LETTER

Ecological, historical and evolutionary determinants of modularity in weighted seed-dispersal networks

Matthias Schleuning,[1]* Lili Ingmann,[1] Rouven Strauß,[2] Susanne A. Fritz,[1] Bo Dalsgaard,[3] D. Matthias Dehling,[1] Michaela Plein,[1,4] Francisco Saavedra,[1,5] Brody Sandel,[6] Jens-Christian Svenning,[6] Katrin Böhning-Gaese[1,7] and Carsten F. Dormann[8]

Abstract

Modularity is a recurrent and important property of bipartite ecological networks. Although well-resolved ecological networks describe interaction frequencies between species pairs, modularity of bipartite networks has been analysed only on the basis of binary presence–absence data. We employ a new algorithm to detect modularity in weighted bipartite networks in a global analysis of avian seed-dispersal networks. We define roles of species, such as connector values, for weighted and binary networks and associate them with avian species traits and phylogeny. The weighted, but not binary, analysis identified a positive relationship between climatic seasonality and modularity, whereas past climate stability and phylogenetic signal were only weakly related to modularity. Connector values were associated with foraging behaviour and were phylogenetically conserved. The weighted modularity analysis demonstrates the dominating impact of ecological factors on the structure of seed-dispersal networks, but also underscores the relevance of evolutionary history in shaping species roles in ecological communities.

Keywords

Avian seed dispersal, current and past climate, ecological networks, evolutionary history, macroecology, modularity, phylogeny, seasonality, traits, weighted bipartite networks.

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INTRODUCTION

Species evolve and coexist entangled in networks of interacting species (Bascompte & Jordano 2007). A recurrent structure of many types of ecological networks is modularity, which describes the existence of sub-communities within networks (Newman & Girvan 2004; Thébault 2013). The modular structure of ecological networks is a consequence of both ecological and evolutionary processes and has been suggested to be important for species coexistence and community stability (Olesen et al. 2007; Thébault & Fontaine 2010).

Interaction frequencies between species pairs are closely associated with the functional interdependence between species (Vázquez et al. 2005) and define the structure of ecological networks (Ings et al. 2009). Neglecting the quantitative nature of species interactions can lead to an incomplete understanding of the processes shaping ecological networks (Scotti et al. 2007; Ings et al. 2009; Staniczenko et al. 2013). In contrast to weighted analysis of other network properties, such as nestedness (Bascompte & Jordano 2007; Staniczenko et al. 2013), algorithms for detecting modularity in weighted bipartite networks have not yet been explored in ecology (Thébault 2013). In consequence, we have an incomplete knowledge of modularity patterns in bipartite networks, such as those describing reciprocal mutualisms between plants and animals (Bascompte & Jordano 2007).

Macroecological analyses of ecological networks have begun to examine the impacts of current ecological and past climatic factors on network structure (Dalsgaard et al. 2011, 2013; Schleuning et al. 2012). First, ecological factors that may influence modularity include gradients in productivity and resource diversity (Trøjelsgaard & Olesen 2013), including seasonal resource fluctuations (Bosch et al. 2009). Ecological responses of species to spatiotemporal resource variability are driven by the ability of consumer species to adapt their foraging behaviour to current ecological conditions (Carnicer et al. 2009; Mulwa et al. 2013). Such processes may lead to generalised interactions at high productivity and resource diversity (Schleuning et al. 2012) and may favour the formation of modules comprising species with overlapping phenological schedules in seasonal climates (Bosch et al. 2009; Martín González et al. 2012). Second, past climate change may be associated with the disruption of co-adapted species pairs, especially in periods of high past climatic instability. Hence, a decrease in modularity with increasing past climatic instability can be expected, as found in pollination networks (Dalsgaard

[1]*Biodiversity and Climate Research Centre (BiK-F) and Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, 60325, Frankfurt am Main, Germany*

[2]*Department of Computer Science, Technion – Israel Institute of Technology, Haifa, 32000, Israel*

[3]*Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, 2100, Copenhagen Ø, Denmark*

[4]*School of Botany, The University of Melbourne, Parkville, VIC, 3010, Australia*

[5]*Institute for Biology/Geobotany and Botanical Garden, Martin-Luther-University, Halle-Wittenberg, Am Kirchtor 1, 06108, Halle (Saale), Germany*

[6]*Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, 8000, Aarhus C, Denmark*

[7]*Department of Biological Sciences, Johann Wolfgang Goethe-Universität Frankfurt, Max–von-Laue-Straße 9, 60438, Frankfurt (Main), Germany*

[8]*Biometry and Environmental System Analysis, University of Freiburg, 79106, Freiburg, Germany*

Correspondence: E-mail: matthias.schleuning@senckenberg.de

et al. 2013). Third, interactions in ecological networks may be phylogenetically conserved (Rezende et al. 2007; Gomez et al. 2010), so related species may form modules that interact with similar sets of species (Krasnov et al. 2012), potentially leading to a positive relationship between modularity and phylogenetic signal in a network. However, there are no integrative studies testing whether current ecological factors, past climatic stability or evolutionary processes are the main determinants of bipartite network structure.

In addition to comparisons of modularity among networks, the variability in species roles within networks is ecologically relevant because ecological networks are composed of individual species that vary in their functional importance (Stouffer et al. 2012). Olesen et al. (2007) adopted a classification system that assigns species roles based on positions of species in modular networks, distinguishing between species defining the modules and species linking different modules (Guimerà & Amaral 2005). Subsequent studies of binary networks have referred to this classification (e.g. Donatti et al. 2011; Mello et al. 2011), but have rarely tested explicitly whether species roles were randomly distributed among species or were associated with species traits or phylogeny (but see Donatti et al. 2011 for a single binary network).

We employ a new method to detect modularity and to describe species roles in bipartite weighted networks, and apply this method to a global data set of 18 seed-dispersal networks describing interactions between about 500 fleshy-fruited plant and about 400 frugivorous bird species. To test the effects of current ecological and past climatic factors on modularity, we obtained information about mean and variance of current climatic conditions and quantified past (late Quaternary) climatic fluctuations at all study locations. To estimate the phylogenetic signal in the interaction networks, we obtained a phylogeny of avian frugivores and computed the co-variation between shared phylogenetic history and interaction similarity across all avian species pairs (Rezende et al. 2007). In addition, we collected information on five important traits of avian frugivores (Schleuning et al. 2011; Menke et al. 2012), related to their morphology (body mass), foraging behaviour (degree of frugivory, social foraging behaviour) and spatiotemporal occurrence (forest dependence, migratory behaviour). We use this unique set of weighted interaction networks and climatic, phylogenetic and trait data to test (1) whether macroecological patterns in modularity are primarily influenced by current ecological factors, past climatic stability or evolutionary history; and (2) whether species traits and phylogeny influence species roles in ecological networks. The weighted modularity analysis finds that (1) the degree of modularity in seed-dispersal networks is most closely related to current ecological factors, and that (2) foraging behaviour and evolutionary history contribute to the variability in avian species roles.

MATERIAL AND METHODS

Data set

We compiled a data set of 18 weighted interaction networks between plants with fleshy fruits and their avian seed dispersers (see Table S1). Other animal seed dispersers (e.g. monkeys,

bats) were not included because a comparative analysis of phylogenetic and trait effects is not meaningful for distantly related groups. Ecologically, the focus on avian seed dispersers is reasonable because birds are the most species-rich group of frugivorous animals (Kissling et al. 2009).

All networks in the data set describe interactions between fleshy-fruited plants and avian frugivores at the community level, although the extent of sampling varied among studies (Table S1). Networks were recorded by observing frugivore visits to plant individuals, except in two studies that were based on faecal samples from birds (Table S1). All studies provided estimates of interaction frequencies, i.e. the number of bird individuals feeding on the fruits *or* the number of bird individuals carrying seeds of a particular plant species. Estimates of interaction efficiencies, such as differences in seed handling, were not available. Interaction frequency is a good proxy for interaction strength, being usually more important than interaction efficiency (Vázquez et al. 2005), and we therefore do not differentiate between seed-dispersal and plant–frugivore networks in this study.

All studies covered at least the main fruiting period in the study area, and species richness per network ranged from 24 to 121 plant and bird species (Table S1). Overall, networks comprised almost 85 000 interaction events. We defined sampling intensity for each network as the ratio between the number of observed interaction events (square root transformed) and the geometric mean of the number of plant and animal species (Schleuning et al. 2012). This measure of sampling effort reflects the number of interaction events observed per species and accounts for higher observation requirements in species-rich than species-poor networks. This matters in macroecological analyses because species richness decreases with absolute latitude ($n = 18$ networks; Pearson correlation, $r = -0.57$, $P = 0.01$).

Modularity algorithm

We employed a new algorithm (QuanBiMo) to calculate the weighted modularity of bipartite interaction networks, which is described in detail in Dormann & Strauß (2014). In principle, this algorithm follows the approach of Clauset et al. (2008). It builds a random binary tree whose leaves represent the interacting species and associates a structure with each tree defining the subdivision of species into modules. To define a new subdivision, random swaps of branches at any level are performed, followed by an evaluation of whether the new subdivision has a higher modularity value than the previous one. The algorithm employs a stochastic hill-climbing approach, i.e. an increase in modularity is always accepted, and a tree with lower modularity is accepted with a probability inversely proportional to the loss in modularity. The objective function is the bipartite version of Newman's quantity of modularity Q (Barber 2007):

$$Q = \frac{1}{2N} \sum_{ij} \left(A_{ij} - K_{ij} \right) \delta \left(m_i, m_j \right),$$

where N is the total number of observed interactions in the network and A_{ij} is the normalised number of interactions

between bird species i and plant species j. The term K_{ij} represents the expected probability of interactions within a module assuming no preferences in the participating species, which is a suitable null model (Barber 2007). When applying the algorithm to binary data, the null model does not constrain the total number of interactions, but the number of links per species. The module to which a species i or j is assigned is m_i and m_j respectively. The indicator function δ (m_i, m_j) is 1 if $m_i = m_j$ (i.e. when species i and j are in the same module) and 0 if $m_i \neq m_j$. The modularity Q ranges from 0, which means that the community has no more links between species within a module than expected by chance, to 1, which equals the maximum degree of modularity.

We searched for the best division of a network into modules in five independent runs of the algorithm. If no further improvement was recorded after 10^7 swaps, the run was terminated and the result interpreted as the optimum. We recorded the degree of modularity Q, the number of detected modules and the affiliation of each species to a module for the run with the highest modularity (see Table S1 for the low variability in Q among runs). To compare the performance of the algorithm in detecting modules in weighted and binary networks, we calculated Q for each network from the weighted matrices and from binary-transformed matrices ($n = 18$; weighted vs. binary Q, $r = 0.49$, $P = 0.04$). To test whether the classification of plant and bird species into modules was associated with their overlap in interaction partners, we employed a multivariate analysis of variance based on Horn–Morisita interaction distances among plant and bird species respectively (Gomez *et al.* 2010).

As modularity tends to be higher in poorly sampled networks (Dormann & Strauß 2014) and as sampling intensity varied among studies (Table S1), we corrected estimates of modularity Q with two alternative null models. First, we randomised interactions with the Patefield algorithm (null model PA, see Blüthgen *et al.* 2008), which randomly redistributes interaction events among all cells of the network while constraining the total number of interactions per species. It assumes that species interact randomly, without constraining the degree of specialisation in a network. Second, we randomised interactions with an alternative null model (null model VA), proposed by Vázquez *et al.* (2007), constraining the total number of interactions per species *and* the network connectance (i.e. the proportion of realised links). This null model assumes that network connectance is an inherent network property (e.g. defined by the number of forbidden links). It redistributes interaction events randomly among species until the number of filled cells in the matrix equals that in the original matrix; remaining interactions are then distributed among filled cells (Vázquez *et al.* 2007). To obtain estimates of Q for both null models, we used the same settings for the modularity algorithm as for the real networks (10^7 swaps, 5 independent runs). For each null model, we obtained 100 randomisations. Null-model estimates of Q were associated with sampling intensity and were not confounded with latitude (Fig. S1a–d). For each network, we calculated two null-model corrected versions of weighted and binary modularity, ΔQ_{PA} and ΔQ_{VA}, as the difference between observed modularity Q and mean $Q_{NULL.PA}$ and $Q_{NULL.VA}$ respectively ($n = 18$; weighted ΔQ: $r = 0.98$, $P < 0.01$; binary ΔQ: $r = 0.35$, $P = 0.16$).

To identify species roles in modular networks, we followed Guimerà & Amaral (2005) and Olesen *et al.* (2007) and for each species defined its standardised within-module degree z and its participation coefficient c (i.e. the evenness of the link distribution across modules) from both weighted and binary matrices. Within-module degree z and participation coefficient c were characterised for a network with M modules as:

$$z = \left(\frac{k_{is} - \overline{k}_s}{SD_{ks}}\right); c = 1 - \sum_{t=1}^{M}\left(\frac{k_{it}}{k_i}\right)^2$$

where k_{is} is the number of links of species i to other species in its own module s, $\overline{k}_s$ is the average k_{is} of all species in module s, SD_{ks} is the standard deviation of k_{is} of all species in module s, k_{it} is the number of links of species i to module t and k_i is the total number of links of species i. Weighted versions of z and c were computed by using species strength instead of species degree (*sensu* Bascompte & Jordano 2007).

Macroecological patterns

We recorded absolute latitude for each study location (range: 0°–52°) and obtained climate estimates at a resolution of 2.5 arc-minutes for mean annual temperature (MAT), temperature seasonality measured as the coefficient of variation in monthly mean temperatures on the Kelvin scale (CV_{MAT}), mean annual precipitation (MAP) and precipitation seasonality (CV_{MAP}), i.e. the coefficient of variation in monthly precipitation (Hijmans *et al.* 2005). MAT and MAP as well as CV_{MAT} and CV_{MAP} were correlated ($n = 18$; MAT vs. MAP: $r = 0.71$, $P < 0.01$; CV_{MAT} vs. CV_{MAP}: $r = -0.59$, $P = 0.01$). Past climate stability was estimated as climate-change velocity since the Last Glacial Maximum (LGM, 21 000 years ago), which describes the rate at which climatic conditions have moved over the Earth's surface (Sandel *et al.* 2011). Climate change since LGM captures one of the strongest climatic shifts of the Quaternary, and the spatial pattern of this change is representative for the last several hundred thousand years (Sandel *et al.* 2011). We derived climate-change velocities for both changes in temperature (VEL_{MAT}) and precipitation (VEL_{MAP}), which were based on 2.5 arc-minute resolution maps of contemporary climate (Hijmans *et al.* 2005) and paleo-climate projections (CCSM3 model; Braconnot *et al.* 2007). VEL_{MAT} and VEL_{MAP} were not significantly correlated ($n = 18$, $r = 0.20$, $P = 0.44$).

To assess the degree of shared evolutionary history among birds, we obtained a phylogeny of avian frugivores from a recently published super-tree (Jetz *et al.* 2012). We obtained a sample of 1000 dated pseudo-posterior trees for the 390 bird species in our networks. As these trees did not vary substantially in topology and branch lengths, we obtained a maximum clade credibility tree across our 1000 samples. To quantify the phylogenetic signal in interaction patterns for each network, we calculated phylogenetic pair-wise distances across all species in the phylogenetic tree (standardised to range between 0 and 1). These were related to an inverse measure of interaction similarity among avian frugivores, i.e. the distances in interaction patterns between all avian species pairs within a network, employing the Horn–Morisita metric

(ranging between 0 and 1). The avian phylogenetic signal in interaction patterns (PHYLO) was then calculated as the correlation coefficient between phylogenetic and interaction distances (separately for weighted and binary matrices), as obtained from parametric Mantel tests (Rezende *et al.* 2007), i.e. high correlations indicate similar interaction patterns in phylogenetically related species. We also ran partial Mantel tests accounting for differences in degree among species which resulted in qualitatively identical results (Table S1).

First, we tested whether modularity Q and ΔQ of weighted and binary interaction matrices were associated with absolute latitude and whether sampling effort and species richness influenced modularity and its relationship with latitude. Second, we fit univariate relationships of MAT, MAP, CV_{MAT} (log), CV_{MAP} (log), VEL_{MAT} (log), VEL_{MAP} (log) and PHYLO with weighted and binary modularity ΔQ with simple linear models and spatial simultaneous autoregressive error (SAR) models. For spatial analyses, we defined the neighbourhood of each study location by the four nearest locations. To test model robustness and the influence of single, potentially inadequately sampled networks, we sub-sampled studies with a jackknife procedure and computed standard deviations of r^2 across the resulting linear models ($n = 18$). Third, we fit multi-predictor models for both weighted and binary modularity ΔQ. We compared model fit according to the small-sample corrected Akaike information criterion (AIC_c) among linear models including all combinations of predictor variables and a null model only including the intercept. We did not include interaction terms between predictor variables because of the limited sample size. We calculated the relative importance of each predictor variable by summing Akaike weights across all models including the respective variable (Burnham & Anderson 2002, p. 168).

Species roles

We selected avian species traits that were related to bird morphology (body mass), foraging behaviour (degree of frugivory, social foraging) or to spatial and temporal patterns in species occurrence (forest dependence, migratory behaviour). We expected that species roles in networks could be simultaneously influenced by each of the five traits. Bird taxonomy followed Clements *et al.* (2012), except for *Chlorophonia cyanea* (Thraupidae, *not* Fringillidae) and *Spindalis portoricensis* (bird family undefined). We were able to compile complete trait information for 345 of the 390 bird species (see Appendix S1 for reference details): (1) Body mass was recorded as mean body mass for male and female individuals; (2) obligate and partial frugivores feeding on fruit as a major food source and opportunistic frugivores that use fruit as a minor complementary food source (according to Kissling *et al.* 2009); (3) social foragers that frequently forage in conspecific and mixed-species flocks, and non-social foragers; (4) forest specialists and species that also inhabit non-forest habitats and (5) short- or long-distance migratory species and residents.

We calculated weighted and binary z values (within-module degree) and c values (participation coefficient), as well as species strength and degree (*sensu* Bascompte & Jordano 2007), and excluded all species with a single observation from these calculations. To ensure comparability among networks, we standar-

dised z and c values as well as species strength and degree to zero mean and unit variance for each network. For each bird species that occurred in more than one network ($n = 81$ species), we calculated an average of standardised z and c values and species strength and degree across all networks (Krasnov *et al.* 2012). We tested phylogenetic signals in z and c values and in species strength and degree, by computing the λ statistic (Pagel 1999), testing it against a random shuffle of values across the tips of the phylogeny. An analysis of phylogenetic signal based on Blomberg's K and the same null model yielded qualitatively identical results (Blomberg *et al.* 2003). We also tested phylogenetic signals in species traits, employing the λ statistic for continuous and the d statistic for binary traits (Fritz & Purvis 2010). We found strong phylogenetic conservatism in all traits (body mass $\lambda = 1$; all binary traits, $0.16 < d < 0.44$; $P < 0.01$ in all cases). Therefore, we tested the influence of species traits on z and c values with phylogenetic generalised linear models (PGLMs), accounting for phylogenetic co-variation among species. This method optimises the degree of phylogenetic co-variation (λ) with a maximum likelihood approach (Freckleton *et al.* 2002). We fit PGLMs of weighted and binary z and c values and of species strength and degree with all combinations of trait variables (but not their interaction terms), and a null model only including the intercept, and identified the minimal adequate model based on the lowest AIC_c. We additionally calculated the relative importance of each trait across all model combinations according to their summed Akaike weights (Burnham & Anderson 2002, p. 168).

RESULTS

Different measures of modularity

In almost all seed-dispersal networks, interaction distances among both bird and plant species were significantly associated with their classification into modules, especially in weighted analyses (Table S2). Weighted networks were significantly more modular than expected from null models (except a single network, $P < 0.01$ for both null models; Table S1). By contrast, only 6 of 18 binary networks were significantly modular according to both null models (Table S1). Weighted and binary Q were positively related to the number of modules detected in a network, although this relationship was significant only for binary networks ($n = 18$; weighted Q, $r = 0.39$, $P = 0.11$; binary Q, $r = 0.67$, $P < 0.01$). The number of modules in a network was closely related to sampling intensity ($n = 18$; weighted analysis, $r = -0.79$, $P < 0.01$; binary analysis $r = -0.76$, $P < 0.01$), as was the case for uncorrected weighted and binary Q (Table S3, Fig. S1e and f). Both null-model corrected modularities (ΔQ_{PA}, ΔQ_{VA}) were not influenced by effects related to sampling effort and species richness (Table S3, Fig. S1e and f) and were therefore used in further analyses.

Macroecological patterns

Weighted network modularity ΔQ_{PA} increased with latitude (Table 1), whereas binary ΔQ_{PA} was also positively, but less strongly related to latitude (Table 1). In univariate linear and

Table 1 Relationships between weighted and binary modularity ΔQ_{PA} (corrected with the Patefield null) and (a) absolute latitude, (b) mean annual temperature (MAT), (c) temperature seasonality (CV_{MAT}), (d) temperature climate-change velocity since LGM (VEL_{MAT}), (e) mean annual precipitation (MAP), (f) precipitation seasonality (CV_{MAP}), (g) precipitation climate-change velocity since LGM (VEL_{MAP}) and (h) the avian phylogenetic signal in interaction patterns (PHYLO). Standardised regression coefficients β and their standard errors (SE) are given for univariate linear (*t* values) and SAR models (*z* values) accounting for spatial sampling locations. For each predictor variable, we provide r^2 values with their standard deviations derived from jackknifing each univariate model, and importance weights (*weight*) by summing up the weights of linear models including the respective predictor variable

	Weighted analysis				Binary analysis			
	β	SE (β)	*t/z*	*P*	β	SE (β)	*t/z*	*P*
(a) Latitude	$r^2 = 0.42 \pm 0.05$				$r^2 = 0.10 \pm 0.05$			
	0.65	0.19	3.42	<0.01	0.32	0.24	1.34	0.20
SAR model	0.68	0.15	4.39	<0.01	0.25	0.10	2.53	0.01
(b) MAT	$r^2 = 0.42 \pm 0.05$/*weight* = 0.23				$r^2 = 0.19 \pm 0.06$/*weight* = 0.51			
	−0.65	0.19	−3.41	<0.01	−0.44	0.23	−1.96	0.07
SAR model	−0.62	0.19	−0.23	<0.01	−0.29	0.11	−0.26	<0.01
(c) CV_{MAT}	$r^2 = 0.50 \pm 0.04$/*weight* = 0.87				$r^2 = 0.14 \pm 0.05$/*weight* = 0.30			
	0.71	0.18	3.99	<0.01	0.38	0.23	1.63	0.12
SAR model	0.79	0.09	8.77	<0.01	0.26	0.11	2.44	0.02
(d) VEL_{MAT}	$r^2 = 0.02 \pm 0.02$/*weight* = 0.25				$r^2 = 0.01 \pm 0.01$/*weight* = 0.22			
	0.15	0.25	0.62	0.54	−0.10	0.25	−0.42	0.68
SAR model	−0.14	0.21	−0.68	0.50	0.09	0.18	0.52	0.61
(e) MAP	$r^2 = 0.29 \pm 0.05$/*weight* = 0.16				$r^2 = 0.10 \pm 0.06$/*weight* = 0.19			
	−0.54	0.21	−2.55	0.02	−0.32	0.24	−1.36	0.19
SAR model	−0.48	0.22	−2.24	0.03	−0.21	0.14	−1.57	0.12
(f) CV_{MAP}	$r^2 = 0.17 \pm 0.08$/*weight* = 0.14				$r^2 < 0.01 \pm 0.01$/*weight* = 0.24			
	−0.41	0.23	−1.81	0.09	−0.28	0.25	−0.11	0.91
SAR model	−0.27	0.23	−1.21	0.23	−0.23	0.13	−1.81	0.07
(g) VEL_{MAP}	$r^2 = 0.05 \pm 0.03$/*weight* = 0.40				$r^2 < 0.01 \pm 0.01$/*weight* = 0.15			
	−0.23	0.24	−0.95	0.36	−0.10	0.25	−0.04	0.97
SAR model	−0.25	0.21	−1.18	0.24	−0.02	0.20	−0.09	0.92
(h) PHYLO	$r^2 = 0.07 \pm 0.03$/*weight* = 0.14				$r^2 = 0.18 \pm 0.04$/*weight* = 0.46			
	−0.26	0.24	−1.07	0.30	−0.42	0.23	−1.85	0.08
	−0.16	0.21	−0.77	0.44	−0.34	0.22	−1. 57	0.12

SAR models, weighted modularity ΔQ_{PA} was associated negatively with current mean annual temperature (MAT) and positively with temperature seasonality (CV_{MAT}), but was unrelated to temperature climate-change velocity (VEL_{MAT}) and the avian phylogenetic signal in interaction patterns (PHYLO) (Table 1, Fig. 1). Effects of temperature variables on weighted modularity were generally stronger than those of precipitation variables (Table 1). In multi-predictor models, all best-fit models of weighted ΔQ_{PA} included CV_{MAT} and its importance was more than twice as high as that of other predictors (Table 1). As null-model corrections removed most variability among binary networks (Fig. S1f), the proportion of explained variance was generally much lower in binary than weighted modularity ΔQ_{PA} (Table 1, Fig. S2). Results based on the second, more constrained null model (ΔQ_{VA}) were qualitatively identical, especially in weighted analyses (Table S4).

Species roles

Weighted and binary measures of *z* and *c* values were positively correlated (*n* = 312 species; *z* values: *r* = 0.46, *P* < 0.01; *c* values: *r* = 0.63, *P* < 0.01). However, the positive correlation was contingent on sampling intensity and decreased exponen-

tially with increasing sampling intensity (Fig. S3). Species strength was positively related to weighted measures of *z* and *c* values, especially to *z* values (*z* values: *r* = 0.78, *P* < 0.01; *c* values: *r* = 0.30, *P* < 0.01), and species degree was positively related to weighted *z* and *c* values (*r* = 0.60, *P* < 0.01 in both cases). We did not detect a phylogenetic signal in within-module degree *z*, neither in weighted ($\lambda < 0.01$, *P* = 1) nor binary analyses ($\lambda = 0.18$, *P* = 0.28), nor in species strength ($\lambda < 0.01$, *P* = 1). By contrast, *c* values exhibited a moderate but significant phylogenetic signal in weighted ($\lambda = 0.37$, *P* < 0.01) and binary ($\lambda = 0.31$, *P* = 0.02) analyses, corresponding to a significant phylogenetic signal in species degree ($\lambda = 0.35$, *P* < 0.01). Mostly tropical lineages, e.g. paleotropical families Pycnonotidae and Lybiidae and neotropical families Pipridae and Thraupidae, showed consistently high *c* values and species degree (Fig. 2).

Effects of species traits on *z* and *c* values and on species strength and degree were generally weak (Table 2). Consistent across all species-level metrics and weighted and binary analyses, values were higher for obligate and partial than for opportunistic frugivores (Table 2). In addition, frugivorous species with social foraging behaviour showed consistently higher weighted and binary *c* values than solitary foragers
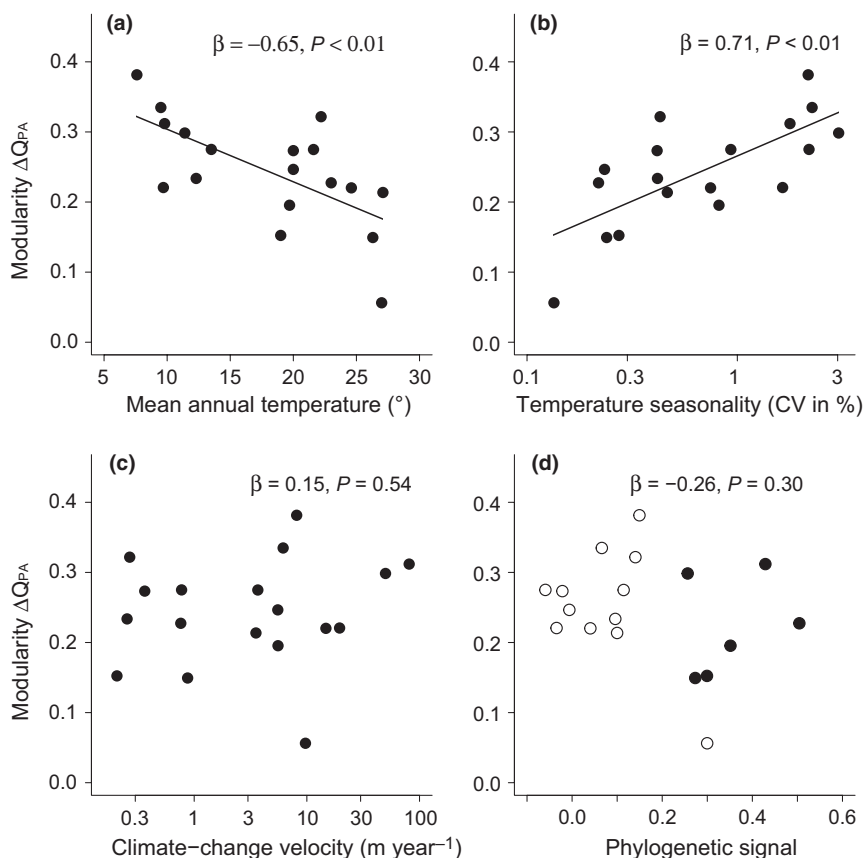
Figure 1 Relationships of weighted modularity ΔQ_{PA} with ecological factors (a, b), past climate (c) and phylogenetic signal (d). Shown are (a) current mean annual temperature, (b) temperature seasonality, (c) temperature climate-change velocity since LGM and (d) the avian phylogenetic signal in interaction patterns, given by the correlation between interaction and phylogenetic distances of bird species in each network; significant correlations in (d) are indicated by filled symbols. Standardised regression coefficients β are given with their P-values; significant relationships ($P < 0.05$) are indicated by trend lines derived from linear models (Table 1).

(Table 2); this difference was not detected in any other metric. All other species traits were not important for explaining the variability in z and c values and in species strength and degree (Table 3).

DISCUSSION

Ecological factors shape modularity in seed-dispersal networks

Weighted seed-dispersal networks were organised in modules, and they were more modular than one would expect in randomly associated communities. This is consistent with previous studies of modularity of binary seed-dispersal and other mutualistic plant–animal networks (Olesen *et al.* 2007; Donatti *et al.* 2011; Mello *et al.* 2011). We found that tropical avian seed-dispersal networks were less modular than temperate networks and that this latitudinal trend in modularity was much stronger in weighted than binary analyses. Uncorrected modularity of weighted and binary networks was strongly influenced by spatially varying sampling intensities (Fig. S1), which cautions against uncorrected comparisons of network metrics among studies. Null-model corrections removed the effects related to differences in sampling intensity, but in binary analysis these corrections erased almost all variability

among networks (Fig. S1). This indicates that null models may separate sampling artefacts from ecological patterns only in weighted analyses. Hence, binary analyses may be less suitable for comparative network analyses because sampling bias may often mask ecological patterns.

The latitudinal pattern of decreasing modularity towards the tropics was also reflected in underlying climatic drivers, as the degree of modularity in avian seed-dispersal networks was positively related to temperature seasonality. Consistently, species communities of temperate seed-dispersal networks vary seasonally (Plein *et al.* 2013). By contrast, seasonal turnover in fruiting plant communities is less pronounced in the tropics, where fruiting phenologies are subject to interannual, but comparatively weak seasonal fluctuations (Howe & Smallwood 1982; Chapman *et al.* 2005). Thus, the latitudinal gradient of weighted modularity in avian seed-dispersal networks may arise from higher seasonal partitioning of fruit and frugivore communities in temperate than tropical ecosystems.

Modularity of avian seed-dispersal networks was only weakly associated with past climatic fluctuations and the shared evolutionary history of avian seed dispersers. Our findings contrast with those from binary pollination networks, where modularity is particularly evident in the climatically stable tropics (Dalsgaard *et al.* 2013; Trøjelsgaard & Olesen
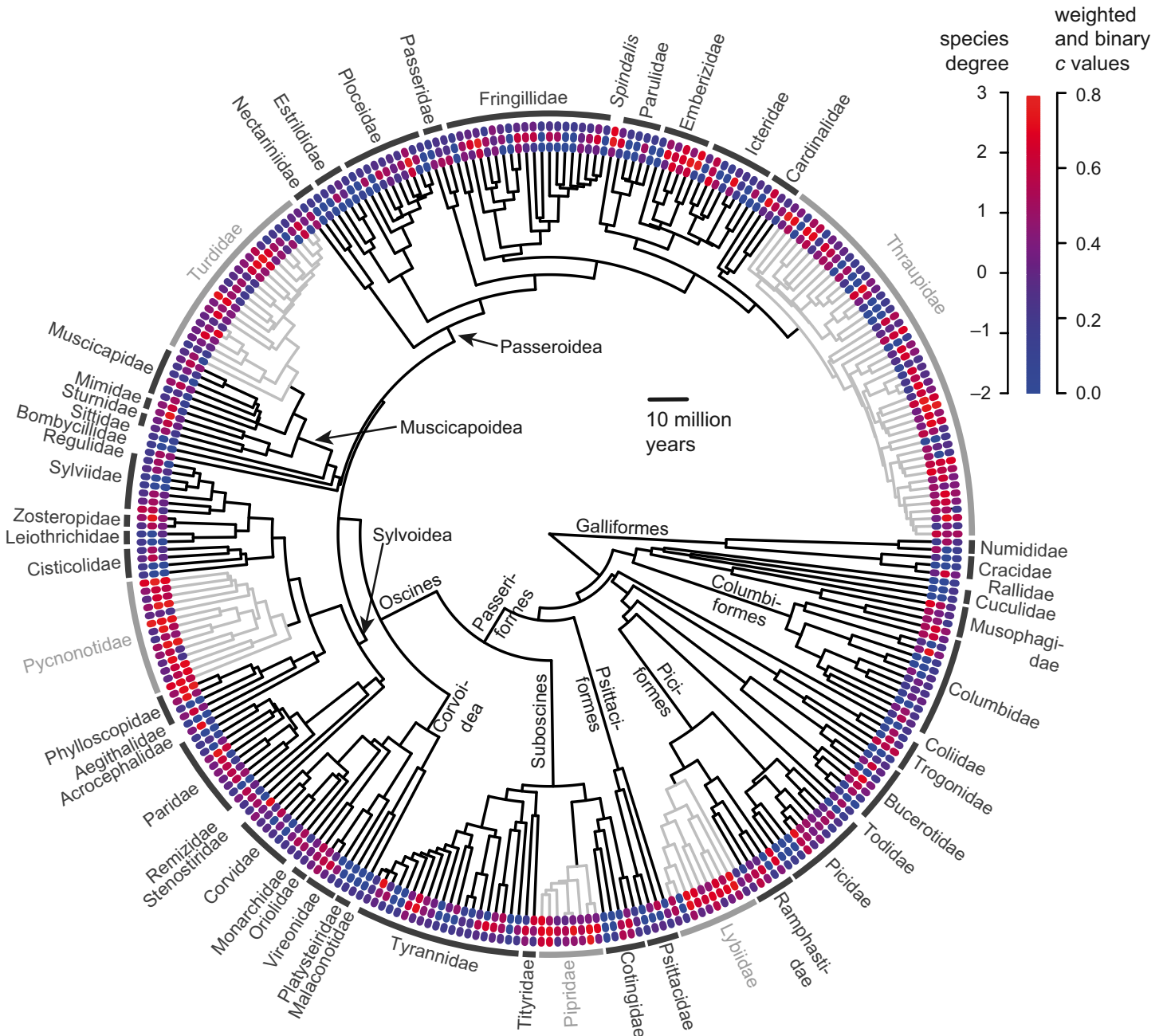
Figure 2 The distribution of weighted (inner circle) and binary (middle circle) *c* values as well as species degree (outer circle) across the phylogeny of avian frugivores. Red tips indicate high, blue tips indicate low values. For improved visualisation, colour scales are based on raw *c* values and standardised species degree (standard deviation units). Branch lengths are proportional to time (see scale bar), ancestral branches of key taxonomic groups and bird families are labelled. Grey branches indicate bird families for which connector values and species degree were significantly larger than the overall mean (only families with > 5 species tested): Lybiidae, Pipridae and Pycnonotidae for weighted and binary *c* and species degree, Thraupidae for weighted *c* and species degree and Turdidae for weighted and binary *c*.

2013). While most animal-dispersed plant species address functionally diverse seed-disperser communities that vary in space and time (Plein *et al.* 2013), animal-pollinated plants depend on transfer of conspecific pollen and thus on flower-constant pollinators (Pellmyr 2002). Hence, selective forces on plants in seed-dispersal systems differ from those in pollination systems, which could explain the observed differences in latitudinal modularity patterns. The observed ecological effects on modularity emphasise that ecological factors, such as seasonal fluc-

tuations in ecological communities (Bosch *et al.* 2009; Martín González *et al.* 2012), should receive the same attention in the interpretation of modularity as evolutionary processes (Donatti *et al.* 2011; Krasnov *et al.* 2012).

Phylogeny and foraging behaviour influence species roles

We found no phylogenetic signal in the within-module degree of bird species, which was also only weakly related to species

Table 2 Effects of species traits on (a) within-module degree z, (b) participation coefficients c and (c) species strength and degree in weighted and binary avian seed-dispersal networks. Minimal adequate phylogenetic generalised linear models (PGLMs), controlling for avian phylogeny, are given (according to AIC_c values), identified in comparisons between PGLMs containing all possible combinations of five traits of avian frugivores, i.e. degree of frugivory, social foraging behaviour, migratory behaviour, forest dependence and body mass. Standardised regression coefficients β with their standard errors, t-statistics and P-values for each predictor as well as r^2 and optimised phylogenetic co-variation λ for each model are given

	Weighted analysis				Binary analysis			
	β	SE (β)	t	P	β	SE (β)	t	P
(a) z values	λ = 0, P = 1; r^2 = 0.03				λ = 0, P = 1; r^2 = 0.05			
Degree of frugivory	0.32	0.10	3.29	<0.01	0.30	0.11	2.78	<0.01
Forest dependence	–	–	–	–	0.25	0.10	2.38	0.02
(b) c values	λ = 0.26, P = 0.06; r^2 = 0.06				λ = 0.18, P = 0.03; r^2 = 0.11			
Degree of frugivory	0.39	0.11	3.56	<0.01	0.48	0.11	4.44	<0.01
Social foraging	0.35	0.13	2.69	<0.01	0.46	0.13	3.48	<0.01
Migratory behaviour	–	–	–	–	–0.10	0.12	–0.78	0.44
(c) Strength/degree	λ = 0, P = 1; r^2 = 0.06				λ = 0.20, P = 0.01; r^2 = 0.09			
Degree of frugivory	0.43	0.09	4.62	<0.01	0.55	0.10	5.42	<0.01

Table 3 The importance of bird traits for explaining variation in within-module degree z, participation coefficients c and species strength and degree in weighted and binary avian seed-dispersal networks. Importance weights were calculated across phylogenetic generalised linear models (PGLMs) including all combinations of main effects of trait variables, and the importance for each predictor variable is given by summing up the Akaike weights of all PGLMs including the respective variable (Burnham & Anderson 2002, p. 168)

	Weighted analysis			Binary analysis		
	z value	c value	strength	z value	c value	degree
Degree of frugivory	0.98	0.99	1.00	0.94	1.00	1.00
Social foraging	0.45	0.89	0.47	0.46	0.98	0.60
Migratory behaviour	0.29	0.31	0.27	0.27	0.57	0.28
Forest dependence	0.31	0.34	0.29	0.86	0.19	0.37
Body mass (log)	0.27	0.20	0.29	0.29	0.34	0.38

traits. This suggests that modules in avian seed-dispersal networks are mostly formed by temporary associations of bird species feeding on the same plants (Plein *et al.* 2013). Species strength, which is closely related to species abundance (Bascompte & Jordano 2007), was correlated with within-module degree and was also unrelated to avian phylogeny. This suggests that factors related to species abundance, rather than phylogenetically conserved traits, were the main determinants of the modular structure of avian seed-dispersal networks.

In contrast to weak effects on within-module degree, phylogeny and selected species traits were significantly related to participation coefficients of frugivores, i.e. to the capacity of species to interact across modules and thus to connect different modules. The connector values of species were related to species degree, which was also phylogenetically conserved (see also Rezende *et al.* 2007). Accordingly, the disposition to feed on a high diversity of different fruit species seems to be concentrated in certain clades in the avian phylogeny. In general, traits related to foraging behaviour were most important for

differences in connector values, whereas avian body size was the trait contributing the least information to weighted analyses. This contrasts with the particular importance of body size in food webs (Woodward *et al.* 2005). It is likely that traits related to foraging behaviour are more important than coarse morphological variables in studies of specific functional groups of species. The apparent importance of body size in previous work on binary seed-dispersal networks (Donatti *et al.* 2011) could potentially be explained by fundamental differences between phylogenetic lineages (i.e. mammals vs. birds) rather than by body size *per se*, calling for rigorous phylogenetic correction in comparative analyses of species roles.

Our study underscores previous findings that opportunistic frugivores fill marginal positions in seed-dispersal networks, whereas the core of interactions is contributed by obligate and partial frugivores (Schleuning *et al.* 2011). Obligate and partial frugivores tend to interact across modules because they have to feed on many fruiting plants to balance their nutritional demands and the spatiotemporal patchiness in fruit availability. The importance of obligate and partial frugivores is particularly high in the tropics (Kissling *et al.* 2009), where they contribute more interactions to seed-dispersal networks (mean ± SE: 80.5 ± 2.2%; n = 18 networks) than in temperate systems (57.3 ± 8.1%). Social foraging behaviour was the other key trait defining avian connector species and may constrain the formation of modules within seed-dispersal networks. In accordance with this, many frugivorous tropical birds are known to forage in mixed-species flocks (Saracco *et al.* 2004). In our study, species that tended to forage in social flocks contributed more than half of the interactions to tropical networks (56.9 ± 6.7%) and significantly fewer interactions to temperate networks (32.1 ± 5.7%).

The results of the species-level analyses correspond well to macroecological patterns in modularity. Low modularity in tropical seed-dispersal systems may be associated with the importance of social and generalist frugivores found in specific phylogenetic lineages of tropical birds. The importance of generalist species for the evolution of seed-dispersal sys-

tems has been noted previously, assuming that these species are primarily large frugivores (e.g. quetzals and large cotingids, Guimarães *et al.* 2011). Our findings suggest that also species-rich lineages of small tropical frugivores, such as bulbuls (Pycnonotidae) and tanagers (Thraupidae), have been key nodes in the evolution of these networks. Hence, the low modularity of tropical seed-dispersal systems may also result from the pervasive connector traits of specific lineages of tropical frugivores.

CONCLUSIONS

Networks of any kind are usually poorly represented by binary links (Barrat *et al.* 2004; Scotti *et al.* 2007). The robustness and relevance of modularity analyses in ecology increase when including information on interaction frequencies (Ings *et al.* 2009). We employ a weighted modularity concept for bipartite networks and show that macroecological patterns in seed-dispersal networks were best resolved in weighted analyses, accounting for sampling bias with null-model corrections. Our approach to weighted modularity was also informative for associating roles of species with phylogeny and species traits, here yielding similar patterns in weighted and binary analyses. This illustrates that modularity analyses of weighted bipartite networks may improve our understanding of the ecological and evolutionary causes of modularity in different types of bipartite ecological networks. For the case of seed-dispersal networks, we demonstrate that the modular structure of plant–frugivore associations is primarily determined by current ecological factors and that phylogeny and foraging behaviour have significant effects on the functional roles of avian seed dispersers in modular networks.

AUTHORSHIP

MS and CFD conceived the idea. RS and CFD developed the modularity algorithm. MS, LI, DMD, MP, FS and KBG contributed network data. BD, BS and JCS contributed climate models. SAF contributed phylogenetic data. MS, LI, RS, SAF and CFD performed analyses. MS and CFD drafted the manuscript. All authors contributed to interpretation and writing.

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