of how structural patterns change across space may provide indirect evidence for the role of biotic interactions in shaping the organization of interacting assemblages. For example, interspecific competition is likely to affect network patterns. Because tropical communities are species rich (Pimm & Brown, 2004) it is expected that competition for resources may favour high modularity and specialization in tropical areas, leading to niche partitioning (Trøjelsgaard & Olesen, 2013). In addition to niche partitioning, some network patterns may be a consequence of the minimization of effects of interspecific competition. For example, multiple ecological and evolutionary processes may lead to nestedness (Bascompte *et al.*, 2003) and theory predicts that nestedness minimizes the effects of interspecific competition and favours species persistence (Bastolla *et al.*, 2009; Thébault & Fountaine, 2010; but see Allesina & Tang, 2012). Moreover, modularity may be favoured by evolutionary constraints (Lewinsohn *et al.*, 2006) and can limit the effects of interspecific competition to subsets of the network, minimizing the destabilizing effects of mutualisms (Allesina & Tang, 2012).

We characterize the structure of mutualistic seed-dispersal networks using a network approach for 34 qualitative and 21 weighted datasets from a wide range of geographical areas: they included not only birds, but also mammals and other vertebrate seed dispersers. As tropical areas are richer in species, we expect that mutualistic assemblages in tropical ecosystems may also show higher nestedness and/or modularity as a consequence of processes minimizing interspecific competition and favouring coexistence (Bastolla *et al.*, 2009; Allesina & Tang, 2012). We also test the effect of taxonomic diversity and site characteristics, both altitudinal range and putative climate predictors used in previous studies (i.e. precipitation, temperature, precipitation/temperature seasonality, historical climate-change velocity and anomaly). Finally, for the first time, we assessed the potential additional role that human impact may have on the structure of seed-dispersal interaction networks.

METHODS

Interaction matrices

We used a global dataset consisting of 34 frugivory interaction networks (Fig. 1; Appendix S1 in Supporting Information)

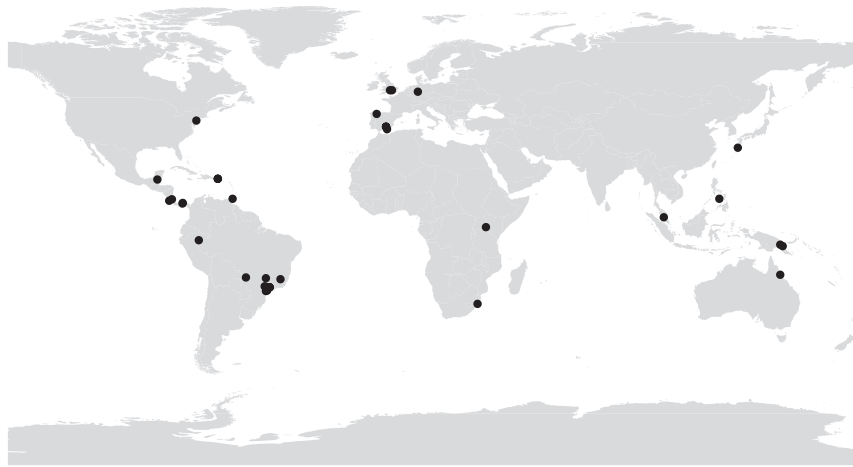


Figure 1 World map showing the approximate location of the 34 studies. Each point represents one seed-dispersal network.

coming from already published studies, mainly from Rezende *et al.* (2007), Mello *et al.* (2011) and the Interaction Web Database (<http://www.nceas.ucsb.edu/interactionweb/index.html>). From each study we collected qualitative information about the interactions between plants and animals. The included studies presented data on frugivory by many animal species, all identified at least to genus level, and presented data from at least two seasons in the year.

Networks of species interactions can be characterized in the form of matrices where species are represented by rows and columns and the interaction between an animal i and a plant j is depicted by the element a_{ij} . Twenty-one of our networks were quantitative, where a_{ij} represents the number of times an interaction was observed. We also conducted analyses on the full set of 34 datasets, treating them as qualitative matrices ($a_{ij} = 1$ when the two species interact and 0 otherwise). Our networks are two-mode as rows and columns represent species from two different groups (i.e. plants and animals).

Measuring network structure

Several measures have already been used to characterize the structure of mutualistic networks, such as nestedness (Bascompte *et al.*, 2003) and modularity (Olesen *et al.*, 2007; Donatti *et al.*, 2011; Mello *et al.*, 2011). These metrics are useful tools because they allow a comparison of the patterns of interactions in communities that differ greatly, and provide ways to quantify and compare the structure of networks across communities (Bascompte & Jordano, 2007). These metrics were first created for qualitative datasets that showed whether an interaction between two species occurred or not. In recent years, generalizations of these metrics to quantitative matrices (i.e. those that also indicate the intensity of the interaction) have also been developed. In this study we use both quantitative and qualitative metrics to characterize both nestedness and modularity.

The qualitative degree of nestedness was calculated for each matrix using the metric NODF (nestedness overlap and decreas-

ing fills; Almeida-Neto *et al.*, 2008), while quantitative nestedness was calculated using WNODF (weighted NODF; Almeida-Neto & Ulrich, 2011). These metrics estimate the degree of nestedness of the matrix and measure the contribution of the different interacting species to the general pattern. Since the variation in the number of interactions across species could also influence the degree of nestedness, we compared the observed value for nestedness of each matrix with the nestedness values of 1000 matrices constructed following a null model. The null model for NODF keeps the heterogeneity in the number of interactions across species (null model 2; Bascompte *et al.*, 2003). In the null model for WNODF, the species-specific probabilities are proportional to the species relative number of interactions (Vázquez *et al.*, 2007). We calculated the NODF values and null model analysis using ANINHADO (Guimarães & Guimarães, 2006) and the WNODF values with the *Bipartite* package in R (Dormann *et al.*, 2009). Both values of nestedness were standardized as Z-scores to allow comparisons among matrices. The Z-NODF was calculated as:

$$Z\text{-NODF} = \frac{(\text{NODF} - \overline{\text{NODF}}_{\text{nullmodel}})}{\text{SD}_{\text{nullmodel}}}$$

where $\overline{\text{NODF}}_{\text{nullmodel}}$ is the mean of all the NODF values of null model matrices and $\text{SD}_{\text{nullmodel}}$ is its standard deviation. The WNODF value was standardized using the same formula.

The second pattern investigated was modularity. A network is considered modular if it is formed by cohesive subgroups of closely connected species. We estimated the degree of modularity of each qualitative (i.e. binary) dataset using the metric M (Newman & Girvan, 2004; Olesen *et al.*, 2007). Because M cannot be computed analytically, we used the simulating annealing algorithm introduced to modularity analysis by Guimerà & Amaral (2005) to estimate it. We used the program MODULAR (Marquitti *et al.*, 2014) to make the calculations. The simulating annealing algorithm attempts to maximize the number of links between nodes belonging to the same module and to minimize the number of links between nodes belonging to different

modules. The quantitative modularity metric Q was calculated using the new algorithm developed by Dormann & Strauss (2013) called QuanBiMo. This algorithm uses the hierarchical random graph approach of Clauset *et al.* (2008), which organizes interacting species in a graph so that close species are more likely to interact. Then it swaps branches at different levels randomly and reassesses the modularity of the network, selecting the more modular organization. We calculated Q using the *Bipartite* package in R. Both M and Q vary from 0 to 1, and large values of M/Q are characteristic of networks with a large number of modules and/or very isolated modules (see Olesen *et al.*, 2007, for additional details). To test the significance of the modularity, we generated 100 random networks fixing the probability that two species interact, based on that observed in the real networks. We then calculated the modularity of the networks and evaluated whether observed modularity fell within the 95% confidence interval calculated from the randomized matrices. We finally standardized the modularity by calculating the Z-score of M and Q (ZM , ZQ), as we did with nestedness.

Many studies have found that modularity and nestedness are negatively correlated, with more nested communities presenting less modular patterns (e.g. Dalsgaard *et al.*, 2013). However, in our dataset, qualitative nestedness and modularity showed a non-significant positive correlation ($r = 0.299$, $P = 0.086$), while the weighted measures showed a non-significant negative association ($r = -0.342$, $P = 0.129$).

Macroecological variables

We analysed how aspects of the site are associated with patterns of interaction at the community level. Based on the site description in each article where the interaction data were published, we extracted latitude, mean annual temperature and mean annual precipitation of the area. When information about precipitation and temperature was unavailable from the articles, we used estimated values extracted from WorldClim (Hijmans *et al.*, 2005). We also extracted the temperature and precipitation seasonality from WorldClim. For temperature, seasonality was calculated as the standard deviation of the temperature values, while for precipitation we used the coefficient of variation of the precipitation ($SD/mean$).

We described long-term climate stability at each site by calculating climate-change anomaly and velocity since the Last Glacial Maximum (LGM; Loarie *et al.*, 2009; Sandel *et al.*, 2011). Climate anomalies at each site are simply the difference between current and LGM climate conditions, whereas climate-change velocity estimates the displacement rate of climate isoclines by scaling the temporal climate gradient against the spatial climate gradient. The temporal climate gradient was calculated as current temperature or precipitation minus LGM temperature or precipitation. Current climate was represented by 2.5' WorldClim (Hijmans *et al.*, 2005) data, while LGM climate was statistically downscaled outputs from two models, CCSM3 and MIROC 3.2 (K-1 Model Developers, 2004; Braconnot *et al.*, 2007). The spatial gradient was calculated as the local slope of the current climate surface at the study site.

We characterized other attributes of the study areas that could be affecting the organization of interactions. For each site, we extracted the human influence index, a composite score which integrates information on human population density, land-cover change, accessibility and electrical infrastructure (Sanderson *et al.*, 2002). We also calculated topographic heterogeneity as the standard deviation of elevation values within a 0.2° (roughly 20 km) window around each site, using the WorldClim digital elevation model (1 km resolution). Finally, as the amount of shared evolutionary history in the community may also influence network configuration, we also calculated the number of animal subfamilies in each of the communities as a measure of taxonomic diversity.

Statistical analyses

We first related the characteristics of the study sites to the network metrics using generalized linear models (GLMs) in R 2.1.1 (R Development Core Team, <http://www.r-project.org>) and model averaging functions as implemented in the 'MuMIn' package (version 1.9.5; Barton, 2013). For each network metric, we fitted models including all the possible combinations and subsets of the predictor variables. As climate velocity and climate anomaly are correlated, we computed two sets of models – one with velocity and the rest of the variables, and one with anomaly and the rest of the variables. We averaged the parameter estimates across all considered models where the respective parameter appeared, weighted by the relative importance of each model (Johnson & Omland, 2004). The number of families and the climate-change velocities were log-transformed for all the analyses. As species richness (S , defined as the number of animal and plant species) may influence the metrics calculated at the network level and because we want to explore network patterns that goes beyond species richness, we included it in all the models. We estimated the relative importance of each predictor variable by summing the weights of the Akaike information criterion (AIC) across all models in the set where a given variable occurred (Burnham & Anderson, 2002).

Then, using the 'ncf' package in R (Bjornstad, 2014), we examined if the residuals of the best model for each variable were spatially autocorrelated. We explored the autocorrelation at 10 different distances. When the residuals of the model were spatially autocorrelated (Z -NODF and ZM), we performed a spatial eigenvector mapping (SEVM) modelling approach removing spatial autocorrelation in the model residuals. We did this by calculating the linear combination of the detected spatial filters, and using it as a covariable in an ordinary least-square framework (Diniz-Filho *et al.*, 2008).

As mainland communities may be more affected by historical climate change than island communities (Dalsgaard *et al.*, 2013, 2014), and as the structure of mutualistic interaction networks may differ between continental and insular communities (e.g. Olesen & Jordano, 2002; Dalsgaard *et al.*, 2013; Schleuning *et al.*, 2014b), we repeated all the analyses using only the continental assemblages. Ideally we would also like to have conducted the analysis only on islands, but there were too few island networks

to allow this analysis. Moreover, as one other macroecological studies on seed-dispersal networks focused on communities formed only by avian dispersers (Schleuning *et al.*, 2014a), for comparative purposes we also repeated all the analyses using just those communities that included only birds.

Methodological limitations of the study

The patterns of interaction between plants and birds are not constant throughout the year. Some fruits are only available during a specific period of the year and some avian species may migrate from the study site for a period of time. In this study we only included the networks that presented data from at least two seasons in the year. However, the fieldwork in some of the studies did not include a complete year, thus it is likely that some interactions were not observed because they occurred in the non-surveyed period. Moreover, when the data were taken from a complete year, the results from different seasons were pooled. Thus, some species that may not coexist temporally were represented together in the same network. Previous studies have already shown that the number of interaction records in mutualistic networks is correlated with the length of the observation period (Schleuning *et al.*, 2012, 2014a), but in general their conclusions were unchanged when accounting for differences in sampling duration.

We also made a substantial effort to cover as many geographical regions as possible, but our dataset is nevertheless unbalanced across space (as in Schleuning *et al.*, 2012, 2014a). We could not find studies that fitted our requirements from continental Asia (we only have one from Japan), from western North America or from North Africa. In contrast, there is an overrepresentation of networks in some areas (e.g. four sites in Spain). However, this is the best representation currently available on a world-wide scale for frugivory networks, making the study comparable to that of Schleuning *et al.* (2012, 2014a). It is also important to underline that the spatial scale of the study sites was not always clear. Finally, some studies included all the possible animal dispersers at the study area, while others focused on a specific group and ignored alternative dispersers from different animal groups (e.g. studying only the avian seed dispersers and not the mammals).

RESULTS

From 34 seed-dispersal interaction networks, we analysed 5665 interactions between animals and plants. Of the 34 networks, 21 were weighted networks totalling 56,968 interactions. Our prediction of increasing nestedness and modularity in the tropics was not corroborated as the structure of the networks (i.e. nestedness and modularity) was non-significantly related to latitude for both the qualitative and quantitative metrics studied (Tables 1 & S1). However, the macroecological patterns in qualitative networks, especially nestedness, were associated with the predictor variables that were included (Tables 2–4, S2 & S3).

Climatic conditions affected the nested structure of seed-dispersal communities. In general, models including historic

Table 1 Generalized linear models relating the nestedness and modularity of the networks with latitude. We show the results including all the study sites. For each test we present the coefficient of the model, the *t*-value and the *P*-value. Z-NODF and ZM are qualitative nestedness and modularity; Z-WNODF and ZQ are weighted nestedness and modularity.

	<i>n</i>	Coefficient	<i>t</i> -value	<i>P</i> -value
Z-NODF	34	0.007	0.232	0.818
ZM	34	−0.013	−0.908	0.371
Z-WNODF	21	0.115	1.745	0.097
ZQ	21	−0.061	−0.745	0.465

climate anomalies performed better than those including climate-change velocities, and models for nestedness had a better fit than those for modularity (Tables 2–4). Nestedness was high where precipitation was low, precipitation anomaly high and temperature anomaly low (Tables 2–4, Fig. 2). Moreover, communities located in areas with high temperature seasonality also had more nested and less modular structures, while high human impact was related to more nested and less modular assemblages (Fig. 2). Finally, the number of species in the network was also related to the structure of the seed-dispersal assemblage, increasing both nestedness and modularity (Fig. 2).

The continental assemblages showed similar macroecological patterns to the global dataset (Tables S4 & S5) although some of the variables lost their significance, for instance, precipitation anomaly was unimportant on the mainland (Table S4). The analyses including the networks that presented only avian species revealed larger changes in the significance of the variables (Tables S6 & S7). For nestedness, many of the climatic variables lost their significance, while both climate-change velocity variables gained significance, reducing nestedness as for the continental-focused analysis. Moreover, networks that included more animal families (i.e. taxonomic diversity) showed more nested patterns. Human impact also decreased modularity and increased nestedness when analysing the continental communities, but for the avian-dispersed assemblages, qualitative modularity was never affected and the quantitative one lost its effect when accounting for the spatial autocorrelation of the models (Tables S4–S7).

The weighted structure of the seed-dispersal networks showed weaker macroecological patterns (Tables 2 & 3), which were almost entirely lost when accounting for spatial autocorrelation in SEVM models (Tables S2 & S3). Both continental and avian networks showed the same structure as the global dataset, i.e. the significance of the macroecological variables explaining their structure was lost when including the spatial filters in the SEVM analyses (Tables S4–S7).

DISCUSSION

Our study on seed-dispersal networks adds to the discussion about whether mutualistic networks are more – or less – spe-

	Z-NODF		ZM		Z-WNODF		ZQ	
	Estimate	w	Estimate	w	Estimate	w	Estimate	w
(Intercept)	0.842		−1.572		13.053		16.260	
Human impact	0.040	0.99	−0.045	0.98	0.125	0.98	−0.291	0.96
# Fam	−0.049	0.27	0.617	0.43	−2.311	0.40	2.338	0.34
# Sp	0.076	1.00	0.018	0.89	0.210	0.81	−0.159	0.50
MAP	−0.001	0.93	0.000	0.35	−0.002	0.62	0.001	0.49
MAT	−0.102	0.45	0.163	0.38	−0.607	0.64	−0.586	0.71
P seasonality	−0.008	0.30	−0.030	0.58	−0.258	0.59	0.029	0.54
T seasonality	0.001	0.95	−0.001	0.84	0.002	0.55	−0.001	0.33
P anom.	0.003	0.94	−0.002	0.66	0.008	0.44	0.007	0.38
T anom.	−0.036	0.95	0.010	0.34	−0.125	0.64	0.082	0.46
Var. elevation	0.002	0.37	−0.002	0.37	0.019	0.49	−0.024	0.32

Table 2 Results of the generalized linear model averaging for the analyses including climate anomaly variables for all the study sites. We present the coefficient (Estimate) and relative importance of the variable (w) for all the macroecological variables explaining modularity (ZM and ZQ) and nestedness (Z-NODF and Z-WNODF). Variables with a relative importance higher than 0.8 are presented in bold. See Table 4 for abbreviations.

	Z-NODF		ZM		Z-WNODF		ZQ	
	Estimate	w	Estimate	w	Estimate	w	Estimate	w
(Intercept)	1.490		−0.560		0.345		13.553	
Human impact	0.035	0.97	−0.053	0.97	0.116	0.94	−0.273	0.97
# Fam	0.171	0.28	0.643	0.44	−0.168	0.31	3.542	0.37
# Sp	0.076	1.00	0.016	0.85	0.260	0.93	−0.147	0.45
MAP	−0.001	0.98	0.000	0.42	−0.002	0.60	0.001	0.53
MAT	−0.007	0.30	0.092	0.66	−0.331	0.59	−0.450	0.69
P seasonality	−0.009	0.29	−0.015	0.37	−0.124	0.43	−0.068	0.31
T seasonality	0.000	0.36	0.000	0.31	0.001	0.39	0.001	0.30
MAP velocity	−0.199	0.31	0.270	0.39	−3.864	0.83	−2.863	0.51
MAT velocity	−0.502	0.58	0.219	0.36	−1.196	0.39	2.343	0.51
Var. elevation	0.003	0.43	−0.001	0.31	0.014	0.41	−0.029	0.52

Table 3 Results of the generalized linear model averaging for the analyses including climate change velocity variables for all the study sites. We present the coefficient (Estimate) and relative importance of the variable (w) for all the macroecological variables explaining modularity (ZM and ZQ) and nestedness (Z-NODF and Z-WNODF). Variables with a relative importance higher than 0.8 are presented in bold. See Table 4 for abbreviations.

cialized, modular and nested in the tropics (Olesen & Jordano, 2002; Ollerton & Cranmer, 2002; Dalsgaard *et al.*, 2011; Schleuning *et al.*, 2012, 2014a; Trøjelsgaard & Olesen, 2013). Whereas pollination networks tend to be more modular in the tropics (Trøjelsgaard & Olesen, 2013), previous work on weighted seed-dispersal networks has reported higher degrees of modularity in temperate regions, not in the tropics (Schleuning *et al.*, 2014a). We find tropical and temperate seed-dispersal networks to be equally modular and nested. These differences between pollination and seed-dispersal systems may be related to more relaxed specialization requirements between the interacting species in frugivory than in plant–pollinator networks (Blüthgen *et al.*, 2007). Many frugivorous birds are able to forage on the fruits of several plant species (Kissling *et al.*, 2012), while pollinators often have more specialized morphology and behaviour (Stang *et al.*, 2007; Maruyama *et al.*, 2014). For the seed-dispersal studies, the differences may be related to the use of different metrics (e.g. qualitative versus quantitative network metrics) and slightly different datasets. Even though we did not detect a significant latitudinal trend, species-rich seed-dispersal communities presented, as expected, both more modular and more nested patterns. More species in the assemblage indicates

greater competition for the resources (i.e. fruits and dispersers), but the modular and/or nested structure may minimize interspecific competition, and hence favour species coexistence (Bastolla *et al.*, 2009; Allesina & Tang, 2012).

The structure of seed-dispersal networks was also influenced by current climatic conditions. Our study indicates that frugivore assemblages in areas with low precipitation are more nested than assemblages in wetter areas. This suggests that resource use in dry environments is organized in such a way that specialist species interact with a subgroup of the interaction partners of the most generalist species. Rainfall has already been identified to affect the organization of other mutualistic interactions. For example, high precipitation favours modularity (Dalsgaard *et al.*, 2013; Trøjelsgaard & Olesen, 2013) and specialization (Dalsgaard *et al.*, 2011) in pollination networks, and increases nestedness in ant–plant mutualistic networks (Rico-Gray *et al.*, 2012). In addition, Schleuning *et al.* (2014a) detected a decrease in weighted modularity with an increase in precipitation for seed-dispersal networks. Climatic seasonality was also related to the structure of seed-dispersal assemblages in our study. Nested communities were located in areas with large seasonal differences in temperature, while the modular commu-

Table 4 Variables included in the best of all the models (i.e. model with the lowest Akaike information criterion) for modularity and nestedness. For each network metric, we show the best model including historic climate anomaly and climate change velocity as putative predictors. The sign before each variable is the sign of the variable in the model. We also include the fit of the model using the percentage of explained deviance, *D*.

Network metric	Best model variables	<i>D</i>
Z-NODF	(+)Human, (-)MAP, (+)# Sp, (+)P anom., (-)T anom., (+)T seasonality	86.13
Z-NODF	(+)Human, (-)MAT velocity, (-)MAP, (+)# Sp	84.33
ZM	(-)Human, (+)MAT, (-)P seasonality, (-)P anom., (+)# Sp	51.14
ZM	(-)Human, (+)MAT, (+)# Sp	42.27
Z-WNODF	(+)Human, (-)MAP, (-)P seasonality, (+)# Sp, (-)T anom., (+)T seasonality	55.90
Z-WNODF	(+)Human, (+)MAP velocity, (-)MAT velocity, (-)P seasonality, (+)T seasonality	18.82
ZQ	(-)Human, (-)MAT, (-)Var. elevation, (-)# Sp, (+)P anom.	35.88
ZQ	(-)Human, (-)MAT velocity, (-)MAP velocity, (-)MAT	32.45

MAT, mean annual temperature; MAP, mean annual precipitation, T seasonality, temperature seasonality; P seasonality, precipitation seasonality; Var. elevation, variability in the elevation range; MAT velocity, historic temperature change velocity; MAP velocity, historic precipitation change velocity; T anom., historic temperature anomaly; P anom., historic precipitation anomaly; # Fam, number of animal families; # Sp, number of animal and plant species.

nities were characteristic of areas with low seasonality in temperature (latter being opposite to the result of Schleuning *et al.*, 2012). Theoretical studies had identified that evolutionary processes in changing environments, such as in seasonal regions, may lead to modularity (Lipson *et al.*, 2002; Kashtan & Alon, 2005) and our results indicate that nestedness may also be prominent in such variable conditions.

In addition to current climatic conditions, historic climate also influenced the structure of seed-dispersal networks. Historic temperature instability was in most analyses related to a decreased level of nestedness; although high precipitation anomalies increased nestedness for the global dataset, this effect disappeared when focusing on the mainland, and precipitation change velocity had a negative effect on nestedness in avian seed-dispersal communities. Thus, especially for avian seed-dispersal and mainland communities, climatic temperature stability seems to lead to more nested networks. On the other hand, modularity was unaffected in most analyses by historical climate stability, as also observed by Schleuning *et al.* (2014a). Interestingly, the increased nestedness in areas with high stability is opposite to what has been observed for pollination studies (Dalsgaard *et al.*, 2013). Similarly, Schleuning *et al.* (2012) indentified a positive association between historical climate instability and specialization in frugivore bird–plant networks,

whereas Dalsgaard *et al.* (2011) observed the opposite for plant–hummingbird pollination networks. Schleuning *et al.* (2012) suggested that pollination systems are more tightly coevolved, and therefore more negatively affected by changing climate and species composition, than frugivore systems where multispecies co-evolutionary selection favours trait convergence. Irrespective of the exact mechanism, it is noteworthy that seed-dispersal and pollination systems consistently show opposite effects to historical climate stability, and that for both systems the effect of historical climate is especially pronounced on the continent. This indicates that how species interact and form networks are shaped differently by historical climate stability on the continent and insular environments (Dalsgaard *et al.*, 2013, 2014).

The structure of our seed-dispersal networks was also affected by the degree of human impact at the study areas, in agreement with previous studies suggesting that seed-dispersal assemblages may be affected by human impact in several ways. Breitbach *et al.* (2010) found a reduced number of interacting species along a human land-use gradient but a maintenance of the ecosystem function, because the number of seeds removed per tree in human-affected areas did not decline (see also Benítez-Malvido *et al.*, 2014). However, Staggemeier & Galetti (2007) detected that plant species in areas with a high degree of human impact had fewer visits and lower consumption rates than more undisturbed areas. In a recent meta-analysis, Markl *et al.* (2012) concluded that forest fragmentation, hunting and selective logging had different effects on visitation rate, dispersal distance and number of removed seeds. Thus, the effect of human impact on seed dispersal by birds depends on the type of affect and the consequences are case specific. In our work, at network level, the highly human-affected and transformed environments showed more nested and less modular structures. Mutualistic networks show a significantly higher degree of reciprocal specialization than expected under neutral conditions (Blüthgen *et al.*, 2008). These highly specialized interactions are more easily lost from the networks because the extinction of one of the species may have fatal consequences for its specialist interacting partners (Ollerton *et al.*, 2006). Thus, highly human-affected communities may show more nested and less modular structures because the most specialized interactions have been lost due to human activities.

Contrary to the study by Schleuning *et al.* (2014a), who found that the macroecological structure of seed-dispersal networks was better described using weighted than binary network metrics, our binary metrics showed much stronger macroecological signals than our quantitative analyses. The low sample size for weighted analyses may cause this contrasting result, as we could only access weighted information for 21 seed-dispersal networks (16 when considering only continental or bird-mediated assemblages) while Schleuning *et al.* (2014a) studied 18 assemblages. Our results suggest that macroecological studies with small sample sizes should be considered with caution as the results may change because of a few data points. This highlights the need for macroecological analysis of weighted networks using bigger databases.

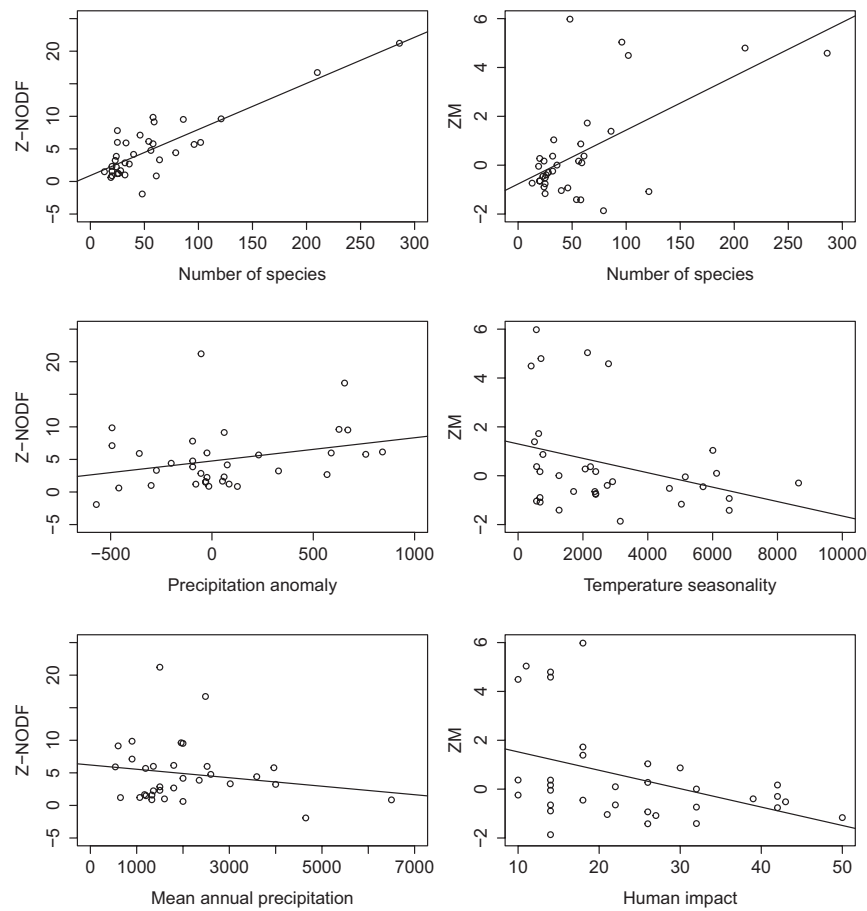


Figure 2 Representation of significant (relative importance of the variable, $w > 0.8$) relationships by means of the GLMs models averaging in table 2 between the qualitative network metrics and the study area characteristics in the seed-dispersal mutualistic networks. The line represents a linear regression. We represent the relationships between nestedness (Z-NODF) and: number of species in the network, precipitation anomaly, and precipitation. We also show the relationships between modularity (ZM) and: number of species in the network, temperature seasonality, and degree of human impact.

In this study on macroecological patterns of seed-dispersal networks, we analysed a relatively large number of binary networks. Our data include seed dispersal mostly by birds but also bats, non-flying mammals and some species of fish and reptiles, so the results may be generalizable to most seed-dispersal assemblages. Our results complement previous studies on the specialization and modularity of seed-dispersal assemblages (Schleuning *et al.*, 2012, 2014a), and can be compared with similar macroecological studies in other mutualistic interactions, especially pollination (Olesen & Jordano, 2002; Dalsgaard *et al.*, 2011, 2013; Schleuning *et al.*, 2012; Trøjelsgaard & Olesen, 2013). All these studies suggest that mutualistic assemblages are not structured randomly and that several factors, notably climatic conditions, are affecting their organization. Our findings highlight that not only climate, but also human impact, are important for understanding the processes that shape the structure of seed-dispersal networks at large spatial scales.

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Additional references to the data sources used in this study can be found at the end of Appendix S1 in the Supporting Information.

SUPPORTING INFORMATION

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

Appendix S1 List of papers used for the analyses and network characteristics of the studied dataset.

Table S1 GLM relating the nestedness and modularity of the networks with latitude.

Table S2 Results of the model averaging for the spatial eigenvector mapping (SEVM) analyses including climate anomaly variables for all the study sites.

Table S3 Results of the model averaging for the SEVM analyses including climate velocity variables for all the study sites.

Table S4 Results of the model averaging for the analyses including climate anomaly variables for the continental sites.

Table S5 Results of the model averaging for the analyses including climate change velocity variables for the continental sites.

Table S6 Results of the model averaging for the analyses including climate anomaly variables for the sites that presented only avian species.

Table S7 Results of the model averaging for the analyses including climate change velocity variables for the sites that presented only avian species.

BIOSKETCH

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