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Opposed latitudinal patterns of network-derived and dietary specialization in avian plant–frugivore interaction systems

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Latitudinal patterns of biodiversity have been studied for centuries, but it is only during the last decades that species interaction networks have been used to examine the proposed latitudinal gradient of biotic specialization. These studies have given idiosyncratic results, which may either be because of genuine biological differences between systems, different concepts and scales used to quantify biotic specialization or because the methodological approaches used to compare interaction networks were inappropriate. Here we carefully examine the latitudinal specialization gradient using a global dataset of avian plant–frugivore assemblages and interaction networks. In particular, we test whether network-derived specialization patterns differ from patterns based on assemblage-level information on avian dietary preferences on specific food types. We found that network-derived measures of specialization (complementary specialization H_2' and $<d'>$, modularity Q) increased with latitude, i.e. frugivorous birds divide the niche of fruiting plants most finely at high latitudes where they also formed more modular interaction networks than at tropical latitudes. However, the strength and significance of the relationship between specialization metrics and latitude was influenced by the methodological approach. On the other hand, assemblage-level information on avian specialization on fruit diet (i.e. the proportion of obligate frugivorous bird species feeding primarily on fruit) revealed an opposed latitudinal pattern as more bird species were specialized on fruit diet in tropical than in temperate assemblages. This difference in the latitudinal specialization gradient reflects that obligate frugivores require a high diversity of fruit plants, as observed in tropical systems, and fulfil more generalized roles in plant–frugivore networks than bird species feeding on different food types. Future research should focus on revealing the underlying ecological, historical and evolutionary mechanisms shaping these patterns. Our results highlight the necessity of comparing different scales of biotic specialization for a better understanding of geographical patterns of specialization in resource–consumer interactions.

In biogeography, one of the most prominent patterns is the increase in species richness toward the tropics. This pattern is so universal across taxa that it may be one of the few general patterns in ecology (Lawton 1999, Hillebrand 2004). Another long-held tenet in ecology is that tropical species are more specialized, i.e. have a finer partitioning of niche space, which may facilitate the coexistence of a higher number of species in the tropics than in temperate regions (Dobzhansky 1950, MacArthur 1969, Schemske 2002, Schemske et al. 2009). A priori, one might indeed expect that species with broad niches inhabit temperate environments, as lower productivity and more seasonal and inter-annual fluctuations in climate and resources should select for morphological, physiological and behavioral traits that allow foraging on a broad range of food types (Waser et al. 1996, Dynesius and Jansson 2000, Dalsgaard et al. 2011, 2013, Rech et al. 2016). However, it remains debated whether biotic specialization in fact decreases toward temperate regions.

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During the last decades, there has been a renewed interest in evaluating the latitudinal gradient in biotic specialization using species interaction networks. Studies have used mutualistic plant–pollinator networks (Olesen and Jordano 2002, Ollerton and Cranmer 2002, Dalsgaard et al. 2011, Schleuning et al. 2012), plant–frugivore networks (Schleuning et al. 2012, 2014) and antagonistic host–parasite and host–parasitoid networks (Guilhaumon et al. 2012, Morris et al. 2014) to ask whether biotic specialization shows a latitudinal pattern. These empirical studies have given idiosyncratic results, finding higher specialization in the tropics (Olesen and Jordano 2002, Dalsgaard et al. 2011, Trøjelsgaard and Olesen 2013), no latitudinal pattern (Ollerton and Cranmer 2002, Morris et al. 2014), or higher specialization in temperate regions (Schleuning et al. 2012, Pauw and Stanway 2014). For instance, hummingbirds and their nectar plants were shown to be more specialized toward the tropics, consistent with the hypothesis that biotic specialization of tropical organisms is caused by high productivity and climatic stability in the tropics (Dalsgaard et al. 2011). On the other hand, plant–frugivore networks were shown to be most specialized in temperate regions, associated with low plant richness and high climatic seasonality at high latitudes (Schleuning et al. 2012, 2014). This suggests that there may not be a universal direction of the latitudinal specialization gradient (Moles and Ollerton 2016).

Another possible explanation for these contrasting results could be that geographical patterns could be falsely detected, or rejected, if the methodological approach is inappropriate (Almeida-Neto et al. 2008, Chagnon 2015, Fründ et al. 2016, Vizentin-Bugoni et al. 2016). To date, no consensus on the best practice for comparative analyses of species interaction networks has been achieved. Notably, network metrics are influenced by sampling effort (Fründ et al. 2016, Vizentin-Bugoni et al. 2016) and studies have dealt differently with the heterogeneity in sampling across networks: some ignoring differences in sampling effort (Olesen and Jordano 2002), some using null models to standardise its effects across networks (Schleuning et al. 2012, Trøjelsgaard and Olesen 2013, Pauw and Stanway 2014), and some accounting for differences in sampling by using a measure of sampling effort as a covariate in regression models (Ollerton and Cranmer 2002, Dalsgaard et al. 2011). These analytical differences may affect the interpretation of geographical patterns of network-derived metrics, such as the latitudinal specialization gradient (Ollerton and Cranmer 2002, Rivera-Hutinel et al. 2012, Kissling and Schleuning 2015, Fründ et al. 2016, Vizentin-Bugoni et al. 2016).

Network-derived estimates of specialization usually focus on a specific interaction type, e.g. mutualistic plant–pollinator or plant–frugivore interactions (Blüthgen et al. 2006), and illustrate how consumer species partition a specific type of resource (e.g. fleshy-fruited plants for frugivorous birds) under the given conditions. Interaction networks thus rarely represent the complete diet of species as many species interact in different types of interaction systems (Fontaine et al. 2011, Kissling et al. 2012, Mello et al. 2015, Dalsgaard et al. 2016). For instance, most fruit-consuming bird species have an omnivorous diet, which includes animal food in addition to fruits (Kissling et al. 2012), thus participating simultaneously in different types of ecological networks. Although we currently lack comprehensive information on the structure of such networks of networks (but see Pocock et al. 2012, Albrecht et al. 2014, Boccaletti et al. 2014), classifications of the general dietary requirements of consumer species have been established and provide information on a species' major and minor food sources, such as insects, fruits or nectar (Kissling et al. 2012, Wilman et al. 2014). Information derived from such databases have also been used to test gradients in biotic specialization, e.g. by comparing assemblage-level information on the dietary niche breadth of species, and have found increasing trends of avian dietary specialization toward tropical latitudes (Belmaker et al. 2012). Comprehensive analyses of biotic specialization gradients, thus, should aim at comparing different scales of biotic specialization simultaneously (Ollerton et al. 2007). Specifically, differences in the extent (single vs many types of interaction systems) and the grain (e.g. taxonomic units vs food categories) at which biotic specialization is quantified could result in different spatial patterns.

Here, we critically evaluate geographical patterns of specialization in bipartite species interaction networks, i.e. the interaction pattern between two parties of species such as plants and animals. We focus on the latitudinal gradient in biotic specialization in terms of niche partitioning among species within interaction networks (Blüthgen 2010) and in terms of dietary specialization of consumer species on specific food types (Belmaker et al. 2012). Specifically, we use an established global dataset of 21 weighted networks of plants and frugivorous birds with the aim to: 1) test whether different analytical approaches to compare network-derived specialization yield similar specialization–latitude relationships; and 2) contrast the network-derived latitudinal specialization gradient with the latitudinal pattern of dietary preferences of bird species (i.e. an assemblage level measure of avian dietary specialization). We demonstrate that network-derived specialization increases with latitude, although the strength and significance of the latitudinal specialization gradient depend on the specific analytical approach taken. The latitudinal pattern of dietary preferences of bird species showed an opposite latitudinal pattern, i.e. more bird species in tropical assemblages were specialized on fruit diet than in temperate assemblages. Our results highlight the necessity of comparing different scales of biotic specialization when evaluating latitudinal and other geographical patterns of biotic specialization.

Material and methods

Plant–frugivore networks and measures of biotic specialization

We used an updated version of the global dataset of Schleuning et al. (2012, 2014) consisting of 21 weighted plant–frugivore birds networks (for details see Supplementary material Appendix 1) to contrast network-derived and dietary specialization along the latitudinal gradient. In the interaction networks, a plant and a frugivorous bird species are linked if a given bird species is recorded eating fruits of a given plant species (Schleuning et al. 2011, 2014, Mello et al. 2015).

The more times a given link between a plant and a bird species is observed, the higher its interaction frequency. The resulting weighted plant–frugivorous bird networks illustrate the interaction pattern of entire assemblages of plants and their frugivorous birds. Compared to binary networks, weighted networks better reflect dependencies between species and the structure of interaction networks (Vázquez et al. 2005, Lewinsohn et al. 2006). Additionally, metrics based on binary networks have been shown to be more sensitive to sampling bias than metrics based on weighted networks (Banašek-Richter et al. 2004, Fründ et al. 2016, Vizentin-Bugoni et al. 2016). When conducting geographical analyses, it is therefore desirable to use metrics based on weighted networks to measure the partitioning of interactions among species, i.e. biotic specialization (Blüthgen 2010). Network-derived specialization is here characterized by two metrics that quantify niche partitioning among species ('niche-based metrics', sensu Blüthgen 2010). First, complementary specialization H_2' quantifies to what extent interaction frequencies deviate from an expected probability distribution of interactions, given by random encounter probabilities of species in proportion to species' total frequencies. The biological assumption here is that if species have preferences for specific interaction partners, these preferences would be captured as deviation from random encounters given by partner availability (Blüthgen et al. 2006). Values of H_2' are scaled to range from 0 to 1 indicating the extremes of generalization and specialization, respectively. Following the same rationale, complementary specialization may be quantified for each species, d', and summarized to represent guild-level specialization $<d'>$ as the weighted mean across species, with weights given by the total interaction frequency of each species (Blüthgen et al. 2006). Second, we calculate bipartite modularity Q, computed by the QuanBiMo algorithm (Dormann and Strauss 2014), which identifies network modules, i.e. weakly connected subsets of species that are internally strongly connected (Olesen et al. 2007, Blüthgen 2010). Thus, Q quantifies the prevalence of interactions within modules in relation to interactions among modules. The metric ranges between 0 (no more links within modules than expected by chance) and 1 (maximum degree of modularity). Modularity can be interpreted as a measure of niche-based specialization, as the division of networks into modules reflects the specialization of species on specific groups of interaction partners (Olesen et al. 2007), such as phylogenetically or phenotypically related groups of species (Maruyama et al. 2014, Schleuning et al. 2014, Martín González et al. 2015).

An important step in geographical analyses of interaction networks is to take into account potential sampling bias which might affect networks metrics, as not all networks require the same effort to accurately estimate network structure (Costa et al. 2015, Kissling and Schleuning 2015). This is usually done by either adding sampling-related covariates to regression models or by employing null model corrections (Schleuning et al. 2012, Trøjelsgaard and Olesen 2013, Sebastián-González et al. 2015). We here apply both approaches. Sampling covariates include sampling intensity, sampling completeness and time span of the study (Chacoff et al. 2012, Schleuning et al. 2012). Sampling intensity is defined as the square-root of the number of interaction events in the network divided by the square-root of the product of the number of animal and the number of plant species in the network (Schleuning et al. 2012). Thus, it quantifies how many interaction events have been observed per species. Sampling completeness of a network is estimated by dividing the observed richness of links by an estimated richness of links (Chacoff et al. 2012). The estimated link richness can be approximated by the Chao 1 estimator of asymptotic richness (Chao 1984). In this method, each pairwise link between a plant and animal species is regarded as the equivalent of a 'species' and the frequency of each pairwise link as 'abundance' (Vizentin-Bugoni et al. 2016). Here, and in geographical analyses in general, null model corrections include Δ- and z-transformations, which both quantify differences between observed and null-model derived metrics (Schleuning et al. 2012, Sebastián-González et al. 2015). In Δ-transformation, the mean value of a metric obtained by multiple randomizations of a network is subtracted from the observed value. In z-transformation, the Δ-transformed value is additionally divided by the standard deviation of values across all randomized networks. Both the Δ- and z-transformation describe to what extent an empirical observation departs from a random pattern defined by a specific null model. The idea behind these procedures is to correct observed network metrics by fixing certain properties of the network that may be influenced by sampling (Fründ et al. 2016). Here, we used the Patefield (PA) null model which fixes the network size as well as the marginal totals of each row and column, given by the species' total frequencies of interaction (Patefield 1981). Thus, it constrains both the species richness and the total number of interactions per species (Dormann et al. 2008). We additionally used a second null model, Vázquez (VA), which constrains network size and connectance, i.e. the proportion of realized links between consumer and resource species relative to the total number of possible links (Vázquez et al. 2007).

In addition, we also quantified avian specialization on specific food types as another measure of biotic specialization, corresponding to a larger extent (multiple instead of single interaction systems) and a smaller grain (food categories instead of taxonomic species) of specialization compared to network-derived specialization measures. We used the classification by Kissling et al. (2012) to identify bird species in the networks with an obligate fruit diet. Obligate frugivores are species that primarily feed on fruits and have fruits as their only major food type. Based on this classification of species, we calculated the proportion of obligate frugivorous bird species for each assemblage as a measure of avian specialization on fruit diet.

Latitudinal patterns of specialization in plant–frugivore interactions

To assess latitudinal patterns of specialization, first we used ordinary least squares regression to evaluate the association between network-derived specialization measures and latitude, both with and without sampling-related covariates (Table 1, Supplementary material Appendix 3). Sampling intensity (log-transformed) and sampling

Table 1. Latitudinal patterns in biotic specialization for weighted plant–frugivore networks. For each of H_2' and Q, we calculated both observed (obs) and null model corrected specialization (Δ and z), using both the Patefield (PA) and Vázquez (VA) null models. We used ordinary least squares regression to evaluate the association between specialization and latitude: (a) without including sampling effort, (b) controlling for sampling intensity (Intensity), (c) controlling for sampling completeness (Complet.), (d) controlling for sampling intensity and time span (number of days), and (e) controlling for sampling completeness and time span (number of days). Associations are reported as standardized regression coefficients. For each model, we also report the coefficient of determination (R^2_{adj}). See Supplementary material Appendix 3 for similar calculations using $<d'>$. We additionally computed the proportion of obligate frugivorous birds in the respective networks (i.e. avian dietary preference), and tested the association between latitude and dietary preference both using ordinary least squares regression (on arcsine-sqrt transformed values; $\beta = -0.72$, $p < 0.001$) and a logistic regression (untransformed values; $\beta = -0.04$, $p < 0.001$).

		Complementary specialization (H_2')					Modularity (Q)				
		obs	Δ-PA	Δ-VA	z-PA	z-VA	obs	Δ-PA	Δ-VA	z-PA	z-VA
(a)	Latitude	$+0.41^{NS}$	$+0.64^{**}$	$+0.69^{**}$	$+0.63^{**}$	$+0.56^{**}$	$+0.12^{NS}$	$+0.59^{**}$	$+0.59^{**}$	$+0.60^{**}$	$+0.60^{**}$
	R^2_{adj}	0.17	0.40	0.48	0.40	0.32	0.02	0.34	0.35	0.36	0.36
(b)	Latitude	$+0.55^{*}$	$+0.46^{*}$	$+0.42^{*}$	$+0.27^{NS}$	$+0.23^{NS}$	$+0.61^{**}$	$+0.41^{NS}$	$+0.36^{NS}$	$+0.26^{NS}$	$+0.25^{NS}$
	Intensity	-0.26^{NS}	$+0.31^{NS}$	$+0.49^{*}$	$+0.64^{**}$	$+0.59^{**}$	-0.88^{**}	$+0.33^{NS}$	$+0.42^{NS}$	$+0.62^{**}$	$+0.63^{**}$
	R^2_{adj}	0.17	0.44	0.62	0.66	0.53	0.53	0.39	0.46	0.61	0.62
(c)	Latitude	$+0.43^{NS}$	$+0.54^{**}$	$+0.58^{**}$	$+0.51^{**}$	$+0.44^{*}$	$+0.28^{NS}$	$+0.47^{*}$	$+0.47^{*}$	$+0.46^{*}$	$+0.46^{*}$
	Complet.	-0.08^{NS}	$+0.32^{NS}$	$+0.36^{*}$	$+0.41^{*}$	$+0.41^{*}$	-0.55^{*}	$+0.38^{*}$	$+0.40^{*}$	$+0.48^{**}$	$+0.47^{*}$
	R^2_{adj}	0.13	0.47	0.58	0.53	0.44	0.25	0.45	0.47	0.55	0.54
(d)	Latitude	$+0.56^{*}$	$+0.47^{*}$	$+0.42^{*}$	$+0.27^{NS}$	$+0.23^{NS}$	$+0.61^{**}$	$+0.41^{NS}$	$+0.36^{NS}$	$+0.26^{NS}$	$+0.25^{NS}$
	Intensity	-0.33^{NS}	$+0.24^{NS}$	$+0.41^{*}$	$+0.69^{**}$	$+0.64^{**}$	-0.89^{**}	$+0.28^{NS}$	$+0.37^{NS}$	$+0.67^{**}$	$+0.68^{**}$
	Time span	-0.24^{NS}	-0.26^{NS}	-0.27^{NS}	$+0.18^{NS}$	$+0.16^{NS}$	-0.04^{NS}	-0.15^{NS}	-0.17^{NS}	$+0.19^{NS}$	$+0.18^{NS}$
	R^2_{adj}	0.18	0.48	0.67	0.67	0.53	0.50	0.38	0.45	0.62	0.63
(e)	Latitude	$+0.41^{NS}$	$+0.50^{**}$	$+0.54^{**}$	$+0.51^{**}$	$+0.47^{*}$	$+0.30^{NS}$	$+0.45^{*}$	$+0.44^{*}$	$+0.47^{*}$	$+0.47^{*}$
	Complet.	-0.09^{NS}	$+0.31^{NS}$	$+0.35^{*}$	$+0.42^{*}$	$+0.41^{*}$	-0.54^{*}	$+0.38^{*}$	$+0.40^{*}$	$+0.48^{*}$	$+0.47^{*}$
	Time span	-0.18^{NS}	-0.29^{NS}	-0.34^{*}	$+0.05^{NS}$	$+0.05^{NS}$	$+0.12^{NS}$	-0.20^{NS}	-0.23^{NS}	$+0.07^{NS}$	$+0.06^{NS}$
	R^2_{adj}	0.12	0.53	0.68	0.51	0.41	0.22	0.46	0.51	0.53	0.51

$^{**}p < 0.01$; $^{*}p < 0.05$; ^{NS}non-significant.

completeness (arcsine-sqrt transformed) were closely related ($r = 0.81$, $p < 0.01$), whereas sampling intensity and sampling completeness were unrelated to the time span of sampling ($r = -0.27$, $p > 0.05$ and $r = -0.08$, $p > 0.05$, respectively). Thus, we did not include sampling intensity and sampling completeness in the same regression models, but included time span as additional co-variate in models with sampling intensity and sampling completeness (Table 1, Supplementary material Appendix 3). Second, we contrasted the analysis of network-derived specialization with latitudinal patterns in dietary preferences of bird species in the respective assemblages, i.e. the proportion of obligate frugivorous bird species within each network. We tested the association between latitude and dietary preference both using ordinary least squares regression (using arcsine-sqrt transformed values) and a logistic regression (untransformed values). None of the ordinary least squares regression models were biased by multicollinearity (CN < 2.0; VIF < 1.6) or positive spatial autocorrelation ($p > 0.05$, based on Moran's I values with 10 distance classes and a permutation test with 10 000 iterations on the model residuals).

Network metrics and null-model transformations were calculated using the 'bipartite' package in R (Dormann et al. 2008); the Chao 1 estimator of asymptotic richness was computed using the 'vegan' package in R (Oksanen et al. 2014). The association between latitude and the proportion of obligate frugivorous bird species was tested with a logistic regression using the 'stats' package in R (R Core Team) and with an ordinary least squares regression using the software Spatial Analysis in Macroecology, SAM 4.0 (Rangel et al. 2010); all other ordinary least squares regressions were likewise calculated with SAM 4.0 (Rangel et al. 2010).

Results

For each of the 21 plant–frugivorous bird networks, we provide the geographic coordinates of the sampling location, report the sampling effort (i.e. time span of the sampling period, sampling intensity, and sampling completeness), the proportion of obligate frugivorous birds, and network-derived specialization metrics (H_2', $<d'>$, Q). The proportion of obligate frugivorous birds in each network varied from 0 to 63%. Observed values of network-derived specialization (H_2', $<d'>$, Q) ranged between 0.18–0.48, 0.13–0.41 and 0.21–0.47, respectively. See Supplementary material Appendix 2 for details, including values of null-model corrected network-derived specialization. All network-derived specialization metrics (H_2', $<d'>$, Q) increased with absolute latitude, but the strength and significance of this relationship was influenced by the methodological approach (Table 1, Supplementary material Appendix 3; Fig. 1). Whereas observed (obs) metric values associated non-significantly with latitude, they were significantly associated with latitude when including sampling intensity as a covariate (Table 1, Supplementary material Appendix 3). All null-model corrected (Δ and z) metrics were significantly associated with latitude in univariate analysis, but some latitudinal associations were non-significant when including sampling-related covarites (Table 1, Supplementary material Appendix 3; Fig. 1). Contrary to network-derived specialization, the proportion of obligate frugivorous birds in each network, i.e. avian specialization on fruit diet, was negatively related to latitude (OLS regression: $\beta = -0.72$, $p < 0.001$; logistic regression: $\beta = -0.04$, $p < 0.001$; Fig. 1).

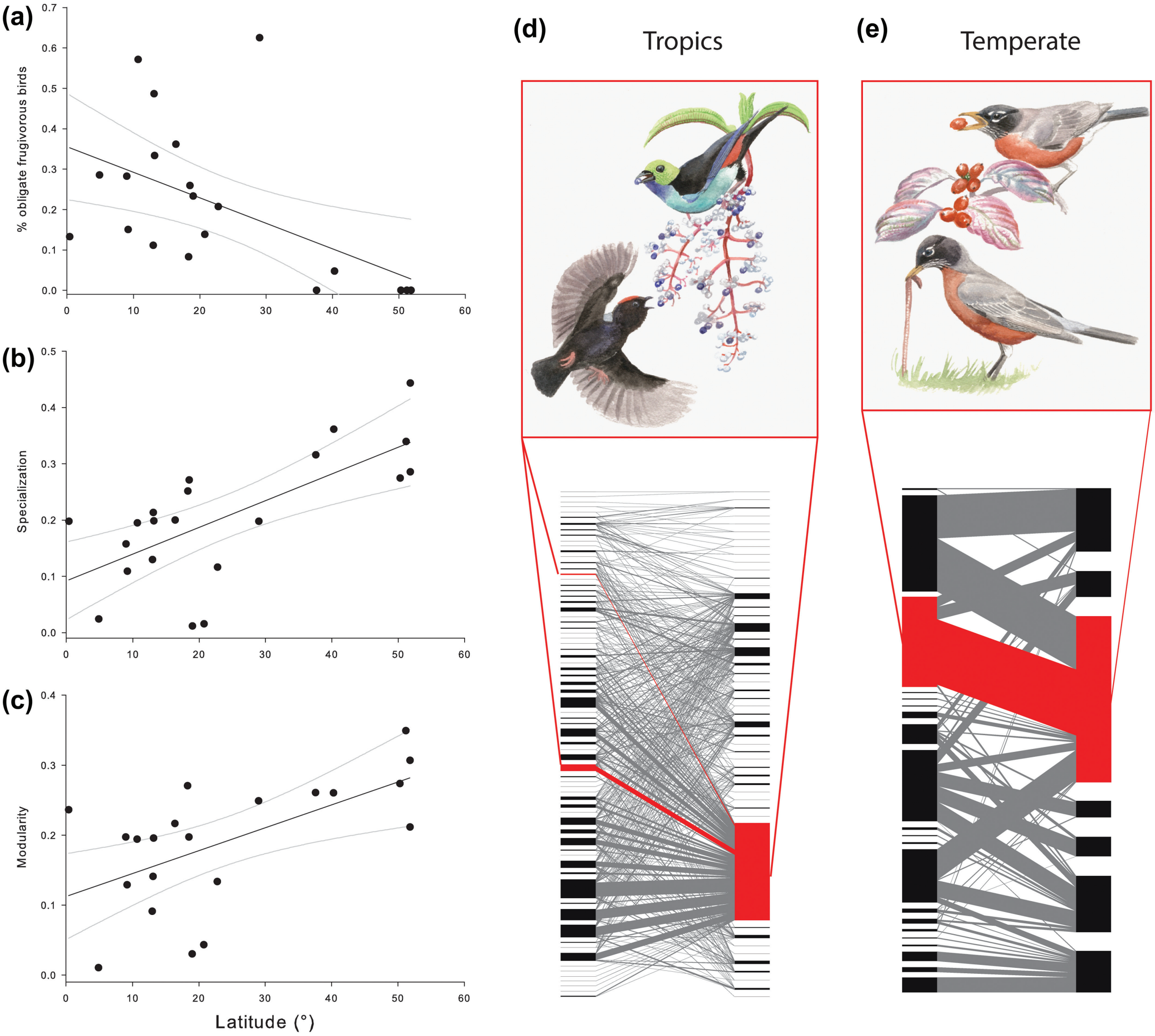

Figure 1. Latitudinal patterns of specialization for frugivorous birds and their fruit plants. There is an opposed latitudinal pattern of network-derived and assemblage-level dietary specialization: (a) the proportion of obligate frugivorous birds decreases with latitude, whereas network-derived (b) complementary specialization (Δ-VA H_2') and (c) modularity (Δ-VA Q) increased with latitude. Note that we illustrate null model corrected specialization and modularity using Δ-transformation and the Vázquez (VA) null model (see Table 1 for similar results when using observed metric values, the Patefield null model and z-transformation). The example interaction networks and species interactions illustrate (d) with a South American network that tropical communities mainly consist of obligate frugivourous birds, which form fairly generalized interaction networks, i.e. the birds often share fruit recourses, as exemplified with *Tangara chilensis* and *Chiroxiphia boliviana* both eating berries from a *Miconia* sp., and (e) with a North American network that high latitude communities consist mainly of bird species with an omnivorous diet containing both fruits and a wide range of other food types, but form specialized networks of interactions with their fruit plants. For instance, *Turdus migratorius* eats both earthworms and fruits of e.g. *Cornus florida*. In the networks, birds are shown to the left and plants to the right; link thickness reflects the pairwise frequency of interaction, and bar size illustrates the total number of interactions for each species. Paintings by Jon Fjeldså.

Discussion

We show that network-derived specialization of plant–frugivore systems is highest in temperate regions, i.e. frugivorous birds divide the niche of fruiting plants most finely at high latitudes where they also form modular subsets of closely associated plant and bird species (Fig. 1). At the same time, however, there are more obligate frugivorous bird species in the tropics than in temperate regions, i.e. more bird species specialize on fruit diet in the tropics (Fig. 1). We note that temperate biomes are also characterized by having less plant species with fleshy fruits than tropical biomes (Chen et al. 2016) and that previous studies have shown that animal species entirely dependent on fruit diet (i.e. obligate frugivores) interact with more plant partners than opportunistic frugivores that interact across different types of interaction systems (Schleuning et al. 2011, 2014, Mello et al. 2015). The evolution of obligate frugivory in the tropics may thus have resulted in a high overlap of fruiting plants among avian frugivores and a low degree of modularity in these systems (Schleuning et al. 2014).

Irrespective of the mechanism causing the detected pattern in plant–frugivore systems, our results show that the scale on which biotic specialization is measured matters. Specifically, we show that dietary specialization across different interaction systems and niche partitioning among species within interaction networks result in opposed spatial patterns. This difference in the scale of biotic specialization is especially relevant for animal groups having both obligate species and species that interact across different types of interaction systems, such as frugivorous birds and many groups of vertebrates. However, it also applies to invertebrates that may use different dietary types during different life stages. For those animal groups, a comprehensive analysis of biotic specialization gradients, should aim at comparing different scales of biotic specialization simultaneously (Ollerton et al. 2007).

Additionally, we note that the comparison between geographical patterns of observed and null-model transformed network metrics may offer an opportunity to gain insights into the mechanisms driving patterns of biotic specialization (Martín González et al. 2015). If differences in species richness are controlled for by the specific null model, one may, for instance, test the importance of species richness for the latitudinal pattern of specialization. In our comparative analyses of different null-model approaches, we found that z-scores were strongly positively associated with sampling intensity and completeness, whereas Δ-transformed metrics were less related to sampling-related covariates (Table 1). In line with our finding, Chagnon (2015) suggested that z-transformed metrics may introduce artefactual differences between networks and should be used with caution. This suggests that Δ-transformed metrics may be better suited for geographical analyses of interaction networks with heterogeneous sampling than z-transformed metrics. We also note that sampling intensity and sampling completeness to some extent influenced the detected pattern for both observed and null-model transformed metrics, and that more work is needed to clarify whether sampling intensity or sampling completeness are better suited to account for differences in sampling effort among interaction networks. Therefore, we suggest to test the influence of sampling on the respective network metric and to include sampling intensity and completeness as covariates in the regression model. If ignoring such sampling-related effects, geographical patterns, such as the latitudinal specialization gradient, may be misinterpreted. Likewise, to ensure that geographical patterns are not biased because of sampling being limited to specific seasons, such as temporal booms of fruits in seasonal climates, we stress that one should also test whether the time span of the studies influences the detected geographical pattern.

In conclusion, we highlight the necessity of comparing network-derived and other metrics of biotic specialization, such as diet preferences, at least for animal groups that interact across different types of interaction systems. Thus, we recommend that geographical studies of species interaction networks should follow a protocol that combines different analytical approaches and uses different sources of information to quantify biotic specialization at different scales. Here, we have shown how this improves our understanding of the latitudinal specialization gradient in avian plant–frugivore systems. Our recommendation equally applies to comparative analyses of biotic specialization in other resource-consumer interaction systems and along other types of geographical and environmental gradients.

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Supplementary material (Appendix ECOG-02604 at <www.ecography.org/appendix/ecog-02604>). Appendix 1–3.