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Abstract

Understanding how the structure of ecological communities varies across biotic and abiotic dimensions is a fundamental goal in ecology. This challenge is now approachable due to the increasing availability of data on community structure across the globe. Ecological communities are often defined with respect to the guilds considered and the interactions they engage in, but it is unclear whether interactions of different types respond similarly to large-scale environmental gradients. Therefore, we don't know whether there exist differences in how the emergent structure of ecological networks varies across biogeographical gradients, depending on their constituent interaction types. Here, using a unique dataset of 952 networks across the globe, we provide a first comparison of network structural metrics and their large-scale variability for five overarching interaction types (feeding, frugivory, herbivory, parasitism, pollination). We show that networks of different types tend to be more modular than expected, but other structural metrics do not deviate from what is expected given the degree distributions of the networks. Our analysis also reveals that network sampling intensity is a particularly relevant factor influencing network degree distribution, and that food webs appear in general more sensitive to environmental factors than other interaction types. By analysing common descriptors from the degree distributions of ecological networks, this study underscores for the first time generalities and differences across different interaction types and their response to environmental, sampling, and anthropic factors.

Introduction

Ecological communities are emergent complex systems that vary across space, time, and in response to external factors (Levin, 1998). Understanding how the structure and dynamics of ecological communities vary with the environment is crucial for developing scientifically sound global change adaptation and mitigation programs (Harvey *et al.*, 2017). This represents, however, a challenging task because of the myriad of interactions and potential confounding factors that may influence these relationships (Tylianakis & Morris, 2017). Conceptualising ecological communities as networks, composed of species and their interactions, allows ecologists to study community structure, and its drivers, by separating these components and their potential feedbacks (Vázquez *et al.*, 2009a).

The variability in network structure across space can be decomposed into the variability attributed to species turnover, and the variability attributed to interaction turnover, i.e. the change in presence and strength of biotic interactions among species (Poisot *et al.*, 2012). While much is known about how species are distributed in space, our knowledge of how interactions change across gradients is still unfolding (Chamberlain *et al.*, 2014; Early & Keith, 2019). Recent studies have shown that biotic interactions are expected to vary with environmental factors (Poisot *et al.*, 2017) or geographical proxies like latitude or altitude (Roslin *et al.*, 2017; Zvereva & Kozlov, 2021, 2022), but the ecological processes behind these patterns or the emerging consequences for community structure and dynamics have not been sufficiently explored.

Different types of interactions can show specific responses in their frequency and intensity to biotic or abiotic drivers. Variability in interaction strength with latitude, for example, shows different trends for herbivory and carnivory than for parasitism, and is further dependent on the metabolism of the involved species (e.g. ectotherms or endotherms) (Zvereva & Kozlov, 2021). Moreover, species-specific responses to temperature variability may trigger phenological mismatches between interacting species, which are more prevalent in species with strong responses to temperature cues, like flowering plants and their insect pollinators (Gérard *et al.*, 2020). Likewise, temperature is directly related to metabolic rates, which influences e.g. movement speeds in ectotherms, with direct consequences for the frequency of interactions between individuals (Early & Keith, 2019).

Pairwise biotic interactions upscale to shape the structure and dynamics of ecological communities. The question of whether there exist differences in the local structure of ecological communities across interaction types has received considerable attention, yet is not fully resolved. An influential study by Thébault & Fontaine (2010) showed that mutualistic bipartite networks were more nested, and less modular, than trophic ones, and these patterns had a positive effect on the stability of these sytems. Further studies have challenged these conclusions, by showing that bipartite binary mutualistic and antagonistic newtorks are impossible to tell apart only based on their structure (Michalska-Smith & Allesina, 2019). Including environmental context (Song & Saavedra, 2020) or meso-scale structural information (Pichon *et al.*, 2024) improves the structural separability of mutualistic and antagonistic networks, as well as explicitly accounting for interaction type (Pichon *et al.*, 2024). Together, these advances suggest that network structure across types of interactions is difficult to tell apart, but that there exist meso-scale patterns and external factors that help discern this variability.

Network structure is not a static property of ecological communities, however. Different descriptors of network structure vary in response to external factors (Tylianakis & Morris, 2017), including environmental, anthropogenic, or other biotic factors (e.g. species richness). Besides the unresolved question of whether there exist fundamental differences between the structure of different types of interaction networks, a related issue is whether different types of networks respond in similar or different ways to variations in such external factors. Evidence regarding this question is elusive, as studies often suggest contrasting relationships between network properties and environmental factors. For example, several studies have analysed the relationship of nestedness, a network structural property (Mariani *et al.*, 2019), with climatic seasonality at biogeographical scales, finding negative (Takemoto & Kajihara, 2016), positive (Song *et al.*, 2017), or no relationship (Brimacombe *et al.*, 2022) for plant-pollination networks, and no relationship for frugivory or host-parasite networks (Brimacombe *et al.*, 2022). Overall, relationships between large-scale environmental variation and network structure have been studied generally independently across different network types, with contrasting aims and methodologies, precluding generalisations.

Combining these lines of evidence, there is an emerging consensus that local community structures potentially vary across interaction types, and in parallel, that pairwise interactions of different types display different trends in their spatial variation and response to external factors. Therefore, we might expect the variation in community structure across large spatial gradients, and in response to external factors, to be different for different interaction types. On the other hand, some factors structuring ecological networks across space may be similar across interaction types. For example, increasing richness towards the tropics may influence fundamental structural network patterns, such as connectance, regardless of interaction type (Dallas & Jordano, 2021; Gibert & Wieczynski, 2021). All together, it is unclear whether different interaction types are structured and change in different ways across large spatial scales. Here, we undertake a comparative analysis of structural network metrics at a global scale by using an unprecedented compilation of 952 ecological networks of five overarching types (pollination, frugivory, herbivory, parasitism, and food webs). This comparative analysis showed that a fundamental property of ecological networks, their degree distribution, explained most of the biogeographical variation in network metrics of all interaction types. Therefore, we further explored the relationship between the degree distribution of ecological networks and their abiotic drivers.

Methods

Network datasets

We compiled observations of ecological networks across the globe, considering binary interactions, uni- or bipartite networks, and with associated spatial coordinates that we could link to a geographical location. We combined networks from open repositories (mangal (Poisot *et al.*, 2016), Web of Life, GATEWAy (Brose *et al.*, 2019)) and from published studies (Boscolo *et al.*, 2023; Dalsgaard *et al.*, 2021; Fricke & Svenning, 2020; Martins *et al.*, 2022; Parra *et al.*, 2022) as well as additional datasets collected by the authors. We classified each network according to their interaction type (pollination, frugivory, herbivory, parasitism, or predation) and topology (unipartite or bipartite). The first set comprised 4341 ecological networks, that we subsequently filtered according to the following criteria: First, we selected networks with > 20 species, or alternatively, > 10 species in each of the groups in bipartite networks. Second, we selected networks that were not fully connected. With these constraints, we aimed to select networks that represented at least moderately diverse communities, with sufficient richness so that structural metrics could be reliably computed and would be ecologically meaningful. In our data collection, we particularly aimed to increased the number of networks of interaction types that are generally less represented in similar analyses (e.g. herbivory). The final dataset is, to our knowledge, the most comprehensive compilation of binary networks across interaction types so far: it comprised 61 frugivory, 444 pollination, 98 herbivory and 39 parasitism networks, as well as 310 food webs, for a total of 952 networks (Fig. 1). All networks considered were bipartite except for the 310 unipartite food webs.

Structural metrics and statistical significance

We calculated a suite of structural metrics for every network in our dataset. In particular, we obtained their interaction overlap (García-Callejas *et al.*, 2023), nestedness (Delmas *et al.*, 2018; Mariani *et al.*, 2019), two modularity algorithms (infomap (Farage *et al.*, 2021) and an algorithm based on betweenness centrality of nodes (Newman & Girvan, 2004)), and two centralization metrics, which represent centrality metrics aggregated at the network level (Delmas *et al.*, 2018):

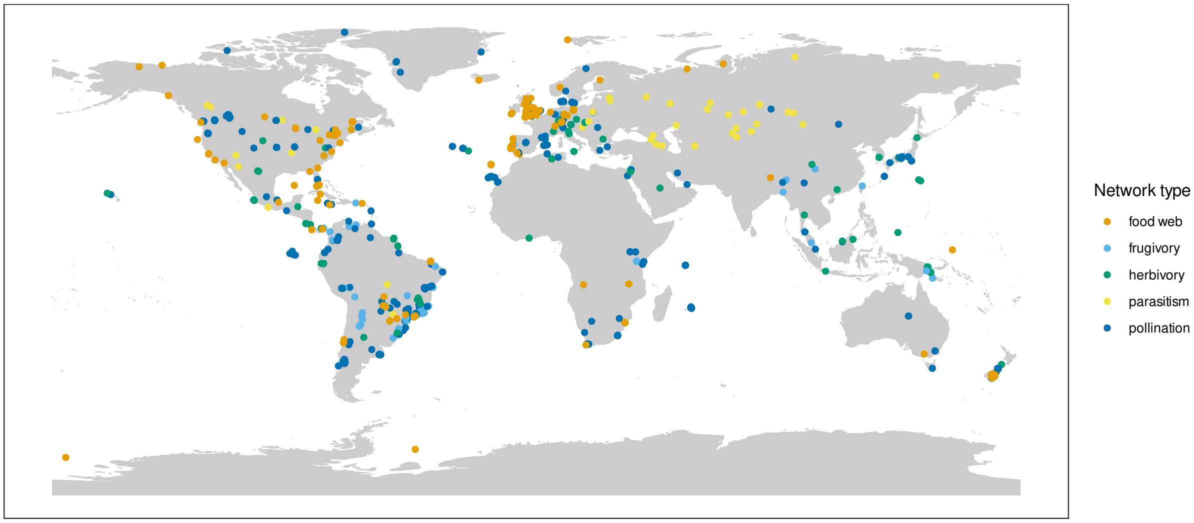

Fig. 1: Spatial location of the ecological networks included in this study. N = 952 networks, of which 310 food webs, 61 frugivory, 98 herbivory, 39 parasitism, and 444 pollination networks.

eigenvector centralization and degree centralization. These metrics represent a variety of structural properties of networks and their interpretation is conceptually similar in uni- and bipartite networks. Furthermore, all these metrics can be applied to networks with more than one component, which was the case for 399 networks. However, in order to be properly interpreted, it is important to quantify their statistical significance, i.e. whether the value of a given metric for a given network can be expected solely by looking at general parameters like the number of nodes or links in the network, or whether there are ecological processes potentially driving it (Delmas *et al.*, 2018). To do so, for each network we generated a set of 100 randomised realisations fixing the degree distribution of the network, while allowing the particular arrangement of interactions to vary. This null model is known as the *configuration model* in network theory (Newman, 2010). We obtained these randomised realisations via a maximum entropy approach, which ensures that these realisations maintain the exact same degree distribution than the original network *on average*, but allow specific realisations to slightly deviate from it (Caruso *et al.*, 2022). These "soft constraints" thus represent situations in which observed network properties (degree distribution in our study) are not fully deterministic and captured by the observation process, but rather are subject to different sources of variability. We implemented this null model following Caruso *et al.* (2022), using the NEMtropy python package (Vallarano *et al.*, 2021).

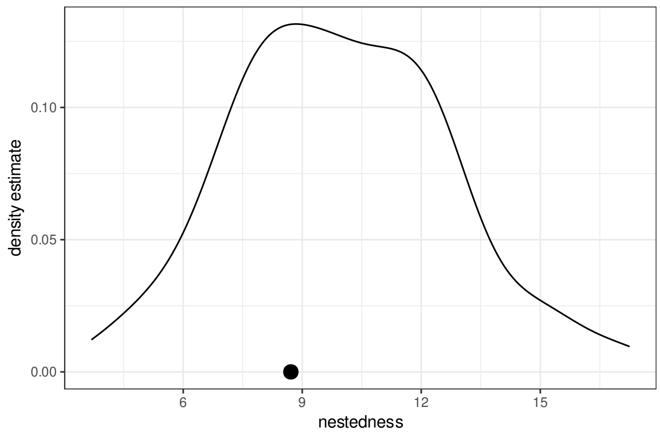

Fig. 2: Observed value (point) and null distribution of the NODF nestedness metric in a plant-pollination network from southern Brazil.

For each network, we compared the values of each metric in the observed network with the distribution of the randomised realisations, as depicted in Fig 2 for the NODF nestedness metric of a plant-pollination network from South-Eastern Brazil extracted from the dataset by Boscolo *et al.* (2023). Then, for each metric, we obtained its associated z-score or standardised effect size (Ford & Roberts, 2019), that quantifies the difference between the observed value and the distribution of null realisations:

$$Z = \frac{X - \mu}{\sigma} \tag{1}$$

where the z-score Z is a function of the observed value of a metric in a network (X), the mean of the metric value for the null realisations (μ) and its standard deviation (σ). Values of $Z > 2$ or $Z < -2$ indicate statistically significant differences between them. In the example from Fig. 2, the nestedness metric of that particular plant-pollinator network has a z-score of -0.42 and is, therefore, not different from what is expected from a random network with fixed richness and degree distribution.

We analysed the differences in the distribution of z-scores across interaction types through linear mixed models, considering interaction type as a categorical predictor and publication as a random effect. To estimate pairwise differences between z-score distributions, we performed Tukey-adjusted post-hoc tests using the R package emmeans v1.10.5 (Lenth, 2024).

Statistical analyses of network degree distributions

We then analysed 1) the variability of degree distribution across interaction types globally, and 2) their environmental, and anthropic determinants. We gathered WorldClim variables at 1km resolution (Fick & Hijmans, 2017) and selected annual mean temperature and precipitation, as well as their seasonality indices, as independent variables. We additionaly included as a predictor variable the Human Footprint Index from Venter *et al.* (2016). This metric represents the Human Footprint Index as of 2009, which may differ substantially from the sampling time of specific networks collected here. Nevertheless, it represents a first approximation to human impacts at particular spatial locations, in the absence of more specific information. To understand the importance of potential sampling bias in the dataset, we further included a measure of network sampling intensity interpreted as the average number of interactions observed per species (Brimacombe *et al.*, 2022; Schleuning *et al.*, 2012):

$$SI_i = \frac{\sqrt{L_i}}{\sqrt{n_i * m_i}} \tag{2}$$

where L_i is the number of links in network i, n_i the number of rows in the adjacency matrix, and m_i its number of columns.

Degree distributions, like any other distribution, cannot be fully reduced to a one-dimensional metric. Hence, we obtained the first four statistical moments of the degree distributions in our data: mean, variance (or standard deviation), skewness, and kurtosis. Mean and standard deviation were positively correlated across the dataset (Pearson's $\rho = 0.76$, $p < 0.05$, Fig. S1), as were skewness and kurtosis ($\rho = 0.902$, $p < 0.05$, Fig. S1). We therefore analysed the determinants of both mean and skewness of our network's degree distributions. Further, as standard deviation is an important descriptor of statistical distributions, we also considered it in the following analyses despite its relatively strong correlation with the mean of the degree distributions.

To understand the patterns of variation of the degree distribution descriptors across interaction types and external factors, we generated three linear mixed models for the relationship of a) degree distribution mean, b) standard deviation, and c) skewness, with environmental, anthropic, and sampling correlates. In these regressions, we considered as independent variables the interaction between biotic interaction type and each of the following factors: human footprint index, network sampling intensity, annual mean temperature, annual mean precipitation, temperature seasonality, and precipitation seasonality. All independent variables were scaled in advance. For these analyses, we included networks with available spatial information for all variables, which resulted in a total of 859 networks (258 food webs, 61 frugivory, 94 herbivory, 37 parasitism, and 409 pollination networks). In addition, variability in network structure is known to be highly driven by publication, both in bipartite networks (Brimacombe *et al.*, 2023) and unipartite food webs (Brimacombe *et al.*, 2024). We therefore included publication as a random intercept effect in our models. While this is not an optimal practice, because many studies -and therefore levels of the random effect- consist of a single network (Brimacombe *et al.*, 2024), preliminary analyses showed that including this random factor consistently improved the AIC of the models compared to standard regressions. Furthermore, in our dataset, 100 studies from a total of 347 included at least 2 networks, so we consider it a valid approximation in the absence of better standardisation in sampling designs. Lastly, for modelling the mean and standard deviation of the degree distributions, we log-transformed these responses, as they were highly skewed. Thus, our models are of the form:

$$\begin{aligned} y_{ij} &= \beta_0 + \beta_1 t_{ij} + \beta_2 a_{2,ij} ... + \beta_n a_{n,ij} + \\ &\beta_{n+1}(t_{ij} \cdot a_{2,ij}) + ... + \beta_{n+n-1}(t_{ij} \cdot a_{n,ij}) + \\ &b_{0j} + \epsilon_{ij} \end{aligned} \tag{3}$$

where y_{ij} is the response variable (log-transformed degree distribution mean, log-transformed standard deviation, or skewness) of observation i from the study j, β_0 is the intercept of the model, β_1 is the fixed effect of interaction type t_{ij}, β_n is the fixed effect of the n_{th} independent variable a_n, the β_{n+1} and subsequent terms are the fixed effects of the interaction between interaction type and the rest of independent variables, $b_{0j} \sim \mathcal{N}(0, \sigma_b^2)$ is the random intercept for study j, and $\epsilon_{ij} \sim \mathcal{N}(0, \sigma_\epsilon^2)$ is the residual error for observation ij. We programmed all models in R v4.3.2 (R Core Team, 2023) using the package glmmTMB v1.1.9 (Brooks *et al.*, 2017), and checked model fits with the DHARMa v0.4.6 package (Hartig, 2022).

Results

Significance of structural metrics across interaction types

In a majority of the analysed networks, regardless of their interaction type, structural metrics are within the expected values of their null distribution (Fig. 3). In other words, the large-scale structural patterns of binary networks of different interaction types can be explained generally by their richness and degree distribution, with the exception of the two modularity metrics, which are on average higher than expected, especially for pollination and herbivory networks. Further, interaction overlap in bipartite networks is, on average, close to being significantly lower than expected. The distributions of z-scores are generally different across structural metrics and interaction types: food webs are significantly different than other interaction types for infomap modularity, interaction overlap and nestedness, whereas all metrics have similar distributions for degree centralization, and finally, eigenvector centralization and betweenness modularity show more heterogeneous patterns.

Biogeographical relationships of network degree distributions

The previous result, hence, raises the question of what are the factors shaping the degree distribution of ecological networks across large spatial scales. Overall, all degree distribution descriptors were highly right skewed, with few networks showing comparatively very high values. There were no outstanding differences between the degree distribution descriptors of the different interaction types (Fig. 4). Unipartite food webs tended to display higher average and standard deviation values than bipartite networks, and similarly lower skewness and kurtosis, as indicated by linear mixed models and post-hoc pairwise comparisons. Among bipartite network types, pollination and herbivory networks tended to show the lowest average values and the highest skewness and kurtosis.

The results from our regression models showed differential effects on the mean, standard deviation, and skewness of the degree distributions of ecological networks (Fig. 5, tables S1,S2,S3). First, most factors displayed non-significant effects on degree distribution descriptors for most interaction types (dashed lines in Fig. 5). The mean and standard deviation of the degree dis-

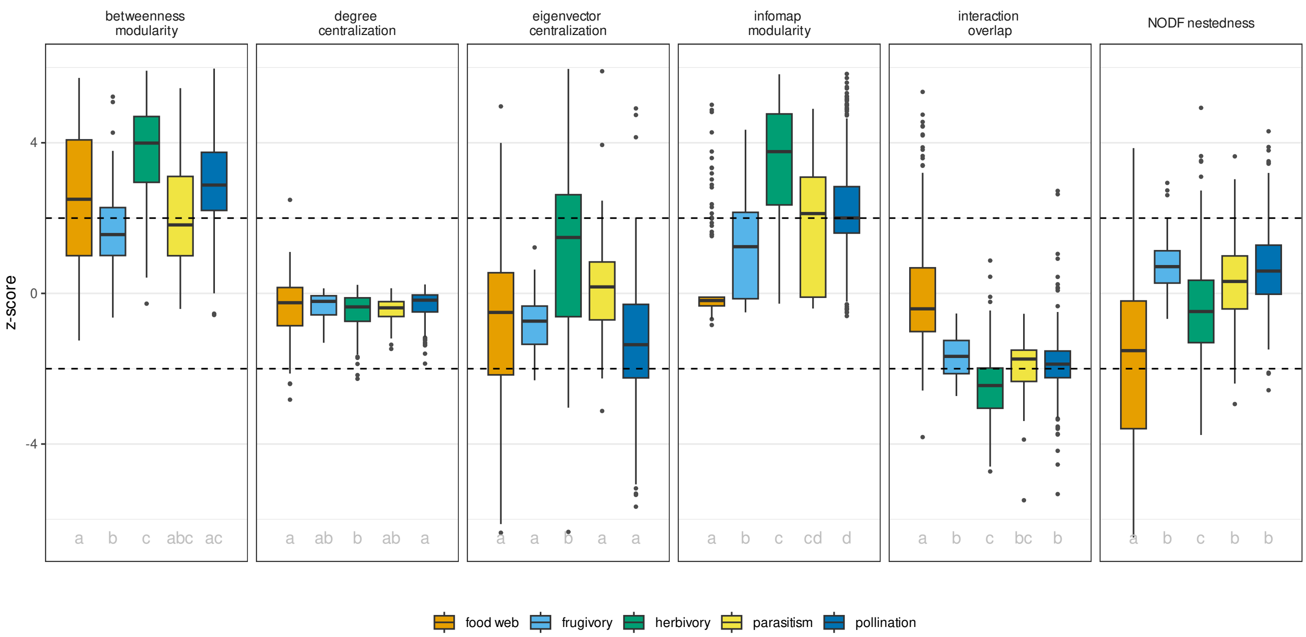

Fig. 3: Distribution of z-scores for all structural metrics and interaction types considered. Boxplots correspond to 310 food webs, 98 herbivory networks, 61 frugivory ones, 39 parasitism ones, and 444 pollination ones. Dashed lines highlight z-scores of -2 and 2. Letters at the bottom of each panel represent statistically significant groupings according to linear mixed models and post-hoc pairwise comparisons. In the boxplots, the vertical black line represents the median, the left and right hinges correspond to the 25th and 75th percentiles, and the horizontal lines extend to the largest/smallest value up to 1.5 times the interquartile range (distance between 25th and 75th percentiles). Single points are observations outside of 1.5 times the interquantile range.

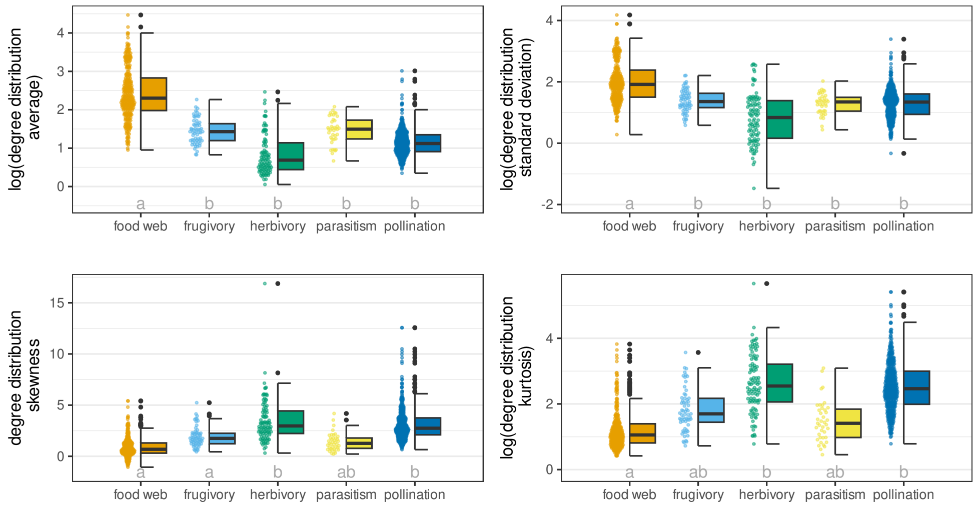

Fig. 4: Statistical moments of the degree distribution of the 952 networks analysed, differentiated by interaction type. Food webs are all unipartite networks; all other interaction types are bipartite. In the vertical axis, values are log-transformed for visibility, except for skewness (lower left panel), that can take negative values. Letters at the bottom of each panel represent statistically significant groupings. Boxplot features as in Fig. 3

tribution (first and second rows of Fig 5) were in general more sensitive to variations in external factors than the skewness, with the exception of sampling intensity (second column of Fig. 5, that showed significant relationships with some or all interaction types for all descriptors. Food webs showed in general the strongest responses to the different environmental factors, especially regarding the average of their degree distributions, which increased with increasing human footprint, with annual mean temperature, but decreased with increasing annual precipitation. Other interaction types showed fewer significant relationships, and sometimes contrasting responses compared to food webs. For example, the degree distribution average and standard deviation of herbivory networks decreased significantly with increasing annual temperature, as opposed to food webs. Models with or without including publication as a random effect showed similar qualitative trends, so here we discuss models including it as they showed consistently lower AIC scores.

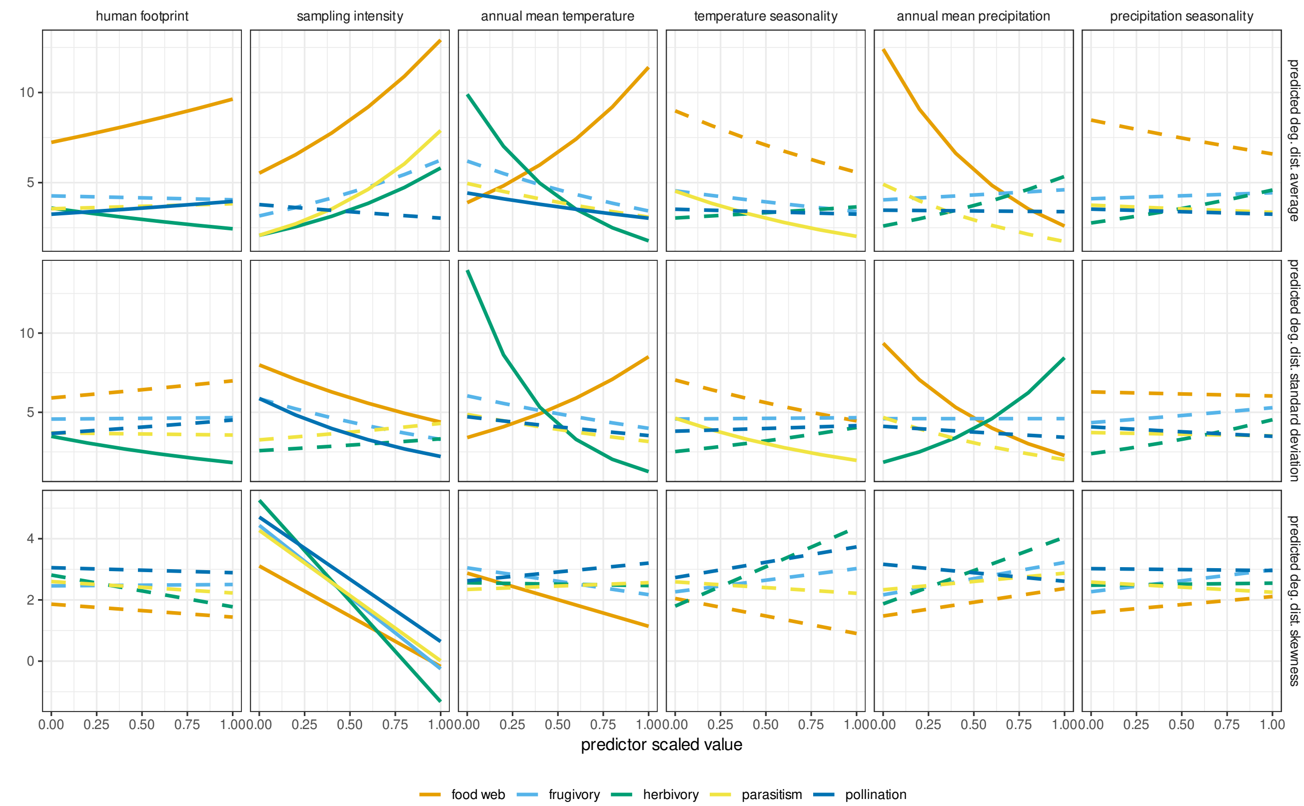

Fig. 5: Marginal effects of each scaled predictor variable on degree distribution average (upper columns), standard deviation (middle columns), and skewness (lower columns), for each interaction type. Effects of each predictor are obtained by setting non-focal predictors to their mean, using the package ggeffects v1.6 (Lüdecke, 2018). Solid lines represent statistically significant effects, dashed lines non-significant ones. Confidence intervals are not shown for visibility, as they are highly overlapping in most cases.

Discussion

Biotic interactions vary in occurrence and intensity at biogeographical scales, in response to factors such as temperature (Dell *et al.*, 2013), precipitation and water availability (Walter, 2018), or human pressure (Sebastián-González *et al.*, 2015). Yet, it is unclear how environmental, sampling, or anthropic factors influence the structure of ecological networks across large spatial scales, and in particular, whether different types of biotic interactions show similar or different patterns in their variation. Here we have shown that biogeographical patterns of ecological networks display both commonalities and differences across interaction types. First, networks of all types considered have a tendency to be significantly modular, and all bipartite networks tend to have fewer interaction overlap than expected by chance, especially herbivory ones (Fig 3), while other structural metrics do not depart from a null expectation. Second, given that the structural metrics considered, and their significance, stem from a fundamental network property (the degree distribution) we showed that the mean, standard deviation, and skewness of network degree distributions vary differently across large gradients for different interaction types. In particular, degree distributions of food webs were most sensitive to environmental variations, whereas variations in sampling intensity influenced all types of ecological networks to some extent (Fig. 5).

The degree distribution of an ecological network informs about the number of interactions that each species has with the rest of the species pool. As such, it is a fundamental property from which, together with connectance (Poisot & Gravel, 2014), several secondary properties can potentially emerge. In our comparative analyses, nestedness and centralization metrics (a network-level generalisation of node centrality metrics) were fully consistent with the degree distributions of the observed networks, suggesting that no other processes are necessary to understand these patterns. In contrast, modularity was in general higher than expected for a given degree distribution, and most importantly, the tendency was similar for all interaction types, and for two different modularity metrics, indicating a robust pattern. Complementarily, the overlap in interactions between species, a low value of which can be indicative of niche differentiation processes (García-Callejas *et al.*, 2023), tended to be lower than expected, i.e. species tended to be more differentiated in their interactions than expected by chance, again, for most interaction types (this time excluding food webs).

Our broad analysis lacks the detail to analyse the processes, ecological or otherwise, driving the significant modularity of the studied networks (reviewed in Dormann *et al.* (2017)). In particular, we analysed binary networks due to their availability, which are incomplete representations of ecological networks (Banašek-Richter *et al.*, 2004), and pooled together many networks of different types and sampled with different methods and objectives. With that in mind, we can only stress that even considering these sources of uncertainty, modularity appears as a significant structural pattern, consistently for different types of ecological interactions. Therefore, processes structuring the modularity of ecological networks may be common to some extent across interaction types, including interaction networks generally thought to be more driven by trait matching (e.g. predator-prey interactions driven by body size (Brose *et al.*, 2006) or plant-bird interactions driven by morphological traits (Maglianesi *et al.*, 2014)) and those for which abundance-driven structure has been demonstrated, e.g. some host-parasite (Canard *et al.*, 2014) and plant-pollination networks (Vázquez *et al.*, 2009b).

Given that several structural metrics emerged directly in our analyses from the degree distribution of the studied networks, we analysed the relationship between the average, standard deviation, and skewness of network degree distributions and several variables at the biogeographical scale (Fig. 5). As a first insight from this analysis, we found that the only factor consistently related to the degree distribution descriptors for different interaction types is the sampling intensity of the network, as defined in Brimacombe *et al.* (2022), and after controlling for publication-level variability in network structure (Brimacombe *et al.*, 2024, 2023). In particular, as sampling intensity increased, the average number of links per species tended to increase (in food webs, parasitism, and herbivory networks), the variability in number of links per species tended to decrease (in food webs and pollination networks), and the asymmetry of the distribution also decreased, for all types of interactions. The overall picture is that higher sampling effort uncovers more interactions from rare species, and the number of species with a disproportionate (low or high) number of interactions decrease. This is consistent with previous studies relating sampling intensity to network structure (Chacoff *et al.*, 2012; de Aguiar *et al.*, 2019), in particular the degree of specialisation in networks (Fründ *et al.*, 2016). Besides sampling intensity, we observed that external factors showed more significant effects on degree distribution averages, i.e. in the mean number of links per species (11 statistically significant effects out of 30 relationships), followed by their standard deviations (8 significant effects), whereas skewness was the least sensitive metric.

A second insight from our degree distribution analyses is that environmental factors are differentialy related to degree distributions of different interaction types. In this case, food webs showed clearly different, and more significant, relationships than the rest of networks. Annual mean temperature was positively related to the number of links in food webs, and their standard deviation, but negatively so with their asymmetry. The pattern was exactly the opposite for annual mean precipitation, that decreased the number and variability of links per species and their variability. Together, these results suggest a higher environmental sensitivity of food web structure to large-scale environmental gradients than that of other interaction types. Previous studies have empirically demonstrated higher predation intensity with increasing temperature (Roslin *et al.*, 2017; Zvereva & Kozlov, 2021), via an increase in predator attack rates (Tylianakis & Morris, 2017). Whether these direct effects of temperature in pairwise interactions translate into food web structural metrics is contested: Gibert (2019) found that connectance increased with increasing temperature, through a concomitant reduction in the number of basal species, whereas Gauzens *et al.* (2020) found no strong environment-structure relationships in intertidal food webs across the globe. These inconsistent results may be due to several reasons, including the habitat type(s) of the food webs analysed. In particular, we pooled together food webs from marine (153), freshwater (91), and terrestrial (66) ecosystems, whose species and interactions may be driven by different eco-evolutionary drivers and responses to environmental factors.

Other community types were also directly affected by environmental factors, for example plants and their pollinating arthropods (Forrest, 2017; Settele *et al.*, 2016), but we found generally weaker or non-significant effects on degree distribution metrics. These may result from one or a combination of the following factors: intrinsic ecological patterns, such that direct effects on species composition or metabolism may not be evident at the network level; limitations of our dataset, e.g. in the number of networks included, binary as opposed to quantitative networks, or spatial coverage; or our analysis choices. We analysed together the potential effect of environmental, anthropic, and sampling factors, and the results showed the relative effect of each factor in the degree distribution metrics. Effect sizes are generally larger for network sampling intensity than any other factor (Fig. 5 and Supplementary Tables S1,S2 and S3), thus suggesting that previous environment-structure relationships at large scales may be incomplete or comparatively weak in relation to sampling issues, as recently observed in bipartite networks (Brimacombe *et al.*, 2022). Robustly disentangling environment-structure relationships across large spatial scales, as well as potential variations across habitat types e.g. in food webs, will thus likely need larger, standardised data collection efforts (Brimacombe *et al.*, 2024) combined with novel methodological approaches.

Overall, we have shown that currently available global data on ecological network structure suggests that 1) ecological networks have a tendency towards being more modular than expected for most interaction types, and usually have less interaction overlap than expected, whereas other structural metrics are not statistically different from a null expectation; 2) that degree distribution descriptors of all interaction types are more sensitive to sampling effects when compared to environmental factors; 3) that food webs in our dataset, and to a lesser extent herbivory networks, are more sensitive to environmental factors than other types of interaction networks. These insights highlight that focusing on fundamental network properties such as degree distribution may bring novel perspectives in the biogeographical study of ecological networks.

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Data and code availability

The compiled network dataset and the R code necessary to reproduce the findings of this study are available at Zenodo:

https://doi.org/10.5281/zenodo.14277893

and GitHub:

https://github.com/garciacallejas/ecological_network_biogeography

Bibliography

Banašek-Richter, C., Cattin, M.-F. & Bersier, L.-F. (2004). Sampling effects and the robustness of quantitative and qualitative food-web descriptors. *Journal of theoretical biology*, 226, 23–32.

Boscolo, D., Nobrega Rodrigues, B., Ferreira, P. A., Lopes, L. E., Tonetti, V. R., Reis dos Santos, I. C., Hiruma-Lima, J. A., Nery, L., Baptista de Lima, K., Perozi, J., Freitas, A. V. L., Viana, B. F., Antunes-Carvalho, C., Amorim, D. d. S., Freitas de Oliveira, F., Groppo, M., Absy, M. L., de Almeida-Scabbia, R. J., Alves-Araújo, A., de Amorim, F. W., Antiqueira, P. A. P., Antonini, Y., Aoki, C., dos Santos Aragão, D., Balbino, T. C. T., da Silva Ferreira Bandeira, M., Barbosa, B. C., de Vasconcellos Barbosa, M. R., Baronio, G. J., Barros, L. O., Beal-Neves, M., Bertollo, V. M., de Melo Bezerra, A. D., Buzatto, C. R., Carneiro, L. T., Caron, E., Carpim, C. S., Carvalho, E. S., Carvalho, T. L., Carvalho-Leite, L. J., Cascaes, M. F., de Castro, F. S., Cavalleri, A., Cazetta, E., Cerezini, M. T., Coelho, L. F. M., Colares, R., Cordeiro, G. D., Cordeiro, J., da Silva Corrêa, A. M., da Costa, F. V., Covre, C., Cruz, R. D. M., Cruz-Neto, O., Correia-da-Rocha-Filho, L., Delabie, J. H. C., da Costa Dórea, M., do-Nascimento, V. T., Alves dos-Santos, J. M., Duarte, M., Duarte, M. C., Duarte, O. M. P., Dutilh, J. H. A., Emerick, B. P., Fabiano, G. d. S., Farache, F. H. A., de Faria, A. P. G., Fernandes, G. W., Maria Abreu Ferreira, P., Ferreira-Caliman, M. J., Ferreira, L. M. N., Filgueira de Sá, T. F., Franceschinelli, E. V., Franco-Assis, G. A., Fregolente Faracco Mazziero, F., Freitas, B. M., Freitas, J., Galastri, N. A., Galetto, L., Garcia, C. T., Amela García, M. T., Garcia, N. L., Garófalo, C. A., Gélvez-Zúñiga, I., Goldas, C. d. S., Guerra, T. J., Guerra, T. M., Harter-Marques, B., Hipólito, J., Kamke, R., Klein, R. P., Koch, E. B. d. A., Landgref-Filho, P., Laroca, S., Leandro, C. M., Lima, R., de Lima, T. R. A., Lima-Verde, L. W., de Lírio, E. J., Lopes, A. V., Luizi-Ponzo, A. P., Machado, I. C. S., Machado, T., Magalhães, F. S., Mahlmann, T., Mariano, C. d. S. F., Marques, T. E. D., Martello, F., Martins, C. F., Martins, M. N., Martins, R., Mascarenhas, A. L. S., de Assis Mendes, G., Mendonça, M. d. S., Menini Neto, L., Milward-de-Azevedo, M. A., Miranda, A. O., Montoya-Pfeiffer, P. M., Moraes, A. M., Moraes, B. B., Moreira, E. F., Morini, M. S., Moure-Oliveira, D., De Nadai, L. F., Nagatani, V. H., Nervo, M. H., de Siqueira Neves, F., de Novais, J. S., Araújo-Oliveira, É. S., de Oliveira, J. H. F., Pacheco-Filho, A. J. d. S., Palmieri, L., Pareja, M., Passarella, M. d. A., Passos, N. d. M., Paulino-Neto, H. F., Luna Peixoto, A., Pereira, L. C., Pereira, R. A. S., Pereira-Silva, B., Pincheira-Ulbrich, J., Pinheiro, M., Piratelli, A. J., Podgaiski, L. R., Polizello, D. S., do Prado, L. P., Prezoto, F., de Quadros, F. R., Queiroz, E. P., Glebya Maciel Quirino, Z., Rabello, A. M., Rabeschini, G. B. P., Ramalho, M. M. M., Ramos, F. N., Rattis, L., de Rezende, L. H. G., Ribeiro, C., Robe, L. J., Rocha, E. M. d. S. R., Rodrigues, R. R., Romero, G. Q., Roque, N., Sabino, W. d. O., Sano, P. T., Reis, P. d. S. S., dos Santos, F. S., Alves dos Santos, I., dos Santos, F. d. A. R., Silva dos Santos, I., Sartorello, R., Schmitz, H. J., Sigrist, M. R., Silva Junior, J. C., e Silva, A. C. G., da Silva, C. V. C., Alves Vieira Silva, B. S., Silva, B. L. d. F., Silva, C. I., da Silva, F. O., e Silva, J. L. S., Silva, N. S., da Silva, O. G. M., e Silva Neto, C. d. M., Silva Neto, E. R., Silveira, D., Silveira, M. S., Singer, R. B., Soares, L. A. S. S., Locatelli de Souza, E. M., de Souza, J. M. T., Steiner, J., Teixeira-Gamarra, M. C., Trentin, B. A., Varassin, I. G., Vila-Verde, G., Yoshikawa, V. N., Zanin, E. M., Galetti, M. & Ribeiro, M. C. (2023). Atlantic flower–invertebrate interactions: A data set of occurrence and frequency of floral visits. *Ecology*, 104, e3900.

Brimacombe, C., Bodner, K., Gravel, D., Leroux, S. J., Poisot, T. & Fortin, M.-J. (2024). Publication-driven consistency in food web structures: Implications for comparative ecology. *Ecology*, In press, e4467.

Brimacombe, C., Bodner, K., Michalska-Smith, M., Gravel, D. & Fortin, M.-J. (2022). No strong evidence that modularity, specialization or nestedness are linked to seasonal climatic variability in bipartite networks. *Global Ecology and Biogeography*, 31, 2510–2523.

Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T. & Fortin, M.-J. (2023). Shortcomings of reusing species interaction networks created by different sets of researchers. *PLOS Biology*, 21, e3002068.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M. & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378–400.

Brose, U., Archambault, P., Barnes, A. D., Bersier, L.-F., Boy, T., Canning-Clode, J., Conti, E., Dias, M., Digel, C., Dissanayake, A. *et al.* (2019). Predator traits determine food-web architecture across ecosystems. *Nature ecology & evolution*, 3, 919–927.

Brose, U., Jonsson, T., Berlow, E. L., Warren, P., Banasek-Richter, C., Bersier, L.-F., Blanchard, J. L., Brey, T., Carpenter, S. R., Blandenier, M.-F. C., Cushing, L., Dawah, H. A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Ledger, M. E., Martinez, N. D., Memmott, J., Mintenbeck, K., Pinnegar, J. K., Rall, B. C., Rayner, T. S., Reuman, D. C., Ruess, L., Ulrich, W., Williams, R. J., Woodward, G. & Cohen, J. E. (2006). Consumer–resource body-size relationships in natural food webs. *Ecology*, 87, 2411–2417.

Canard, E., Mouquet, N., Mouillot, D., Stanko, M., Miklisova, D. & Gravel, D. (2014). Empirical evaluation of neutral interactions in host-parasite networks. *The American naturalist*, 183, 468–79.

Caruso, T., Clemente, G. V., Rillig, M. C. & Garlaschelli, D. (2022). Fluctuating ecological networks: A synthesis of maximum-entropy approaches for pattern detection and process inference. *Methods in Ecology and Evolution*, 13, 2306–2317.

Chacoff, N. P., Vázquez, D. P., Lomáscolo, S. B., Stevani, E. L., Dorado, J. & Padrón, B. (2012). Evaluating sampling completeness in a desert plant-pollinator network. *Journal of Animal Ecology*, 81, 190–200.

Chamberlain, S. A., Bronstein, J. L. & Rudgers, J. A. (2014). How context dependent are species interactions? *Ecology Letters*, 17, 881–890.

Dallas, T. A. & Jordano, P. (2021). Species-area and network-area relationships in host–helminth interactions. *Proceedings of the Royal Society B: Biological Sciences*, 288, 20203143.

Dalsgaard, B., Maruyama, P. K., Sonne, J., Hansen, K., Zanata, T. B., Abrahamczyk, S., Alarcon, R., Araujo, A. C., Araujo, F. P., Buzato, S. *et al.* (2021). The influence of biogeographical and evolutionary histories on morphological trait-matching and resource specialization in mutualistic hummingbird–plant networks. *Functional Ecology*, 35, 1120–1133.

de Aguiar, M. A. M., Newman, E. A., Pires, M. M., Yeakel, J. D., Boettiger, C., Burkle, L. A., Gravel, D., Jr, P. R. G., O'Donnell, J. L., Poisot, T., Fortin, M.-J. & Hembry, D. H. (2019). Revealing biases in the sampling of ecological interaction networks. *PeerJ*, 7, e7566.

Dell, A. I., Pawar, S. & Savage, V. M. (2013). Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *Journal of Animal Ecology*, 83, 70–84.

Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Riva, G. V. D., Fortin, M.-J., Gravel, D., Guimarães, P. R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D. & Poisot, T. (2018). Analysing ecological networks of species interactions. *Biological Reviews*, 94, 16–36.

Dormann, C. F., Fründ, J. & Schaefer, H. M. (2017). Identifying causes of patterns in ecological networks: Opportunities and limitations. *Annual Review of Ecology, Evolution, and Systematics*, 48, 559–584.

Early, R. & Keith, S. A. (2019). Geographically variable biotic interactions and implications for species ranges. *Global Ecology and Biogeography*, 28, 42–53.

Farage, C., Edler, D., Eklöf, A., Rosvall, M. & Pilosof, S. (2021). Identifying flow modules in ecological networks using Infomap. *Methods in Ecology and Evolution*, 12, 778–786.

Fick, S. E. & Hijmans, R. J. (2017). Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas. *International journal of climatology*, 37, 4302–4315.

Ford, B. M. & Roberts, J. D. (2019). Evolutionary histories impart structure into marine fish heterospecific co-occurrence networks. *Global Ecology and Biogeography*, 28, 1310–1324.

Forrest, J. R. (2017). Insect pollinators and climate change. In: *Global climate change and terrestrial invertebrates*, chap. 69–91. John Wiley Sons, pp. 23–45.

Fricke, E. C. & Svenning, J.-C. (2020). Accelerating homogenization of the global plant–frugivore meta-network. *Nature*, 585, 74–78.

Fründ, J., McCann, K. S. & Williams, N. M. (2016). Sampling bias is a challenge for quantifying specialization and network structure: Lessons from a quantitative niche model. *Oikos*, 125, 502–513.

García-Callejas, D., Godoy, O., Buche, L., Hurtado, M., Lanuza, J. B., Allen-Perkins, A. & Bartomeus, I. (2023). Non-random interactions within and across guilds shape the potential to coexist in multi-trophic ecological communities. *Ecology Letters*, 26, 831–842.

Gauzens, B., Rall, B. C., Mendonça, V., Vinagre, C. & Brose, U. (2020). Biodiversity of intertidal food webs in response to warming across latitudes. *Nature Climate Change*, 10, 264–269.

Gérard, M., Vanderplanck, M., Wood, T. & Michez, D. (2020). Global warming and plant–pollinator mismatches. *Emerging topics in life sciences*, 4, 77–86.

Gibert, J. P. (2019). Temperature directly and indirectly influences food web structure. *Scientific reports*, 9, 5312.

Gibert, J. P. & Wieczynski, D. J. (2021). Constraints and variation in food web link-species space. *Biology Letters*, 17, 20210109.

Hartig, F. (2022). *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models*. URL `https://CRAN.R-project.org/package=DHARMa`. R package version 0.4.6.

Harvey, E., Gounand, I., Ward, C. L. & Altermatt, F. (2017). Bridging ecology and conservation: From ecological networks to ecosystem function. *Journal of Applied Ecology*, 54, 371–379.

Lenth, R. V. (2024). *emmeans: Estimated Marginal Means, aka Least-Squares Means*. URL `https://CRAN.R-project.org/package=emmeans`. R package version 1.10.5.

Levin, S. A. (1998). Ecosystems and the Biosphere as Complex Adaptive Systems. *Ecosystems*, 1, 431–436.

Lüdecke, D. (2018). ggeffects: Tidy data frames of marginal effects from regression models. *Journal of Open Source Software*, 3, 772.

Maglianesi, M. A., Blüthgen, N., Böhning-Gaese, K. & Schleuning, M. (2014). Morphological traits determine specialization and resource use in plant–hummingbird networks in the neotropics.

Ecology, 95, 3325–3334.

Mariani, M. S., Ren, Z.-M., Bascompte, J. & Tessone, C. J. (2019). Nestedness in complex networks: Observation, emergence, and implications. *Physics Reports*, 813, 1–90.

Martins, L. P., Stouffer, D. B., Blendinger, P. G., Böhning-Gaese, K., Buitrón-Jurado, G., Correia, M., Costa, J. M., Dehling, D. M., Donatti, C. I., Emer, C. *et al.* (2022). Global and regional ecological boundaries explain abrupt spatial discontinuities in avian frugivory interactions. *Nature Communications*, 13, 6943.

Michalska-Smith, M. J. & Allesina, S. (2019). Telling ecological networks apart by their structure: A computational challenge. *PLOS Computational Biology*, 15, e1007076.

Newman, M. E. J. (2010). *Networks, an Introduction*. Oxford University Press, Oxford; New York. ISBN 978-0-19-920665-0 978-0-19-163776-6.

Newman, M. E. J. & Girvan, M. (2004). Finding and evaluating community structure in networks. *Physical Review E*, 69, 026113.

Parra, S. A., Thébault, E., Fontaine, C. & Dakos, V. (2022). Interaction fidelity is less common than expected in plant–pollinator communities. *Journal of Animal Ecology*, 91, 1842–1854.

Pichon, B., Goff, R. L., Morlon, H. & Perez-Lamarque, B. (2024). Telling mutualistic and antagonistic ecological networks apart by learning their multiscale structure. *bioRxiv*, 2023.04.04.535603.

Poisot, T., Baiser, B., Dunne, J. A., Kéfi, S., Massol, F., Mouquet, N., Romanuk, T. N., Stouffer, D. B., Wood, S. A. & Gravel, D. (2016). Mangal – making ecological network analysis simple. *Ecography*, 39, 384–390.

Poisot, T., Canard, E., Mouillot, D., Mouquet, N. & Gravel, D. (2012). The dissimilarity of species interaction networks. *Ecology Letters*, 15, 1353–1361.

Poisot, T. & Gravel, D. (2014). When is an ecological network complex? Connectance drives degree distribution and emerging network properties. *PeerJ*, 2, e251.

Poisot, T., Guéveneux-Julien, C., Fortin, M.-J., Gravel, D. & Legendre, P. (2017). Hosts, parasites and their interactions respond to different climatic variables. *Global ecology and biogeography*, 26, 942–951.

R Core Team (2023). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL `https://www.R-project.org/`.

Roslin, T., Hardwick, B., Novotny, V., Petry, W. K., Andrew, N. R., Asmus, A., Barrio, I. C., Basset, Y., Boesing, A. L., Bonebrake, T. C. *et al.* (2017). Higher predation risk for insect prey at low latitudes and elevations. *Science*, 356, 742–744.

Schleuning, M., Fründ, J., Klein, A.-M., Abrahamczyk, S., Alarcón, R., Albrecht, M., Andersson, G. K., Bazarian, S., Böhning-Gaese, K., Bommarco, R. *et al.* (2012). Specialization of mutualistic interaction networks decreases toward tropical latitudes. *Current biology*, 22, 1925–1931.

Sebastián-González, E., Dalsgaard, B., Sandel, B. & Guimarães, P. R. (2015). Macroecological trends in nestedness and modularity of seed-dispersal networks: Human impact matters. *Global Ecology and Biogeography*, 24, 293–303.

Settele, J., Bishop, J. & Potts, S. G. (2016). Climate change impacts on pollination. *Nature Plants*, 2, 1–3.

Song, C., Rohr, R. P. & Saavedra, S. (2017). Why are some plant–pollinator networks more nested than others? *Journal of Animal Ecology*, 86, 1417–1424.

Song, C. & Saavedra, S. (2020). Telling ecological networks apart by their structure: An environment-dependent approach. *PLOS Computational Biology*, 16, e1007787.

Takemoto, K. & Kajihara, K. (2016). Human impacts and climate change influence nestedness and modularity in food-web and mutualistic networks. *PLoS One*, 11, e0157929.

Thébault, E. & Fontaine, C. (2010). Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks. *Science*, 329, 853–856.

Tylianakis, J. M. & Morris, R. J. (2017). Ecological Networks Across Environmental Gradients. *Annual Review of Ecology, Evolution, and Systematics*, 48, 16–28.

Vallarano, N., Bruno, M., Marchese, E., Trapani, G., Saracco, F., Cimini, G., Zanon, M. & Squartini, T. (2021). Fast and scalable likelihood maximization for exponential random graph models with local constraints. *Scientific Reports*, 11, 15227.

Vázquez, D. P., Blüthgen, N., Cagnolo, L. & Chacoff, N. P. (2009a). Uniting pattern and process in plant-animal mutualistic networks: A review. *Annals of botany*, 103, 1445–57.

Vázquez, D. P., Chacoff, N. P. & Cagnolo, L. (2009b). Evaluating multiple determinants of the structure of plant-animal mutualistic networks. *Ecology*, 90, 2039–46.

Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., Possingham, H. P., Laurance, W. F., Wood, P., Fekete, B. M. *et al.* (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature communications*, 7, 12558.

Walter, J. (2018). Effects of changes in soil moisture and precipitation patterns on plant-mediated biotic interactions in terrestrial ecosystems. *Plant Ecology*, 219, 1449–1462.

Zvereva, E. L. & Kozlov, M. V. (2021). Latitudinal gradient in the intensity of biotic interactions in terrestrial ecosystems: Sources of variation and differences from the diversity gradient revealed by meta-analysis. *Ecology Letters*, 24, 2506–2520.

Zvereva, E. L. & Kozlov, M. V. (2022). Meta-analysis of elevational changes in the intensity of trophic interactions: Similarities and dissimilarities with latitudinal patterns. *Ecology Letters*, 25, 2076–2087.