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TECHNICAL NOTE

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How network size strongly determines trophic specialisation: A technical comment on Luna et al. (2022)

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Abstract

Luna et al. (2022) concluded that the environment contributes to explaining specialisation in open plant–pollinator networks. When reproducing their study, we instead found that network size alone largely explained the variation in their specialisation metrics. Thus, we question whether empirical network specialisation is driven by the environment.

KEYWORDS
bipartite networks, environmental gradients, network size, plant–pollinator, sampling intensity, specialisation

INTRODUCTION

Recently, there has been a concerted initiative to determine if and how network specialisation is explained by the environment (e.g. Dalsgaard et al., 2011, 2017; Schleuning et al., 2012). Much of this research stems from the venerable proposition that species are more specialised in the tropics, which may arise from the greater number of species requiring resources to be more finely divided (Janzen, 1973; MacArthur, 1984; Moles & Ollerton, 2016). Nevertheless, the strength and direction of this relationship has been debated (e.g. Moles & Ollerton, 2016; Ollerton & Cranmer, 2002).

Luna et al. (2022) added to this discussion by assessing how current and historical environmental factors structure specialisation in *open* (i.e. freely accessible) plant–pollinator networks. Specifically, they explored how net primary productivity [NPP], elevation, temperature (annual mean and historical stability) and precipitation (annual mean and historical stability) influenced three metrics of specialisation—niche overlap, linkage density and mean normalised degree. They found significant relationships with these specialisation metrics and thus concluded that the environment—in particular climate and resource availability—explained global variation in trophic specialisation.

One major limitation from Luna et al. (2022), however, is their use of open networks without appropriate controls for non-systematic sampling and differences in network construction. Without these controls, networks likely contain structural differences due to, for example, differences in the amount of sampling time (CaraDonna et al., 2021), sampled area (Galiana et al., 2018) or from differences in node resolutions (Bodner et al., 2022; Hemprich-Bennett et al., 2021). While these differences can prevent commensurability and therefore should be appropriately identified and controlled (Jordano, 2016), details about open networks are often unavailable, forcing researchers to rely on other approaches to account for these structural differences.

While direct measures of sampling design are largely unavailable, network size could provide a potential proxy measure for some design differences as variation in network size largely reflects sampling differences (Michalska-Smith & Allesina, 2019). Indeed, controlling for this potential bias in open networks can influence results as Morris et al. (2014) found no relationships

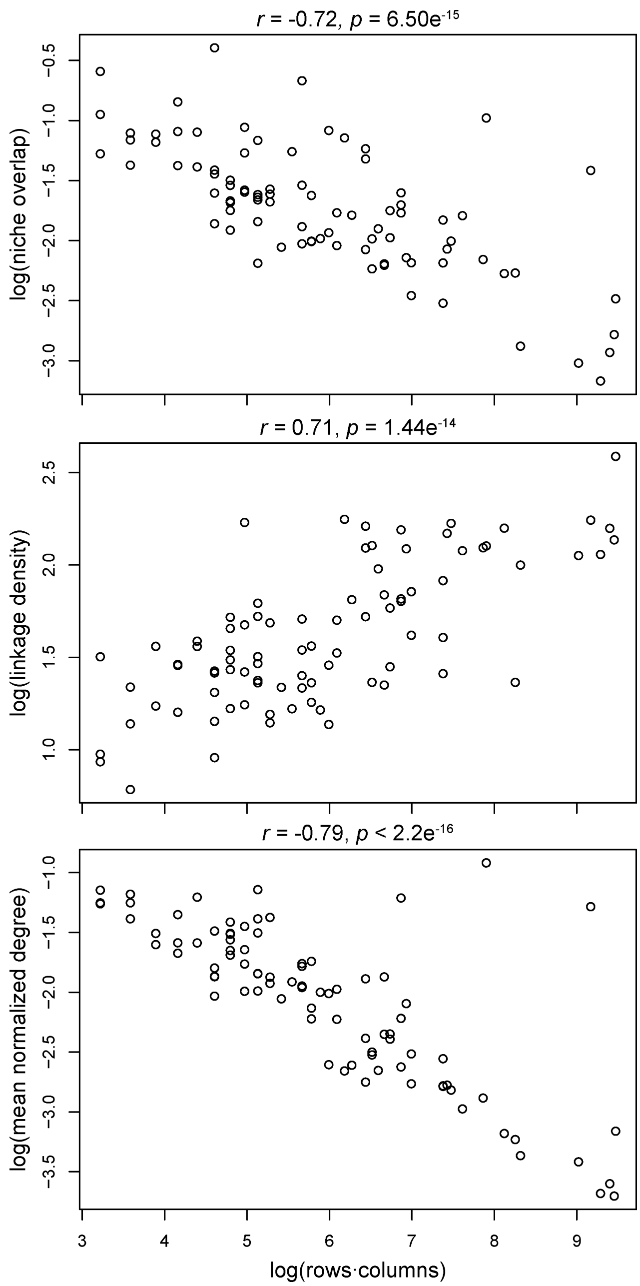

FIGURE 1 Pearson correlation (r) between network size (defined by the product of the number of plant and pollinator species; i.e. rows · columns) and the three specialisation metrics of niche overlap, linkage density and mean normalised degree for 87 plant–pollinator networks.

between latitude and network structure after controlling for network size. One metric commonly adopted to help control for sampling differences, *sampling intensity* (Schleuning et al., 2012), also accounts for network size and is typically used as a covariate to account for sampling bias in network structural metrics (e.g. Ceron et al., 2019). Beyond design differences, network size could also reflect community species richness, which is influenced by environmental factors. Regardless of the primary causes of network size differences, however, capturing true network structural differences requires that specialisation metrics and network size are independent.

ANALYSES

We tested how network size (i.e. the product of the number of rows and columns) influenced the specialisation metrics of Luna et al. (2022) and compared our results to those from models that use their environmental factors as explanatory variables. Given its common adoption in network studies, we also additionally tested how sampling intensity was related to these specialisation metrics. We conducted our analyses using the same methods and open networks as Luna et al. (2022).

First, we tested the relationship between all metrics of specialisation with network size and found for each a strong and statistically significant correlation, that is, all had an absolute correlation between 0.71 and 0.79 (Figure 1). The relationships between sampling intensity and specialisation metrics were also quite strong (Figure S1).

Next, we tested linear mixed models for each specialisation metric using three different fixed effect structures: (i) network size alone; (ii) the five current and historical environmental variables from Luna et al. (2022) and (iii) network size with the five environmental variables (Table 1). For all mixed models, network location was included as a random effect. We found that network size alone best explained the variation captured via the fixed effects in two of the three specialisation metrics—niche overlap and linkage density. For mean normalised degree, while fixed effects structure (iii) explained 55% of the variation, which suggested environmental factors were contributing to the model, network size alone explained over 35% of the variation. Similar results were obtained with sampling intensity (Table S1). Hence, we found that both network size and sampling intensity were the strongest individual contributors for explaining the variation across the specialisation metrics.

CONCLUSION

Environmental factors are correlated with the specialisation metrics of niche overlap, linkage density and mean normalised degree. However, we found that network size alone explained more of the variation than all five environmental variables for two out of the three metrics as presented by Luna et al. (2022), and that network size and metrics related to network size (i.e. sampling intensity) were the best variables for explaining all specialisation metrics. Our results provide a more parsimonious alternative to explain the variation in specialisation metrics and question the conclusion of Luna et al. (2022) that the environment determines specialisation in plant–pollinator communities.

TABLE 1 Linear mixed models (LMMs) for the three specialisation metrics of niche overlap, mean normalised degree and linkage density with log transformed network size (defined by the product of the number of plant and pollinator species), and the environmental variables from Luna et al. (2022) as explanatory variables. Luna et al. (2022) *best model* represents the LMMs that Luna et al. (2022) used for showing how the environment explains each specialisation metric. The amount of variation explained by the fixed effects is represented by $R^2_{marginal}$ and the amount explained by both the fixed and random effects is represented by $R^2_{conditional}$. The random effect used in all models is network location

Specialisation metric	Description	Fixed effects variables	$R^2_{marginal}$	$R^2_{conditional}$
Niche overlap	Only network size	Network size	0.407	0.643
	Luna et al. (2022) *best model*	*NPP, mean annual temp., mean annual precip., historical temp. stability, elevation*	0.133	0.465
	Network size + Luna et al. (2022) *best model*	Network size, *NPP*, *mean annual temp.*, *mean annual precip.*, *historical temp. stability*, *elevation*	0.427	0.628
Mean normalised degree	Only network size	Network size	0.357	0.881
	Luna et al. (2022) *best model*	*NPP, mean annual precip., historical temp. stability, historical precip. stability, elevation*	0.467	0.749
	Network size + Luna et al. (2022) *best model*	Network size, *NPP*, *mean annual precip.*, *historical temp. stability*, *historical precip. stability*, *elevation*	0.550	0.859
Linkage density	Only network size	Network size	0.434	0.739
	Luna et al. (2022) *best model*	*NPP, mean annual temp., mean annual precip., historical precip. stability, elevation*	0.285	0.801
	Network size + Luna et al. (2022) *best model*	Network size, *NPP*, *mean annual temp.*, *mean annual precip.*, *historical precip. stability*, *elevation*	0.429	0.823

AUTHOR CONTRIBUTION

CB and KB created the analyses. CB, KB and M-JF wrote the manuscript.

DATA AVAILABILITY STATEMENT

https://osf.io/q23vz/ (https://doi.org/10.17605/OSF.IO/Q23VZ).

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.14029.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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