





RESEARCH ARTICLE

No strong evidence that modularity, specialization or nestedness are linked to seasonal climatic variability in bipartite networks

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Abstract

Aim: Given the influence of seasonality on most ecological systems, an emerging research area attempts to understand how community network structure is shaped by seasonal climatic variations. To do so, most researchers conduct their analyses using *open* networks due to the high cost associated with constructing their own community networks. However, unwanted structural differences from the unique sampling and construction methods used to create each open network likely make comparing these networks a difficult task. Here, with the largest set of open bipartite networks collected to date, we test whether seasonal climatic variations explain network structure while additionally accounting for construction/sampling differences between networks.

Location: Trying to approach global.

Time period: Contemporary.

Major taxa studied: Plants and animals.

Methods: Using 723 open bipartite networks, we test whether temperature and/or precipitation seasonality explains (un)weighted metrics of nestedness, modularity or specialization across plant–pollinator, seed–dispersal, plant–ant, host–parasite or plant–herbivore systems.

Results: Generally, seasonality only weakly explained network structure: at most 16% of the variation in weighted metrics and 5% of the variation in unweighted metrics. Instead, a control for sampling bias in networks, sampling intensity, often better explained many of the network structural metrics. When limiting our analyses to only intensely sampled networks, however, about 33% of the variation in weighted modularity and specialization was explained by seasonality, but only in plant–pollinator networks.

Main conclusions: Altogether, we do not find strong evidence that seasonality explains network structure. Our study also highlights the large amount of structural differences in open networks, likely from the many different sampling and network construction techniques adopted by researchers when constructing networks. Hence, a definitive test for the relationship between network structure and seasonality across large spatial extents will require a dataset free from sampling and other biases, where

networks are derived from a consistent sampling protocol that appropriately characterizes communities.

KEYWORDS

antagonistic, climate, environmental gradient, mutualistic, networks, sampling intensity

1 | INTRODUCTION

Representation of ecological communities as networks has increased dramatically in the past few decades (Delmas et al., 2019; Fortin et al., 2021; Poisot et al., 2016; Tylanakis & Morris, 2017). With the growing availability of *open* (i.e., freely available) networks (Salim et al., 2022), there has also been an initiative in evaluating if and how empirical community networks are structured across large biogeographical gradients (Pellissier et al., 2018; Poisot et al., 2021). Indeed, given that the structure of a network is shaped by external perturbations experienced by the modelled community (Cadotte & Tucker, 2017; Song et al., 2017), it is now recognized that community structure may only be understood in relation to the environment that the represented community occupies (Cenci et al., 2018; Song & Saavedra, 2020).

While ecologists have long understood that temporal periodicity, in particular seasonality, is an important component of ecological systems (Firkowski et al., 2022; Tonkin et al., 2017), few studies have actually investigated the relationship between community structure and seasonality in empirical communities (White & Hastings, 2020). Increasingly, studies are finding that seasonality plays an important role in shaping empirical ecological communities and their species interactions (Brimacombe et al., 2021; McMeans et al., 2015; Rudolf, 2019; Tonkin et al., 2017), for instance, by influencing species coexistence and community stability (McMeans et al., 2015, 2020). Seasonal climatic variability, therefore, is likely a key factor influencing community network structure at the global scale (Liu et al., 2021; Schleuning et al., 2014).

To date, most researchers investigating the relationship between climate and community structure across large spatial extents have primarily used specialization, modularity and nestedness as measures of network structure. Specialization measures the degree of species' niche partitioning in a community (Blüthgen et al., 2006; Figure 1a). Modularity captures the degree to which species interact more strongly with a specific subset of species in a community (Dalsgaard et al., 2017; Figure 1b). Nestedness measures the extent to which specialists interact with perfect subsets of species that generalists also interact with in a community (Song et al., 2017; Figure 1c).

Using these structural measures, researchers have developed some theoretical expectations of how networks may respond to climatic variability. In seasonal climates where resources can vary greatly across time, selection may favour networks consisting of generalists and less specialized consumers that can utilize a broad range of food types (Dalsgaard et al., 2017) leading to increased

specialization towards the tropics. Of course, we would be remiss if we failed to mention that a venerable proposition of ecology also predicts that specialization increases towards the tropics (Brimacombe et al., 2022; MacArthur, 1972; Xing & Fayle, 2021), which may be in part due to less seasonality. Similarly, modularity may also increase towards tropical regions since selection may favour generalist species in seasonal environments who in turn interact with the whole community as compared to more specialist species in tropical regions that interact with only a subset of species (Welti & Joern, 2015). In contrast, it has been proposed that seasonality may lead to decreased nestedness in the tropics as compared to the temperate regions (Song et al., 2017) since an ordered network structure may enhance community tolerance to random perturbations (Saavedra et al., 2016).

Current empirical findings do not always support these theoretical expectations (Xing & Fayle, 2021; see Table 1 for a list of publications that test for these expectations, or variations thereof). While some studies find that specialization tends to increase towards the tropics (Dalsgaard et al., 2011), others find the opposite – specialization decreases towards tropical regions (Dalsgaard et al., 2017; Schleuning et al., 2012). Furthermore, some empirical studies have found nestedness to increase with temperature seasonality (Song et al., 2017) while others have found nestedness to decrease with increasing temperature variability between years (Welti & Joern, 2015). Empirical studies exploring modularity also have results that parallel those of specialization and nestedness where some studies find that modularity decreases with increasing latitude and temperature variability (Trøjelsgaard & Olesen, 2013; Welti & Joern, 2015), whereas others find modularity increases with seasonality and latitude (Dalsgaard et al., 2017; Schleuning et al., 2014). Other studies have also found no relationships between these measures and climatic variability or latitude (Doré et al., 2021; Morris et al., 2014; Ollerton & Cranmer, 2002).

These conflicting relationships of how networks respond to climate may be due in part to the differences in how particular systems respond to external perturbations (Song & Saavedra, 2020; Zvereva & Kozlov, 2021). Since antagonistic and mutualistic interactions can lead to different dynamics (Allesina & Tang, 2012) and can have distinct fitness outcomes for interacting species (Guimarães, 2020), it had been hypothesized that antagonistic and mutualistic networks could be structured differently (Lewinsohn et al., 2006; Thebault & Fontaine, 2010). Only recently has it been shown that antagonistic and mutualistic networks exhibit differences in their respective nestedness and modularity values after controlling for temperature seasonality (Song & Saavedra, 2020). Therefore, evaluating how

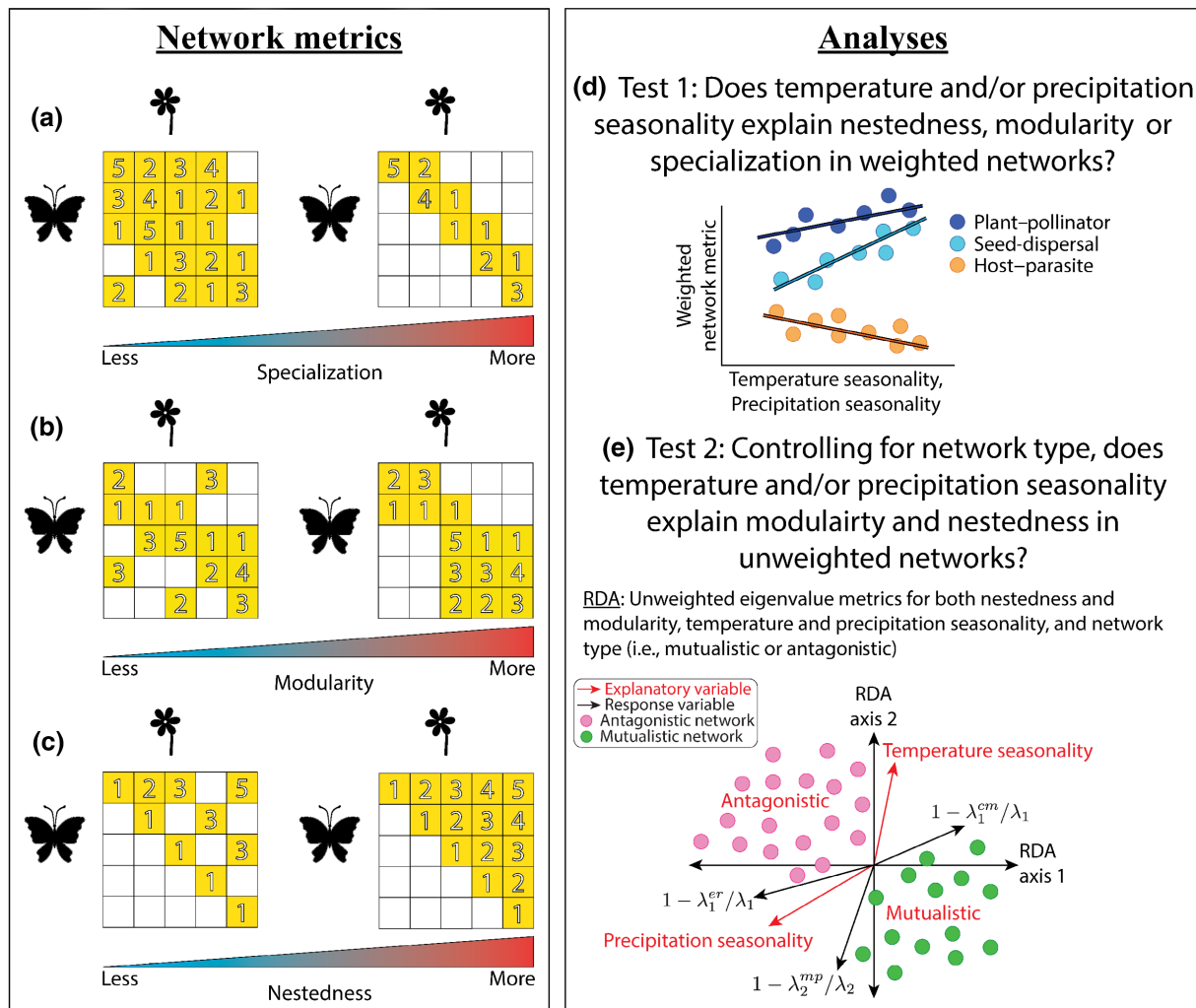


FIGURE 1 Left: Illustration of specialization, modularity and nestedness in connected weighted plant-pollinator systems, where white boxes indicate a lack of pairwise species interaction, and yellow numbered boxes indicate a weighted interaction between plant (columns) and pollinator (rows) species. Right: First, as shown in (d) we test the relationships between temperature and precipitation seasonality with the weighted network metrics of specialization (a), modularity (b) and nestedness (c) in plant-pollinator, seed-dispersal and host-parasite networks. Second, as illustrated in (e) we test the relationship between seasonality and unweighted network metrics using a redundancy analysis (RDA). Specifically, we attempt to explain normalized measures of nestedness ($1 - \lambda_1^{cm} / \lambda_1$, $1 - \lambda_2^{mp} / \lambda_2$) and modularity ($1 - \lambda_1^{er} / \lambda_1$) using precipitation and temperature seasonality, while controlling for whether networks were antagonistic (plant-herbivore and host-parasite) or mutualistic (plant-pollinator, seed-dispersal and plant-ant)

communities and their network representations respond to climatic seasonality may at the very least require appropriate control for the effects of whether networks are classified as antagonistic or mutualistic.

While climatic seasonality may structure networks in theory, detecting and quantifying the nature of such relationships may be extremely difficult to capture in practice. First, of the studies that investigate network structural variation across large spatial extents, most only consider a small number of communities that are not representative of the vast heterogeneous environmental gradients across the Earth (Poiso et al., 2021). Consequently, even if a statistically significant trend is found between network structure and seasonality, this relationship may not be an accurate delineation of the true relationship since few networks have been used to find such a trend.

Given the very real practical difficulty of collecting community-wide pairwise interaction data (Jordano, 2016; Pellissier et al., 2018), it is understandable that most studies are limited to few networks, for example, $n < 30$ (e.g., Dalsgaard et al., 2017; Olesen & Jordano, 2002; Schleuning et al., 2014). Second, of the networks available, there are other practical sampling effects that could impede and blur the potential theoretical signal that may exist between network structure and seasonality. For instance, the length of time used to characterize a community, for example, days, months, or years (CaraDonna et al., 2017, 2021; Schwarz et al., 2020), the amount of geographical area used to characterize ecological communities (Galiana et al., 2018), or the type of sampling procedure used when collecting ecological data (de Aguiar et al., 2019; Jordano, 2016), can all influence the depiction of a community as a network. Altogether, we may

TABLE 1 A list of some publications that test for, or variations of, latitudinal gradients in empirical ecological networks

Publication	Type of networks	Number of networks	Approx. range of absolute latitude (°)	Relationships with network metric(s)
Dalsgaard et al. (2011)	Plant–pollinator	31	0–40	Specialization decreases with absolute latitude.
Schleuning et al. (2012)	Plant–pollinator, seed-dispersal	282	0–82	Specialization increases with absolute latitude.
Trøjelsgaard and Olesen (2013)	Plant–pollinator	54	0–82	Modularity decreases with absolute latitude.
Schleuning et al. (2014)	Seed-dispersal	18	0–52	Modularity increases with temperature seasonality and absolute latitude.
Dalsgaard et al. (2017)	Seed-dispersal	21	0–50	Specialization increases with absolute latitude. Modularity increases with absolute latitude.
Welti and Joern (2015)	Plant–pollinator, seed-dispersal, plant–herbivore	68	0–35	Nestedness in mutualistic networks decreases with increasing temperature variability between years. Modularity in plant–herbivore networks decreases with increasing temperature variability within years.
Song et al. (2017)	Plant–pollinator	43	0–80	Nestedness increases with temperature seasonality.
Ollerton and Cranmer (2002)	Plant–pollinator	126	0–82	No relationship found with specialization.
Morris et al. (2014)	Host–parasite	216	0–75	No relationships found with specialization or modularity.
Doré et al. (2021)	Plant–pollinator	295	0–80	No relationship found with specialization.

then expect that these unwanted sources of structural differences could mask any trend that may exist between network structure and seasonality. Unfortunately, many of these unwanted sources cannot be controlled for given that the necessary information is not contained in corresponding metadata, for example, the amount of area used to characterize a community for each network is often not indicated, and so researchers must rely on other approaches to attempt to control for sampling differences across networks (Brimacombe et al., 2022).

In this study, we test whether seasonal climatic variability explains the structure of bipartite networks. While previous studies have performed similar tests, they are often limited to a small number of networks and/or a few ecological systems (Table 1), and thus fail to effectively determine whether there exist global trends across all networks. Our study then represents the single largest test of the effect of seasonal variability on plant–pollinator, seed-dispersal, plant–ant, host–parasite and plant–herbivore networks.

We consider two approaches. First, we test if the variations in modularity, specialization or nestedness of weighted plant–pollinator, seed-dispersal or host–parasite networks are explained by temperature and/or precipitation seasonality in either linear mixed models or linear models (Figure 1d). To help remove detectable structural differences that are due to sampling effects when characterizing a community as a network via observation, we control for both sampling intensity and the publication source of each network. We adopt the latter as networks from the same publication

may have more similar network structure than those originating from other publications since these networks may be sampled in similar ways, for example, consistency in the amount of time spent sampling and geographical area used to characterize the community. Second, we test if temperature and/or precipitation seasonality explain variation in unweighted metrics of modularity or nestedness while controlling for whether networks are antagonistic (host–parasite and plant–herbivore) or mutualistic (plant–pollinator, seed-dispersal and plant–ant) in a redundancy analysis (RDA; Legendre & Legendre, 2012; Figure 1e). To help ensure differences in modularity and nestedness are not driven by differences in sampling design and sampling effort, each modularity and nestedness metric used in the RDA is normalized by a random matrix with an equivalent number of nodes and edges.

2 | METHODS

2.1 | Data: Bipartite networks and climatic seasonality

A total of 723 ecological bipartite networks and their sampling locations were collected (Figure 2). This dataset was made up of 298 plant–pollinator, 10 ant–plant and 277 seed-dispersal networks (total of 585 mutualistic networks), as well as 97 host–parasite, and 41 plant–herbivore networks (total of 138 antagonistic networks).

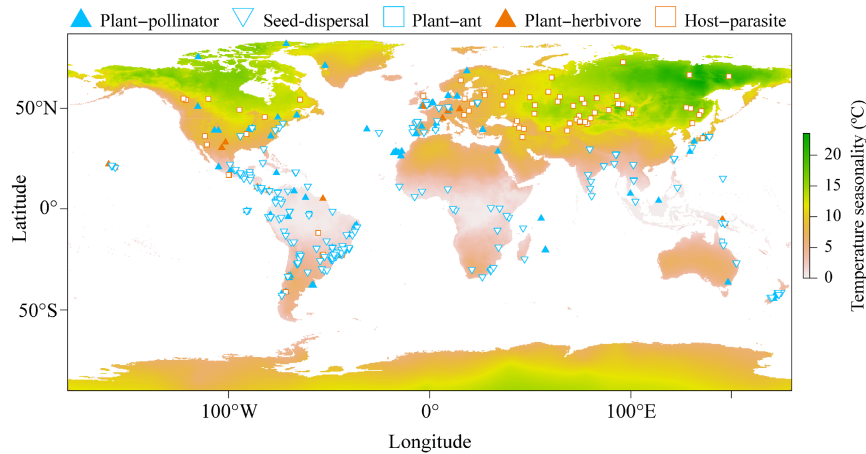


FIGURE 2 The location of the empirical bipartite networks ($n = 723$) used in this study, and their corresponding temperature seasonality ($^{\circ}\text{C}$) from Fick and Hijmans (2017) where blue symbols indicate mutualistic networks (plant-pollinator, seed-dispersal and plant-ant) and orange symbols indicate antagonistic networks (plant-herbivore and host-parasite)

Networks were obtained from open databases (e.g., datadryad.org and web-of-life.es) and from other studies' supplementary material (e.g., Fricke & Svenning, 2020; Michalska-Smith & Allesina, 2019; see Supporting Information Appendix S1 for literature sources for each network). Only networks that had at least five species in either disjoint set of species partitions were included in our study to avoid including small networks which may otherwise bias our analyses (Michalska-Smith & Allesina, 2019; e.g., minimum requirement of five pollinators and plant species per plant-pollinator network). Additionally, for simplicity, only the giant component of each network was used [i.e., the largest connected component of a graph (Dale & Fortin, 2014)] since all ecological networks used in this study are typically connected (Guimarães, 2020) when sampled correctly.

Temperature and precipitation seasonality were obtained from WorldClim (Fick & Hijmans, 2017), specifically BIO4 and BIO15, respectively. Temperature seasonality (in units of $^{\circ}\text{C}$) was defined as the standard deviation of mean monthly temperature values. Precipitation seasonality (unitless) was defined as the coefficient of variation of monthly precipitation. Both temperature and precipitation seasonality were measured spatially at a resolution of 2.5 arc minutes.

2.2 | Weighted network metrics

Of the 723 bipartite networks collected, 164 plant-pollinator, 166 seed-dispersal and 68 host-parasite networks were weighted. Networks were classified as weighted when interactions in the network had an associated measure of interaction frequency, for example, the number of times a pollinator pollinated a plant.

Only weighted networks were used to evaluate the effects of seasonality on network structure in all our linear models as they are often better descriptors of community structure than unweighted networks (Blüthgen, 2010; Blüthgen et al., 2007; Vizentin-Bugoni et al., 2016). Each weighted network was represented as a weighted incidence matrix, where for n rows (e.g., n plant species) and m columns (e.g., m pollinator species), a weighted interaction was

represented by a non-zero integer value between row j and column i if and only if there existed a connection between species j and i .

2.2.1 | Weighted modularity (ΔQ)

Weighted modularity (Q) for each weighted network was quantified using the `DIRT_LPA_wb_plus` function from the `bipartite` package (Dormann et al., 2008). This algorithm attempts to maximize Barber's modularity (Barber, 2007) of a given weighted network, where modules are more likely to form when there are strong node-node interactions (Beckett, 2016). We used the weighted modularity metric ΔQ , where $\Delta Q = Q_{\text{empirical}} - \bar{Q}_{50:\text{Vaznull}}$, the difference between the empirical weighted modularity of a given network ($Q_{\text{empirical}}$) and the mean weighted modularity of an ensemble of 50 null models based on the empirical network ($\bar{Q}_{50:\text{Vaznull}}$). The Δ -transformed metric was used to correct for the influences of sampling on empirical network properties (Dalsgaard et al., 2017). For the null model, we chose to adopt *Vaznull* (Vázquez et al., 2007), which fixes network size and weighted connectance as the empirical network.

2.2.2 | Weighted specialization ($\Delta H'_2$)

Weighted complementary specialization (H'_2), hereafter referred to as weighted specialization, was quantified for each weighted network using the `H2fun` function in the `bipartite` package. This function uses the two-dimensional Shannon entropy to calculate the specialization of an empirical network. In addition, `H2fun` normalizes empirical specialization using the maximum and minimum entropy possible when network configuration is constrained by the same row and column totals as the empirical network (Blüthgen et al., 2006). Hence, H'_2 ranges from 0 to 1 indicating the extremes of generalization and specialization, respectively. We controlled for potential sampling bias in specialization by using the Δ -transformed metric $\Delta H'_2$, where $\Delta H'_2 = H'_{2,\text{empirical}} - \bar{H}'_{2,50:\text{Vaznull}}$, the difference between the empirical weighted specialization of a given network ($H'_{2,\text{empirical}}$) and the mean

weighted specialization of an ensemble of 50 *Vaznull* models based on the empirical network ($\overline{H'}_{2,50;Vaznull}$).

2.2.3 | Weighted nestedness (ΔN)

Weighted nestedness (N) for each weighted network was quantified using the *wnodf* function (Almeida-Neto & Ulrich, 2011) in the *MBI* package (Chen, 2013). This function is a weighted extension of *nodf* (Almeida-Neto et al., 2008) and measures the degree to which rows and columns show decreasing marginal totals. We controlled for potential sampling bias in nestedness by using the Δ -transformed metric ΔN , where $\Delta N = N_{\text{empirical}} - \overline{N}_{50;Vaznull}$, the difference between the empirical weighted nestedness of a given network ($N_{\text{empirical}}$) and the mean weighted specialization of an ensemble of 50 *Vaznull* models based on the empirical network ($\overline{N}_{50;Vaznull}$).

2.3 | Weighted network linear models

2.3.1 | Plant-pollinator, and seed-dispersal linear mixed models (LMMs)

Linear mixed models (LMMs) were used to determine whether variations in the weighted measures of modularity (ΔQ), specialization ($\Delta H'_2$) or nestedness (ΔN) were explained by temperature and precipitation seasonality. We constructed separate models for each of the three weighted metrics. We focused on these three metrics since they are commonly used in the literature; but we note that relationships between the metrics could also be present (e.g., Fortuna et al., 2010) so finding relationships with one metric is likely to indicate relationships with the others. We also constructed LMMs for explaining normalized weighted modularity (ΔQ_n ; Equation A1), normalized weighted specialization ($\Delta H'_{2,n}$; Equation A2) and normalized weighted nestedness (ΔN_n ; Equation A3), wherein each metric of ΔQ , $\Delta H'_2$ and ΔN was normalized by the standard deviation of its corresponding metric from the 50 *Vaznull* models (Supporting Information Appendix S3: Section 2).

Separate sets of LMMs were constructed: one set for plant-pollinator networks and one set for seed-dispersal networks. In each LMM, combinations of temperature and precipitation seasonality, as well as sampling intensity (Equation 1), were included as fixed effects, and publication was included as a random effect. We included sampling intensity, interpreted as the average number of interaction events observed per species (Schleuning et al., 2012), to control for the amount of effort used to characterize each network and to use as a baseline measure to evaluate the degree to which seasonality contributed to explaining variations in each network metric. Additionally, we included publication as a random intercept to control for possible publication effects that may make networks from the same publication more similar in structure than networks from different publications. Networks from the same publication each formed their own group (when there were more

than four networks per one publication) while the remaining networks were aggregated into their own group. Networks from publications with fewer than four networks were aggregated together as including them as separate intercepts may cause over-fitting in the models. All LMMs were constructed using the *lme4* package (Bates et al., 2015). The proportion of variance explained by the fixed effects (marginal R^2) and the proportion of variance explained by both the fixed effects and random effects (conditional R^2) were measured using the *MuMIn* package (Bartoń, 2020).

$$\text{Sampling intensity (network}_i) = \frac{\text{number of interactions in network}_i}{\sqrt{\text{number of rows (n) in network}_i \cdot \text{number of columns (m) in network}_i}} \quad (1)$$

If the variation explained by the random effect of publication was greater than zero for the weighted structural metrics of modularity, specialization or nestedness, we deemed publication to be important for explaining network structure and hence we continued to evaluate the effect of seasonality using LMMs with publication as a random effect. When assessing the random effect, we used the complete LMM that contained all fixed effects (including an interaction between temperature and precipitation seasonality) in addition to the random effect of publication, that is compactly written as sampling intensity + temperature seasonality \times precipitation seasonality + (1|publication). When the random effect of publication was important, we further investigated which combinations of fixed effects explained the variation in the corresponding structural metrics via Akaike information criterion (AIC; Akaike, 1973). If multiple models had similarly low AIC values (i.e., the absolute difference between their AIC values was less than 2), the model explaining the response variable with the lowest AIC was selected. While we acknowledge that models differing by less than an absolute AIC value of 2 did not differ in their performance, for simplicity, we only report the model with the lowest AIC (hereafter, 'chosen') in the main text. Hence, while there may be multiple models that performed equally well at explaining the response variable, as our primary objective was to assess the contributions of seasonality, we only needed to compare one of the 'best' performing models with models containing only sampling intensity. In cases where the marginal $R^2 < .15$, we did not investigate the individual contributions of each fixed effect since we deemed these models to not provide strong evidence of a relationship between seasonality and network structure. All analyses were conducted in R version 4.1.2 (R Core Team, 2021).

LMMs were only adopted for plant-pollinator and seed-dispersal networks as they were the only systems with the requisite number of publication categories (e.g., > 5 ; Bolker, 2021). Additionally, we constructed linear regression models (LMs) using the same combinations of fixed effects as the LMMs and then compared the amount of variation explained by seasonality in both sets of models. This was done to ensure that the random effect of publication was not masking the effects of seasonality in the LMMs (Supporting Information Appendix S3: Table A5).

2.3.2 | Plant–pollinator, seed-dispersal and host–parasite linear regressions (LMs)

When LMMs were not appropriate (i.e., systems had fewer than five publication categories or the variation explained by random effects of publication was 0), we used simple linear models (LMs) to explain the variation in weighted modularity (ΔQ , ΔQ_n), weighted specialization ($\Delta H'_2$, $\Delta H'_{2,n}$) and weighted nestedness (ΔN , ΔN_n). LMs were tested with all possible combinations of terms involving sampling intensity (Equation 1), temperature and precipitation seasonality given by the equation: sampling intensity + temperature seasonality \times precipitation seasonality.

We also constructed LMs using only networks with higher sampling intensity values in their respective system to test whether networks that were more extensively sampled showed any relationship with seasonality. To do so, we constructed LMs using only networks whose sampling intensity values were larger than the median sampling intensity value for each ecological system to explain variations in weighted modularity ($\Delta Q_{>Samp.int.}$), weighted specialization ($\Delta H'_{2,>Samp.int.}$), and weighted nestedness ($\Delta N_{>Samp.int.}$). These LMs were only constructed for plant–pollinator and seed-dispersal networks since these ecological systems had sufficient numbers of networks to build models with at most four explanatory variables (i.e., sampling intensity + temperature seasonality \times precipitation seasonality). We did not perform these analyses using LMMs since there would not have been enough random effect groups to warrant their use.

LM configurations of temperature and precipitation seasonality, and sampling intensity for explaining variations in network structure were chosen using AIC values in the same way as was done for LMMs. Specifically, when models had similarly low AIC values (i.e., the absolute difference between their AIC values was less than 2) for explaining the response variable, the model with the lowest AIC value was selected and presented in the main text along with a model containing only sampling intensity as an explanatory variable.

2.3.3 | Testing for spatial autocorrelation in models for weighted structural metrics

We tested for spatial autocorrelation, based on each network's sampling location, in the residuals of the chosen LMMs and LMs for weighted modularity (ΔQ , ΔQ_n , $\Delta Q_{>Samp.int.}$), weighted specialization ($\Delta H'_2$, $\Delta H'_{2,n}$, $\Delta H'_{2,>Samp.int.}$) and weighted nestedness (ΔN , ΔN_n , $\Delta N_{>Samp.int.}$) using Moran's I from the *DHARMA* package (Hartig, 2021). This was done to ensure that the assumptions of the models were not violated. Since none of the models' residuals had strong positive autocorrelation (Supporting Information Appendix S2), we did not include a term for autocorrelation in any of our models.

2.4 | Unweighted network metrics

Unweighted networks were used to evaluate the effects of seasonality on the structure of ecological networks while controlling for differences in how antagonistic or mutualistic systems may respond to seasonality, in a redundancy analysis. We used the modularity and nestedness metrics originally proposed by Michalska-Smith and Allesina (2019), since they have previously been shown to capture differences in antagonistic and mutualistic network structure when using climatic seasonality in a principal component analysis (Song & Saavedra, 2020).

To evaluate the modularity and nestedness of unweighted networks, the two largest eigenvalues of each network's adjacency matrix were used, where each eigenvalue was normalized to account for size and connectance of the networks. In theory, the first eigenvalue (λ_1) is maximized in perfectly nested networks (Staniczenko et al., 2013), while the second eigenvalue (λ_2) separates from the bulk of the eigenvalue spectrum in strongly modular networks (Newman, 2013). In our analysis, λ_1 of each network was normalized with respect to the first eigenvalues of two null models: (a) the Erdős–Rényi (λ_1^{er}) random bipartite graph (Erdős & Rényi, 1959) in which the numbers of nodes and connections were preserved, but nodes were connected at random, and (b) a configuration model (λ_1^{cm}) (Bender & Canfield, 1978; Strona et al., 2014) in which the numbers of nodes and connections were preserved as well as each node's degree (i.e., number of edges per node), but connections were made at random. Additionally, the λ_2 of each network was normalized by the second eigenvalue of a Erdős–Rényi model, approximated by $\lambda_2^{mp} \approx \left[1 + \sqrt{\frac{m}{p}}\right] \cdot \sqrt{np(1-p)}$, where $p = \frac{\text{total number of connections}}{n \cdot m}$, and (mp) stands for Marchenko–Pastur (Marčenko & Pastur, 1967). See Michalska-Smith and Allesina's (2019) supporting information for a more thorough derivation of all eigenvalue metrics.

Altogether, the three matrix algebra properties of each network evaluated were:

$$1 - \lambda_1^{cm} / \lambda_1 \quad (2)$$

$$1 - \lambda_1^{er} / \lambda_1 \quad (3)$$

$$1 - \lambda_2^{mp} / \lambda_2 \quad (4)$$

Since these modularity and nestedness metrics have only been rigorously tested using unweighted networks, we converted our weighted networks into unweighted networks for this analysis.

2.4.1 | Redundancy analysis with unweighted networks

We used redundancy analysis (RDA) to evaluate whether temperature and/or precipitation seasonality explained the variation in modularity and nestedness for unweighted networks while also

controlling for antagonistic and mutualistic network types. In the RDA, we included modularity and nestedness as the response variables (specified by Equations 2–4). Temperature and precipitation seasonality as well as a binary variable to identify networks as either antagonistic or mutualistic were included as explanatory variables.

3 | RESULTS

3.1 | Weighted network linear models

3.1.1 | Plant–pollinator and seed-dispersal linear mixed models (LMMs)

For plant–pollinator networks, the complete configuration LMM with all the fixed effects of sampling intensity (Samp. int.), temperature (Temp.) and precipitation (Precip.) seasonality (i.e., Samp. int. + Temp. × Precip.) only minimally contributed to explaining variations in weighted modularity (ΔQ) and weighted specialization ($\Delta H'_2$) (marginal $R^2 = .055$ and $.116$, respectively; Table 2). In both cases, the random effect of publication (which consisted of six categories) contributed to explaining most of the accounted variation (conditional $R^2 \approx .328$). For weighted nestedness (ΔN), since the random effect of publication did not contribute to explaining network structure, we explored seasonality's influence on ΔN in plant–pollinator networks using LMs (see Section 3.1.2). When testing the normalized versions of our metrics, the chosen model for normalized weighted nestedness (ΔN_n) only explained about 16% of the variation using the fixed effect of Temp. (Supporting Information Appendix S3: Table A3). We did not investigate models to explain the variation in normalized weighted modularity (ΔQ_n) or in normalized weighted specialization ($\Delta H'_{2,n}$) since residuals violated model assumptions.

For seed-dispersal networks, the complete configuration LMM with all the fixed effects of temperature and precipitation seasonality

(and their interaction), and sampling intensity only explained a minimal amount of the variation for weighted modularity (ΔQ ; marginal $R^2 = .082$) and weighted nestedness (ΔN ; marginal $R^2 = .051$) (Table 2). For both weighted modularity and weighted nestedness, the random effect of publication (which consisted of nine categories) contributed most to explaining the accounted variation of both metrics (conditional $R^2 = .232$ and $.293$, respectively). In the case of weighted specialization ($\Delta H'_2$), the chosen model moderately explained the variation in $\Delta H'_2$ but contained only sampling intensity as a fixed effect (marginal $R^2 = .279$, conditional $R^2 = .357$; Table 2 and Supporting Information Appendix S3: Table A1). Regarding the normalized metrics, we only explored seasonality's influence on normalized structural metrics using LMs (Section 3.1.2) as the inclusion of random effects did not improve the models.

3.1.2 | Plant–pollinator, seed-dispersal and host–parasite linear models (LMs)

As the marginal and conditional R^2 were equal for weighted nestedness (ΔN) in plant–pollinator LMMs, LMs were instead adopted to evaluate the relationship between temperature and precipitation seasonality with ΔN . The chosen model (i.e., the model with the lowest AIC) for ΔN included sampling intensity, temperature seasonality, and precipitation seasonality (i.e., Samp. int. + Temp. + Precip., $R^2_{\text{adj}} = .206$, Table 3 and Supporting Information Appendix S3: Table A2). While this LM contained both seasonality variables as explanatory variables, sampling intensity contributed most as a model with only sampling intensity explained more than half – about 12% – of the variation in ΔN (i.e., $R^2_{\text{adj}} = .117$).

For the normalized metrics of seed-dispersal networks, only LMs for normalized weighted nestedness (ΔN_n) were explored as model assumptions were violated when explaining both normalized weighted modularity (ΔQ_n) and normalized weighted specialization

TABLE 2 Linear mixed models (LMMs) for explaining the variation in weighted modularity (ΔQ), weighted specialization ($\Delta H'_2$) and weighted nestedness (ΔN)

Network type	Dependent variable	Fixed effect(s)	Marginal R^2	Conditional R^2
Plant–pollinator ($n = 164$)	ΔQ	Samp. int. + Temp. × Precip.	.055	.332
	$\Delta H'_2$	Samp. int. + Temp. × Precip.	.116	.323
	ΔN	Samp. int. + Temp. × Precip.	.218	.218
Seed-dispersal ($n = 166$)	ΔQ	Samp. int. + Temp. × Precip.	.082	.232
	$\Delta H'_2$	Samp. int. + Temp. × Precip.	.293	.377
		Samp. int.	.279	.357
	ΔN	Samp. int. + Temp. × Precip.	.051	.293

Note: Marginal R^2 is the proportion of variation explained by the fixed effects, and conditional R^2 is the proportion of variation explained by both the fixed and random effects. Publication, a factor variable that grouped networks from the same publication, was included as a random intercept in all models. Precipitation seasonality (Precip.), temperature seasonality (Temp.) and log-transformed sampling intensity (Samp. int.) were included as fixed effects. If the marginal $R^2 < .15$, we did not investigate which combinations of fixed effects were chosen. See Supporting Information Appendix S3: Table A1 for the associated models that were tested when evaluating which fixed effects were to be chosen. When marginal and conditional R^2 are equal (indicating that the random effect did not contribute to explaining the variation), model explorations were performed with linear models (Table 3).

TABLE 3 Linear models (LMs) for explaining the variation in weighted modularity (ΔQ), weighted specialization ($\Delta H'_{2n}$) and weighted nestedness (ΔN)

Network type	Metric	Independent variable(s)	Intercept	Temp. coeff.	Samp. int. coeff.	Precip. coeff.	Temp. × Precip. coeff.	R^2_{adj}	ΔAIC
Plant–pollinator (n = 164)	ΔN	Samp. int. + Temp. + Precip.	-7.6***	-4.6e-4*	-3.9***	4.0e-2	-	.206	0.00
		Samp. int.	-7.3***	-	-4.1***	-	-	.117	15.52
Host–parasite (n = 68)	ΔQ	Samp. int. + Temp. × Precip.	-3.4e-2	3.4e-5***	-4.8e-2*	5.1e-3*	-4.7e-7***	.175	0.00
		Samp. int.	2.3e-1***	-	4.1e-3	-	-	-.015	11.17
	$\Delta H'_{2n}$	Samp. int.	2.9e-1***	-	9.2e-2***	-	-	.144	0.00
		ΔN	-1.3e+1***	-	-1.1e+1***	-	-	.467	0.00

Note: Temp. = temperature seasonality; Precip. = precipitation seasonality; Samp. int. = the log-transformed sampling intensity for each network; coeff. = the coefficient's value; R^2_{adj} = the adjusted R^2 of the model; ΔAIC = the difference between the Akaike information criterion (AIC) of a given model and the model with the lowest AIC value. When Samp. int. alone is not the chosen model, we also provide the model with the lowest AIC value. See Supporting Information Appendix S3: Table A2 for all possible model configurations using the independent variables for explaining weighted metrics. * $p < .05$; ** $p < .01$; *** $p < .001$.

($\Delta H'_{2n}$). We found that seasonality only weakly explained the variation in ΔN_n ($R^2_{adj} = .045$; Supporting Information Appendix S3: Table A4), as the chosen LM included sampling intensity and temperature seasonality as explanatory variables (i.e., Samp. int. + Temp.).

Altogether for host–parasite networks, we found no strong relationships to suggest that seasonality explained any weighted structural metrics (Table 3 and Supporting Information Appendix S3: Table A2). Specifically, the chosen models for both weighted specialization ($\Delta H'_{2n}$) and weighted nestedness (ΔN) only included sampling intensity as an explanatory variable ($R^2_{adj} = .144$ and $.467$, respectively). While the chosen model for weighted modularity (ΔQ) was the complete model of Samp. int. + Temp. × Precip. ($R^2_{adj} = .178$; Figure 3), the total amount of variation explained by seasonality was low as a model with the seasonality terms only explained a small amount of variation in ΔQ (i.e., Temp. × Precip., $R^2_{adj} = .136$, Supporting Information Appendix S3: Table A2). Additionally, since model assumptions for both normalized weighted modularity (ΔQ_n) and normalized weighted specialization ($\Delta H'_{2n}$) violated model assumptions, we only explored LMs for normalized weighted nestedness (ΔN_n) in host–parasite networks (Supporting Information Appendix S3: Table A4). Although we found that the chosen model for normalized weighted nestedness (ΔN_n) included both sampling intensity and precipitation seasonality as explanatory variables ($R^2_{adj} = .619$), most of the variation explained was via sampling intensity since a model with only sampling intensity had an R^2_{adj} of $.572$.

3.1.3 | Higher sampling intensity networks: Plant–pollinator and seed-dispersal linear models (LMs)

When limiting our LM analyses to networks whose sampling intensity was greater than the median sampling intensity for their respective systems, we found moderate relationships with seasonality for two weighted metrics in plant–pollinator networks but none in seed-dispersal networks (Supporting Information Appendix S3: Table A6). Specifically, for plant–pollinator networks, the chosen model for explaining the variation in weighted modularity ($\Delta Q_{>Samp.int.}$) included sampling intensity, temperature, and precipitation seasonality (i.e., Samp. int. + Temp. × Precip., $R^2_{adj} = .323$), while the chosen model for explaining the variation in weighted specialization ($\Delta H'_{2n>Samp.int.}$) was Temp. × Precip. ($R^2_{adj} = .326$). Yet, when explaining the variation in weighted nestedness ($\Delta N_{>Samp.int.}$) in plant–pollinator networks, we found a much weaker relationship with seasonality ($R^2_{adj} = .146$) as the chosen model included only temperature seasonality as an explanatory variable. Conversely for seed-dispersal networks, the only noteworthy relationships we found (i.e., $R^2_{adj} > .15$) to suggest that seasonality explained any of the three network metrics were the models for weighted specialization ($\Delta H'_{2n>Samp.int.}$) wherein the chosen model contained all explanatory variables (i.e., Samp. int. + Temp. × Precip., $R^2_{adj} = .246$). However, most of the variation in $\Delta H'_{2n>Samp.int.}$ was explained by sampling intensity alone as a model with only sampling intensity had a moderate relationship with $\Delta H'_{2n>Samp.int.}$ ($R^2_{adj} = .199$; Supporting Information Appendix S3: Table A6).

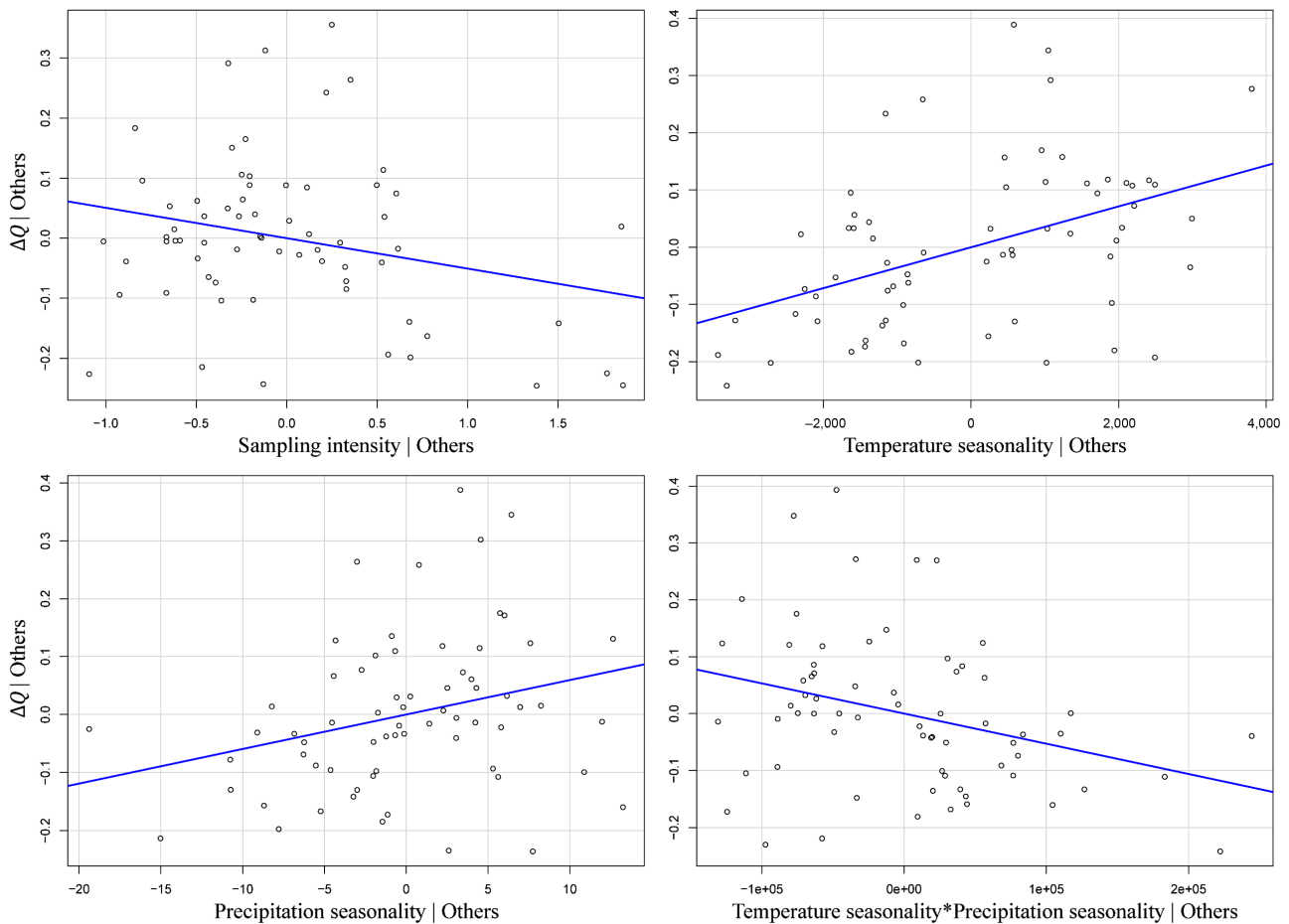


FIGURE 3 Added variable plot for the chosen linear model explaining the variation in weighted modularity (ΔQ) using the explanatory variables sampling intensity + temperature seasonality \times precipitation seasonality ($R^2_{\text{adj}} = .178$) for host–parasite ($n = 67$) networks. A single outlier was removed from the analyses presented here, but see Figure A1 of Supporting Information Appendix S3 for the linear model with all ($n = 68$) networks. Each panel represents the relationship between ΔQ and each explanatory variable in the model while controlling for all other variables

3.2 | Redundancy analysis with unweighted networks

We found only very weak relationships between seasonality and the unweighted network metrics for nestedness and modularity when controlling for antagonistic and mutualistic systems using RDA. Specifically, temperature and precipitation seasonality, and network type (i.e., antagonistic/mutualistic) only explained about 5% ($R^2_{\text{adj}} = .052$) of the total variation in unweighted nestedness (Equations 2 and 3) and unweighted modularity (Equation 4) metrics. When projecting these results in an RDA triplot (Figure 4), antagonistic and mutualistic systems did not show evidence of having different structures as they overlapped in RDA space.

4 | DISCUSSION

The representation and analyses of ecological communities using networks have increased dramatically over the last few decades (Delmas et al., 2019; Fortin et al., 2021; Poisot et al., 2016; Tylianakis

& Morris, 2017). Despite the growing number of ecological networks and statistical tests available, how climate and environmental conditions contribute to detectable differences in network structure is still heavily debated (Brimacombe et al., 2022; Pellissier et al., 2018; Poisot et al., 2021). In our large-scale analyses using the largest open dataset of bipartite networks yet compiled, we find (a) only weak evidence that temperature and/or precipitation seasonality explains the variation in the weighted metrics of modularity, specialization and nestedness in plant–pollinator, seed–dispersal or host–parasite systems and (b) that precipitation and/or temperature seasonality does not explain unweighted metrics of nestedness or modularity even when controlling for antagonistic (host–parasite and plant–herbivore) or mutualistic (plant–pollinator, seed–dispersal and plant–ant) network types.

Generally, in cases where seasonality contributed to explaining some of the variations in unweighted and weighted structural metrics, the contributions were always small. Specifically, seasonality explained at most only about 16% of the total variation in weighted network metrics [i.e., normalized weighted nestedness (ΔN_n) for plant–pollinator networks (Supporting Information Appendix S3: Table A3)] and about 5% of unweighted metrics (RDA; Figure 4). Importantly, the results for

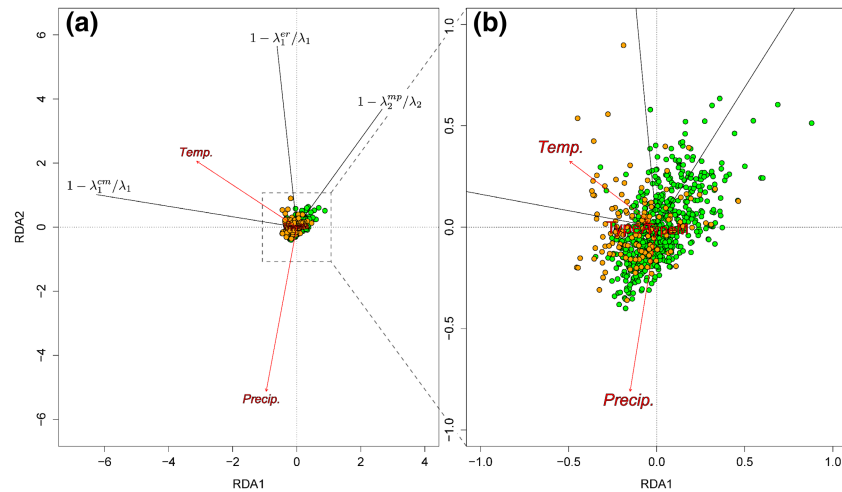


FIGURE 4 Redundancy analysis (RDA) distance triplot explaining metrics of unweighted nestedness ($1 - \lambda_1^{cm} / \lambda_1$, $1 - \lambda_1^{er} / \lambda_1$) and unweighted modularity ($1 - \lambda_2^{mp} / \lambda_2$) using precipitation (*Precip.*) and temperature (*Temp.*) seasonality while controlling for whether networks are classified as antagonistic (type A – plant–pollinator, plant–ant and seed–dispersal; orange circles) or mutualistic (type M – plant–herbivore and host–parasite; green circles). Panel (b) is a closer perspective of panel (a). Points are clustered together in the plots since *Temp.*, *Precip.* and *network type* only weakly explain the variation in the unweighted nestedness and modularity metrics ($R^2_{adj} = .052$)

the unweighted metrics also indicate that there are no structural differences between mutualistic and antagonistic networks since both overlap in RDA space, contrasting the findings of Song and Saavedra (2020).

The prominence of sampling intensity rather than temperature and/or precipitation seasonality throughout our analyses highlights how non-biological factors can influence the representation of ecological communities as networks. Nevertheless, beyond the variation captured by sampling intensity, other study design differences including the unique sampling strategies and unique construction methodologies that each publication adopted to create available open networks likely confound and contribute to our findings that there exist only weak relationships between network structure and seasonality. For example, previous studies have already found that the amount of time used to characterize an ecological community (CaraDonna et al., 2021; Schwarz et al., 2020), and the amount of area used when sampling *in situ* (Galiana et al., 2018) can influence network structure, and that the taxon resolution of nodes determined during network construction can contribute to large fluctuations in network metrics (Hemprich-Bennett et al., 2021). It is thus likely difficult to compare open species interaction networks (Salim et al., 2022) since each network may be structurally distinct due to the unique (a) biotic conditions each community experiences, the unique construction method used to create each network, and the unique sampling protocols adopted to characterize each ecological system as a network. Hence, study design differences are especially important to consider when using open networks as they can vary substantially between each publication that provides these networks. Although we acknowledge that we did find moderate relationships (i.e., $R^2_{adj} \approx .325$) of seasonality with weighted modularity and weighted specialization, this occurred only with plant–pollinator networks when three or more variables were included, and only when we limited our analyses to networks with the highest sampling intensity (Supporting Information Appendix S3: Table A6).

Most studies that attempt to measure network structure on a global scale use open networks that have been sampled and

constructed via different methodologies. Given the structural differences that can arise due to differences in sampling and construction methodologies, we advocate, as did Jordano (2016), for a consistent and rigorous protocol for reporting ecological network structure, particularly when measuring changes across large spatial extents. While not an exhaustive list, we recommend that this protocol includes consistency in: (a) the ways interactions are recorded, (b) the time and area allotted for observing interactions, and (c) the node resolution in networks. Such a protocol would help ensure measurement commensurability between networks, resulting in a definitive test of the relationship between structure and climatic gradients (Gravel et al., 2019). Until proper protocols have been adopted, we recommend exercising caution when using networks from multiple sources since the amount of time, area, effort, and node resolution used to characterize a community can vary greatly.

Beyond network heterogeneities that may arise due to differences in study design and methodologies, inherent biological properties may beget a lack of biological commensurability, creating even greater challenges when comparing networks. For example, given success for disentangling how traits influence pairwise species interactions (e.g., Dalsgaard et al., 2021), it may then be difficult to compare systems made up of very different species. While some traits may be generalizable across organisms like body size, finding other common traits that govern different organisms, for example, both insect and hummingbird interactions within plant–pollinator networks, may not be easy. Moreover, the life stage resolution of nodes can contribute to significant differences in network structure (Bodner et al., 2022; Clegg et al., 2018). For example, separate nodes are likely required to represent different life stages of species for those in which life stages act and behave entirely differently from one another, for example, tadpole and frog, resulting in even greater difficulties when comparing with networks without such variations between ontogenetic stages.

5 | CONCLUSION

Despite accumulated network data, it is unknown if and how ecological systems show detectable patterns in network structure across seasonal climatic gradients. Here, using a collection of open bipartite networks, we find no strong evidence that there exists a relationship between network structure and temperature and/or precipitation seasonality across large spatial extents, even when controlling for whether networks were antagonistic or mutualistic. Instead, we find much of the variation in network structure is better explained by the sampling intensity used to characterize each network. Hence, a definitive test for the relationship between network structure and seasonality across large spatial extents likely requires a dataset that is free from sampling bias, and networks whose communities are characterized using a consistent sampling protocol. Such a protocol would help ensure measurement commensurability between networks, resulting in a definitive test for the relationship between network structure and climatic gradients. However, given the large amounts of structural differences in currently available networks that likely result from sampling design differences, it is unlikely that such meaningful relationships with seasonal climatic variability exist within the network data.

AUTHOR CONTRIBUTIONS

CB and KB conceptualized the paper, with help from MMS, DG and MJF. CB and KB conducted the analyses. CB and MMS collected the data. CB and KB wrote the manuscript, and all authors made contributions to subsequent revisions.

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CONFLICT OF INTERESTS

We declare no conflict of interests.

DATA AVAILABILITY STATEMENT

Data and code are available here: <https://osf.io/h2m7j/>.

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BIOSKETCH

Our research team is broadly interested in understanding ecological communities via network approaches. Generally, we seek to understand how environmental covariates contribute to network structure across space and time, as well as evaluating the utility of open networks for answering these questions.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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