ON THE EFFECTIVENESS OF ANALYSING ECOLOGICAL
COMMUNITIES AS NETWORKS

by

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Abstract

Despite general recognition that ecological communities are dynamic, few studies evaluate how species interactions vary across time and space. Those that do commonly model and study the topology of communities as species interaction networks. Due to the high cost of *in situ* observations, researchers are often forced to reuse published *open* (i.e., freely available) species interaction networks to test their ecological hypotheses. Reused networks, however, can be problematic to adopt as data since they were likely built using differing methodologies and sampling protocols that are underreported, leading to inherent topological differences that are difficult to account for. My PhD aims to quantify the dynamic topology of species interaction networks and assess if open networks can be effectively reused to understand their topological drivers. In Chapter 2, I use an inferential method to construct seasonal multi-trophic networks from freshwater stream fish abundances collected using standardized protocols. The resulting networks show significant topological changes, even over short seasonal durations. In Chapter 3, I use a global dataset of open bipartite networks to test whether topology is explained by seasonal climatic variability. I find that seasonality does not structure networks; instead, an imperfect control variable for the amount of effort used to build each network, *sampling intensity*, best explains topology. In Chapter 4, I reevaluate previously published relationships suggesting abiotic and biotic variables explain open bipartite network topology. I uncover again that *sampling intensity* better explains topology than multiple ecological variables. In Chapter 5, I quantify topological similarity between open bipartite networks from Chapter 3 to better attempt to identify drivers of their structure. I find open networks sourced from the same publication are very topologically similar, highlighting the strong influence of publication-specific approaches on the structure of species interaction networks. Likewise, in Chapter 6, I evaluate the topological similarity between open food webs. I confirm again that the structure of open food webs sourced from the same publication are very similar. Altogether, my thesis enhances understanding of network dynamics and reveals the strong influence of publication on network structure, challenging the unbridled reuse of open networks for deducing topological drivers.

It is important that students bring a certain ragamuffin, barefoot, irreverence to their studies; they are not here to worship what is known, but to question it.

Jacob Bronowski

The first principle is that you must not fool yourself and you are the easiest person to fool.

Richard P. Feynman

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The core of my thesis consists of five chapters, all of which have been published in academic journals. As the first author of each paper, I was the lead investigator, performing the majority of the conceptualization, analysis, and writing. Nevertheless, all co-authors contributed by assisting in different aspects of each study, which have been invaluable in enhancing the quality of the research. The five chapters are:

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Chapter 4—**Brimacombe, C.**, K. Bodner, and M.-J. Fortin. How network size strongly determines trophic specialization: A technical comment on Luna et al. (2022). Ecology Letters, 2022, **25**:1914–1916.

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Chapter 6—**Brimacombe, C.**, K. Bodner, D. Gravel, S. J. Leroux, T. Poisot, and M.-J. Fortin. Publication-driven consistency in food web structures: Implications for comparative ecology. *Accepted:* Ecology.

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Chapter 1

Introduction

For almost all practical purposes, it is assumed that matter currently on earth will remain on the planet, reflecting the property of a closed system (Jacobson et al., 2000). According to the law of conservation of mass then, this matter is neither created nor destroyed (Bodner et al., 2021a). Consequently, the elements that make up life as we know it—mainly carbon, nitrogen, oxygen, hydrogen, calcium, and phosphorus—are perpetually reused and interconnected through all biological processes when formed into new molecules (Sterner et al., 2011).

This recycling of materials, and the ability to track it, is an important part of science. In chemistry, the mass of reactant elements in a reaction must equal the mass of the products (Silberberg et al., 2006). In physics, differential equations quantitatively describe relationships between functions and their derivatives (Boyce et al., 2021). In biology, carbon in the bodies of heterotrophs must have originated from autotrophs (Bolin, 1970).

The ability to track organic matter was likely an attractive feature for early ecologists who represented species and their feeding interactions as food webs. While the genesis of food webs is unknown, early concepts can be traced to Al-Jāḥiẓ in the eighth century who conceived food chains (Egerton, 2002; Delmas et al., 2019). The more recognizable and contemporary food webs produced by Summerhayes and Elton (1923) in the 1920s, can perhaps also be regarded as a beginning (Dunne, 2006). In their study, Victor Summerhayes and Charles Elton represented terrestrial and aquatic organisms—of various levels of taxonomic classification—as unique and discrete entities (specifically boxes), with their corresponding pairwise trophic feeding interactions as edges connecting organisms.

Since its inception, the interest, application, and study of networks in ecology has grown, especially in recent decades (Proulx et al., 2005; Ings et al., 2009; Delmas et al., 2019; Fortin et al., 2021). This rapid adoption can perhaps be attributed to their utility in representing complex systems as tractable networks, which can be further analyzed using mathematical techniques (Poisot et al., 2016b). For instance, beyond a *consumption road map*, analyzing who eats whom has important consequences for entire communities; direct and indirect interactions provide pathways that can facilitate trophic cascades (García-Callejas et al., 2019).

With network science's rich and extensive history, we as ecologists are equipped with a wealth of knowledge about networks that we can apply to our own studies (Michalska-Smith and Allesina, 2019). My thesis is devoted to building and analyzing *species interaction networks*, and so most of the discussion is focused here. Given the immense literature encompassing ecological networks (Poisot et al., 2015), this chapter serves only as a cursory introduction. In the following sections, I briefly introduce species interaction networks, how they are constructed, as well as some simple measurements that inform about their corresponding ecological communities. These ideas and concepts will be further explored in subsequent chapters, offering richer insights into their broader

implications.

1.1 General network history

Network science is a powerful discipline, originally rooted in the quantitative field of pure mathematics as *graph theory*. Celebrated as its first proof (Newman, 2003), the "Seven Bridges of Königsberg" problem resolved by revered mathematician Leonhard Euler in 1736, rigorously formalized the impossibility of navigating the City and returning to the place of departure, by only crossing each of the seven bridges once (Euler, 1741). The abstraction of Königsberg (now Kaliningrad, Russia) and its bridges as a mathematical object consisting of nodes (i.e., identifiable locations of the City separated by a river) and edges (i.e., bridges need to cross the river) is an illustration of the power of topology (Newman et al., 2006). Specifically, concerning the properties of a shape—in this case a network—that remain unchanged when that shape is deformed (Totaro, 2008), e.g., the Cartesian locations of bridges are disregarded when modelled as a network but still help to answer the aforementioned problem.

While the study of networks largely remained within the confines of graph theory for the next 200+ years, certain discoveries significantly punctuated through to contemporary network science (Lewis, 2011). In 1959, Edgar Gilbert (Gilbert, 1959) and Paul Erdős and Alfréd Rényi (Erdős and Rényi, 1959) independently introduced generative random graphs, which are now often adopted as network null models. In 1967, Stanley Milgram (Milgram, 1967) provided evidence for the "six degrees of separation", suggesting that anyone is socially connected to another by five intermediate acquaintances. More recently in the late 1990s and early 2000s, seminal work by Duncan Watts, Steven Strogatz, Albert-László Barabási, Reka Albert, Michelle Girvan, and Mark Newman applied network tools to understand real-world physical systems (e.g., the internet), which helped to usher in the study of complex networks (Molontay and Nagy, 2020). Complex networks exhibit properties and behaviors that do not appear in simple networks such as random graphs (Mitchell, 2006).

Today, network science is known as the science of systems (Lewis, 2011). This umbrella term includes parts of chemistry, physics, biology, and social science (Cottrell and Pettiford, 2000), but these same subjects in turn also inform network science; by innovating and developing novel approaches to analyze their own types of networks (Molontay and Nagy, 2020). Hence, the network tools available are vast, and sophisticated in their ability to uncover cryptic properties in the topology of networks. Added with the ability to analyze networks consisting of millions of nodes and edges, especially in our current data age (Newman et al., 2006), where "data is the new oil" as termed by mathematician Clive Humby, network science will undoubtedly continue to flourish.

1.2 Ecology and networks

The definition of species interaction networks are partly proceeded by their name, in that nodes represent species and edges connecting nodes represent their corresponding pairwise species interactions (Filotas et al., 2023). Specifically, in precise mathematical language (Lewis, 2011), a species interaction network G can be defined in set notation as

$$G = \{N, L, f\}, \tag{1.1}$$

where N is the set of all nodes representing species identities, L is the set of all edges representing species interactions, and $f: N \times N$ is a mapping function which informs about the nodes/species that interact with each other pairwise (i.e., one link connects two nodes). Species interaction networks are also commonly used and referred to as a model for the corresponding *ecological community* from which they were sampled, e.g., Dunne (2006); Delmas et al. (2019).

Undoubtedly, species interactions are important for species themselves (Thompson, 1999). In fact, the whole discipline of community ecology is devoted to the "study of the interactions that determine the distributions and abundances of organisms" (Krebs, 2009). Because species not only rely on interactions for sustenance, but also exist within interconnected webs, their evolution is directly shaped by these relationships (Cohen et al., 1993). Interactions are also integral to community stability (Landi et al., 2018), resilience (McCann, 2011), and often serve as a more nuanced indicator of richness than simple lists of species abundance counts (Valiente-Banuet et al., 2015). For these reasons, among others, studying species and their interactions within a network framework has helped to illuminate many different subdisciplines within ecology.

1.2.1   About ecological networks

One way to delve into the nitty-gritty of species interaction networks is by first classifying networks into mutually exclusive categories according to the rules by which their nodes can form edges with other nodes. Starting with the base case, unipartite networks allow any node to form an edge with any other node in a given network (Delmas et al., 2019). Food webs are the most recognizable unipartite networks in ecology and have historically been the most commonly studied type of species interaction network (Dormann et al., 2017). For instance, Polis (1991) described the trophic interactions between different vertebrates, invertebrates, and vascular plants of California's Coachella Valley desert. Under more constrained rules, bipartite networks separate nodes into two disjoint sets, where edges only occur between nodes of opposite sets (Williams, 2011). Like the plant-pollinator networks described by CaraDonna et al. (2017), there is clear differentiation between sets of nodes which represent animal pollinator species and plant species, and interactions only occur between a single plant node and a single pollinator node. Inductively, multipartite networks are a generalization of bipartite networks, whereby nodes belong to n disjoint sets (i.e., *multi*-sets), and edges between nodes can only occur between nodes of different sets. For example, Pocock et al. (2012) constructed a species interaction network consisting of 11 distinct sets of animals (e.g., seed-feeding insects, rodent ectoparasites) found in Somerset, United Kingdom. Keen awareness of the different types of networks is essential as their topology is dictated by the rules which interactions are allowed to occur between species.

Beyond just their nodes, species interaction networks can be further classified by their links. Binary networks consist of edges where an interaction is simply defined to exist between two nodes in a network. For example, Schneider (1997) built binary food webs for seven temporary pond communities in northern Wisconsin. In contrast, weighted networks are those that have edges with associated non-zero numerical values that reflect some element of realism. For instance, in the predator-prey bipartite networks of Gelmi-Candusso et al. (2023), the weight of links correspond to the number of times a predator species was observed eating a prey species. Edges can also be directed. In this way, an edge may indicate the flow of matter or energy. For example, Valiela (1974) described the food web of an arthropod community found in manure, where arrows point away from lower trophic organisms and towards higher trophic organisms. While obvious, it should be explicitly

stated that interactions also represent different types of species interactions. For instance, the edges of plant-pollinator networks are mutualistic and reflect an animal species pollinating a plant species, whereas the edges of food webs are antagonistic and reflect a consumer species eating a resource species.

Certainly, networks in ecology encompass more than just species interaction networks. Landscape ecology originally adopted networks to "generalize the consequences of habitat loss for patch connectivity and its implications for metapopulations" (Bascompte, 2007). In conjunction with differential equations describing species population changes, the patches of resources in metacommunity theory can also be modelled using networks (Thompson et al., 2017). Since ecological processes occur in a closed system, many other well-known topics in ecology can also be modelled as a network. Accordingly, Lotka-Volterra equations can be modelled as a network (Haerter et al., 2016), where interactions represent the rates of change of species population sizes. Similarly, susceptible-infected-recovered dynamics can be modelled by taking a network approach (Newman, 2002).

1.2.2 Constructing species interaction networks

Perhaps unsurprisingly, the biggest hurdle ecologists must overcome when evaluating network topology is the task of starting out, namely, gathering *in situ* data to be able to build species interaction networks (Strydom et al., 2021*a*). Generally most empirical networks at some point require field data (Jordano, 2016), where researchers must observe interactions between individuals of different species for those interactions to be represented in the network (Faisal et al., 2010). For example, when constructing food webs, ecologists often rely on evidence of predator-prey interactions through gut content analyses, via the presence of biological material of one species present in the stomach of another species (McLeod et al., 2020). However, it is often logistically and financially prohibitive for researchers to obtain interaction evidence to build their own food webs (Hegland et al., 2010; de Aguiar et al., 2019; Xing and Fayle, 2021).

The observational evidence requirement likely forces many researchers that do build networks to focus on studying ecological communities of more localized and small organisms. This may explain the recent increased interest in bipartite communities, such as those represented by plant-pollinator networks (Poisot et al., 2021; Xing and Fayle, 2021). In such cases, to obtain interaction evidence, a researcher may simply record all animal pollinators seen contacting the reproductive structures of sessile flower species during some observational period, e.g., CaraDonna et al. (2017).

Inferring community structure may also be an alternative and effective approach to help alleviate some sampling challenges (Morales-Castilla et al., 2015). Unlike traditional methods that rely on direct observation, inferential techniques circumvent the need for physical evidence of species interactions by instead employing proxies. For example, inference of interactions has been accomplished with varying levels of success, including via traits (Gravel et al., 2013), species co-occurrence (Harris, 2016), and phylogenetics (Strydom et al., 2022).

1.2.3 Topological measures of species interaction networks

For ecologists, constructing a species interaction network is likely a means to further analyze its corresponding topological properties which may reveal profound biological insights (Blüthgen et al., 2007). For example, *node centrality* can be used to identify keystone species in food

webs (Martín González et al., 2010). But before applying any metrics, it is essential to be aware of the type of network being analyzed. Different network types often necessitate distinct analytical approaches due to the rules governing the ways in which interactions are allowed to occur between nodes. For example, weighted metrics are designed to analyze the topology of networks with weighted interactions, and so should only be used with weighted networks. It should be stated that although not usually specified throughout this chapter, most of the metrics mentioned here have variants that have been developed to analyze weighted, unweighted, or directed networks.

One of the earliest discussions involving network metrics centered around *connectance*, spurred by the enduring complexity-stability debate (Dunne, 2006). Specifically, the hypothesis that a greater number of species interactions increases community stability (MacArthur, 1955). This notion was challenged by Robert May in his landmark works which outlined that stability occurs in random networks only when the number of species (S), connectance (C), and interaction strength (i) obey the inequality: $i\sqrt{SC} < 1$ (May, 1972, 1973). In essence, connectance measures the proportion of realized links to all possible links in a species interaction network (Blüthgen et al., 2006). For instance, in a food web with cannibalism, connectance is the ratio between the number of links L and the squared number of nodes S (or species) in the network, expressed as L/S^2. This metric also emphasizes the perspective of the graph as a binary symmetric matrix, where S is the number of rows and columns, and L is the number of 1s. Naturally, weighted matrices replace the binary entries with some other non-binary real number. While interactions in communities certainly do not occur at random, May's work provided a quantitative method to test the influence of complexity using empirical data [i.e., plugging in for the variables in the above equation] (Dunne, 2006). However, recent discourse about empirical networks generally views connectance as a sampling artifact, whereby connectance increases as sampling effort increases (Michalska-Smith and Allesina, 2019).

Today, more *in-vogue* metrics generally evaluate bipartite network topology, with three of the most popular being *modularity*, *nestedness*, and *specialization*. Modularity measures for clustering within a species interaction network, whereby clusters occur when a subset of species interact more strongly with each other than with other species (Olesen et al., 2007). For instance, Schleuning et al. (2014) demonstrated that modularity was related to seasonal climatic variability in seed-dispersal networks. Nestedness measures the degree to which specialist species interact with *proper* subsets of species interacting with generalists species (Bascompte et al., 2003). Guimarães Jr. et al. (2006) evaluated ant-plant networks in Mexico, and found generally high nestedness in species rich communities. Specialization measures the proportion of niche overlap—as measured by interaction partners—between species in the community (Blüthgen et al., 2007; Poisot et al., 2012*b*). Dalsgaard et al. (2011) found that the specialization of plant-hummingbird networks was associated with species richness and climatic variables.

Recognizing the significant loss of information incurred when summarizing network structure to a single metric, ecologists have begun to look for "distributions of forms within network structure" (Stouffer et al., 2007). Among these, motifs have gained considerable interest. Motifs are configurations of subsets of nodes and edges within a network that form connected circuits, and their over expressed frequency within an analyzed network is considered as displaying importance (Milo et al., 2002; Alon, 2007). In ecology, applications of motifs have included investigating the role of bee species in plant-pollinator networks (Simmons et al., 2019*a*), the role of ontogenetic structure in food webs (Clegg et al., 2018), and prey selection in food webs (Stouffer et al., 2007).

1.2.4   *Open* species interaction networks

Due to the substantial investment required to create any species interaction network (Polis, 1991; McLeod et al., 2021), many researchers opt to forgo *in situ* sampling, and instead adopt empirical networks already built as data for testing their own hypotheses (Winemiller, 1990; Goldwasser and Roughgarden, 1993). These freely available (i.e., open) species interaction networks are often made available on online repositories, after the articles which explored their topology have been published. Open food webs have been reused to investigate how the topology of communities are influenced by the amount of sampled area that was used to delineate the community (Galiana et al., 2018), and how communities are influenced by their proximity to anthropogenic sources (Mestre et al., 2022b). Open bipartite networks are also commonly reused, in particular, to evaluate how the structure of plant-pollinator, seed-dispersal, and host-parasite systems are influenced by latitude and climactic variability (Olesen and Jordano, 2002; Ollerton and Cranmer, 2002; Dalsgaard et al., 2011; Schleuning et al., 2012; Morris et al., 2014; Dalsgaard et al., 2017).

Of course, there are drawbacks with reusing collections of open species interaction networks for deducing topological properties therein (Dunne, 2006; Pringle and Hutchinson, 2020). In particular, open networks have been built by different sets of researchers using different definitions for their nodes and edges, based on observational data collected in different ways (May, 1983). Hence, these networks are topologically different, but in unknown ways, since the protocols used to build each network are missing, if not extremely underreported (Poisot et al., 2021). This makes it impossibly difficult to appropriately use collections of open networks—without effective controls—to infer drivers of their topology.

Lacking comprehensive information regarding how each open network was built, researchers often resort to using proxies derived from the network's topology to attempt to control for inherent topological differences that are presumably not the result of ecological drivers. A commonly adopted control included in statistical analyses is *sampling intensity* (Schleuning et al., 2012), defined as

$$\text{sampling intensity} = \frac{\sqrt{\text{number of interactions in network}}}{\sqrt{\text{number of rows in network} \cdot \text{number of columns in network}}}, \qquad (1.2)$$

which can be thought of as a normalizing statistic that measures the average amount of effort used to characterize the interactions of each species in a network. Various null models (e.g., link randomization of an empirical network) are also commonly adopted as a baseline for comparison (Dormann et al., 2017). However, challenges persist in understanding how statistical significance relates to biological relevance (Artzy-Randrup et al., 2004; Fründ et al., 2016).

1.2.5   Seasonality and species interaction networks

Communities are well documented to undergo structural changes when measured across time and space, yet most studies that examine these changes typically focus solely on variations in their species composition (Anderson et al., 2011). While it is trivial that the presence of two species is a prerequisite for an interaction to occur, it is not the only condition, as interactions may or may not occur even when both species are present (Poisot et al., 2015).

A particularly prevalent global driver of community topological change across time and space is seasonality, although it remains understudied. These predictable environmental oscillations

(e.g., temperature, precipitation) exert profound effects on species diversity, abundance, and interactions (Grøtan et al., 2012; Tonkin et al., 2017). For example, seasonality has been invoked to explain latitudinal structuring of bipartite species interaction networks (Song et al., 2017), the topology of stream food webs (Thompson and Townsend, 1999), community structure (Chesson, 2000), and community productivity (Robinson et al., 2013).

1.3   Thesis outline

The primary goal of my thesis is to investigate processes and drivers that shape ecological community topology using network theory. Generally, I investigate how species interaction network topology changes across both time and space in response to seasonality, as well as study how the ways in which researchers model ecological communities as networks perhaps determines their topology.

1.3.1   Chapter 2:—Inferred seasonal interaction rewiring of a freshwater stream fish network

The study of seasonal climatic variability on community topology is typically limited to communities consisting of species with small body sizes, which have interactions that are easily tractable. To overcome this issue, I apply a novel network construction method that uses time series abundance data to infer interactions between any species counted in the community. By building a fall and a spring network from freshwater fish abundances measured during these two seasons, I am able to quantify the two ways in which network topology can change across seasons, which are: (i) differences in species composition across the two seasons, and (ii) differences in interactions between species present in both seasons.

1.3.2   Chapter 3—No strong evidence that modularity, specialization, or nestedness are linked to seasonal climatic variability in empirical bipartite networks

While seasonal climatic variability has been invoked to explain community network topology for small bodied species, most studies test their hypotheses using a few networks (i.e., $n < 30$) and across a single type of ecological community. Using the largest dataset of open bipartite species interaction networks yet collected—consisting of five different types of communities (i.e., plant-pollinator, plant-ant, seed-dispersal, plant-herbivore, and host-parasite)—I more comprehensively test whether environmental variability explains nestedness, modularity, or specialization.

1.3.3   Chapter 4—How network size strongly determines trophic specialization: A technical comment on Luna et al. (2022)

Collections of open species interaction networks are often adopted as data for testing hypotheses about the topology of ecological communities. However, few studies attempt to control for differences in how each network was built, severely limiting the rigor of findings derived from open networks. This chapter is devoted to testing the robustness of claims regarding ecological communities from a recent publication that used open networks as their data source. Specifically, I test whether open

plant-pollinator bipartite network specialization is best explained by multiple ecological variables, when I also account for differences in how each network was built via measures of (*i*) sampling intensity, and (*ii*) network size (i.e., total number of species included in the network).

1.3.4 Chapter 5—Shortcomings of reusing species interaction networks created by different sets of researchers

Accounting for differences in how open networks were built is necessary for effective inference when using them. While controls like sampling intensity and network size are sometimes used, their efficacy is likely low as they do not directly account for the many nuances in variations of protocols adopted by researchers that build the networks. In this Chapter, I attempt to uncover the sources of topological differences in open networks by evaluating structural differences within subsets and across subsets of bipartite networks from Chapter 3, with particular focus on open networks sourced from the same publication. Since networks sourced from the same publication are built using consistent *construction methodologies*, *sampling strategies*, and exposed to comparable *biological and environmental factors*, publication may bias their bipartite networks' topology to be similar.

1.3.5 Chapter 6—Publication-driven consistency in food web structures: Implications for comparative ecology

Drawing on the results of Chapter 5, in this Chapter, I extend the network analysis to food webs to investigate whether the publication source of each open food web predominantly influences their topology. Unlike bipartite networks, food webs are less constrained in terms of the interactions nodes can have, making it uncertain if the same publication effect on network topology holds. Given that both bipartite networks and food webs play an eminent role in network ecology for informing our understanding of communities, this generalization holds significant importance.

1.3.6 Chapter 7—Final remarks

As an overview, I discuss the results of all Chapters and their implication for ecology. In particular, I emphasize recommendations for enhancing the utility of species interaction networks, focusing on improvements in data collection and modelling techniques.

Chapter 2

Inferred seasonal interaction rewiring of a freshwater stream fish network

2.1   Abstract

Despite evidence that seasonal variation may lead to the persistence of competing species, studies on the effect of seasonality on community network structures are sparse. Identifying whether seasonal network changes result from species turnover or rewiring (i.e., rearrangement of interactions among species), also remains understudied in multi-trophic communities. Using species abundance data for 38 species over three years (from nine sites across central/eastern United States) and a novel tree-based inference method, we constructed seasonal networks for a multi-trophic freshwater stream fish community. We found that seasonality influences species interactions, particularly through rewiring (81%) compared to species turnover (19%). Moreover, the number of rewiring interactions was best explained by fish status as a piscivore/non-piscivore and species maximum length ($R^2 = 0.41$). Our findings suggest that rewiring may be a dominant process in stream fish communities experiencing seasonal environments and that traits linked to trophic level could be a good indicator of a species' contribution to rewiring. As networks dominated by rewiring may be more robust, this network approach could be a valuable conservation tool for identifying which biological relationships must be retained for communities to avoid extinction.

2.2   Introduction

Ecologists recognize that species interactions are a cornerstone in determining biodiversity and ecosystem functioning (Bascompte and Jordano, 2007; Goudard and Loreau, 2008). Particularly, species interactions are central in the evaluation of community stability which can be measured using a system's resilience, robustness, and resistance to perturbations (Ives et al., 1999; Ives and Carpenter, 2007; Donohue et al., 2013). Indeed, interactions can mediate the negative effects of environmental change (Brooker, 2006; Suttle et al., 2007) and hence are essential for continued ecosystem persistence in the face of global change.

Species interactions vary across both space and time (Hagen et al., 2012; Rasmussen et al., 2013; Tylianakis and Morris, 2017; Pellissier et al., 2018; Olivier et al., 2019). Temporal heterogeneity, in particular seasonality, has been invoked to explain biodiversity and community structure (Tonkin

et al., 2017). For example, seasonality has been shown to minimize competitive interactions and help stabilize total species abundances (Shimadzu et al., 2013), as well as play a role in maintaining structure and diversity in communities [e.g., Fitzgerald et al. (2017)]. Consequently, as environments experience regular seasonal oscillations (Tonkin et al., 2017), the influence of seasonality on species interactions is pervasive (McMeans et al., 2015).

From a community perspective, species interactions can be analyzed using network theory and seasonality can be incorporated by constructing and comparing separate species interaction networks representing different seasons [e.g., CaraDonna et al. (2017)]. The properties of seasonal species interaction networks can then be assessed based on their topological differences due to species turnover and interaction rewiring [i.e., the changes in the interactions between the same species across space or time despite both species remaining present] (Poisot et al., 2012a). While seasonal species turnover or rewiring may dominate a system, they act in concert (Alarcón et al., 2008; Petanidou et al., 2008; Olesen et al., 2011; CaraDonna et al., 2017; Schwarz et al., 2020). Identifying the relative contribution(s) of each to seasonal network topology is important as systems dominated by rewiring may be more robust to perturbations [e.g., Kaiser-Bunbury et al. (2010); Saavedra et al. (2016a); Vizentin-Bugoni et al. (2020)]. Additionally, as traits have been shown to be an important driver of ecological network structure (Eklöf et al., 2013), determining how species traits relate to seasonal rewiring is a critical, yet unexplored component for understanding ecosystem dynamics.

Temperate freshwater stream ecosystems are well-suited to study the effects of seasonality as they experience regular seasonal variations from differences in shading, temperature, disturbance, and productivity (Thompson and Townsend, 1999). This strong influence of seasonality can have consequences for fish community assemblages (Junk et al., 1989; Peterson et al., 2017), making multi-trophic stream fish communities [e.g., Winemiller (1990); Peterson et al. (2017)] an ideal system for studying seasonal rewiring. However, observational interaction data may not always be accessible.

Indeed, due to the sampling effort required (Alarcón et al., 2008) and the difficulty in observing certain types of interactions [e.g., competition] (Faisal et al., 2010), few systems have the observational data required to produce observed temporal interaction networks. These challenges often restrain seasonal species interaction networks to few trackable system such as plant-pollinator networks [e.g., Alarcón et al. (2008); Petanidou et al. (2008); Olesen et al. (2011); Burkle et al. (2013, 2016); Rasmussen et al. (2013), but see Baird and Ulanowicz (1989); Yodzis and Winemiller (1999); Carnicer et al. (2009); Saavedra et al. (2016a); Lopez et al. (2017); Peterson et al. (2017); McMeans et al. (2019) for notable exceptions].

To palliate the limitations related to direct interaction data, inferential methods that estimate species interaction networks have been proposed as an alternative to their empirically derived counterpart (Morales-Castilla et al., 2015). Inferential methods are reproducible, allow for a wider range of species given they require less sampling effort, and can detect interactions that are not readily observable (Faisal et al., 2010). While most inferred ecological interaction networks are constructed using species co-occurrence methods, they have been criticized for elucidating false interactions and for failing to detect true pairwise species interactions (Blanchet et al., 2020). A false interaction may arise due to species responding similarly to the same environmental factors (Peres-Neto et al., 2001) while true interactions may not be detected due to the coarseness of presence/absence data (Sander et al., 2017). Joint species distribution models [e.g., Pollock et al. (2014); Ovaskainen et al. (2016)] have been touted as a more robust method to infer community

structure as they incorporate abiotic factors into their analysis (D'Amen et al., 2018). However, these models are also often built using co-occurrence data and therefore suffer the same limitations as other methods that rely on presence/absence data to infer species interactions (Blanchet et al., 2020). A promising approach proposed by Momal et al. (2020) addresses limitations of presence/co-occurrence data by utilizing species abundances (instead of presence/absence data) and environmental covariates within a joint species distribution modeling framework. Including abundance measures provides richer information for capturing interactions (Blanchet et al., 2020) while the inclusion of environmental factors helps prevent spurious interactions in the network.

In this paper, we investigate seasonal changes in a multi-trophic freshwater stream fish community by creating seasonal networks using stream fish abundances (NEON, 2020) and a novel tree-based inference method proposed by Momal et al. (2020). Using this method, we constructed two inferred fish interaction networks for fall and spring and examined their topological differences. Specifically, our objectives were to: (i) quantify the influence of seasonal interaction rewiring and species turnover (i.e., β-diversity); and, (ii) evaluate whether seasonal changes in species interactions were related to species-specific traits.

2.3   Materials and methods

2.3.1   Overview

Using the sampled freshwater fish abundances carried out by the National Science Foundation's National Ecological Observatory Network (NEON), we analysed abundance data by season (either fall or spring). Due to convergence issues in the network inference methods, yearly information had to be ignored during network construction. To ensure that year did not substantially influence the dynamics of the system, LASSO Poisson regressions (Friedman et al., 2010) were used to test the effect of year on species abundances. We found that the addition of year did not substantially improve the species abundance predictions, allowing us to pool data based on the season the sample was taken. Inferred seasonal interaction networks were created via a two step-process: (i) construct fall and spring Poisson lognormal (PLN) models (Chiquet et al., 2018, 2019), a type of joint species distribution model that measure species interactions while controlling for environmental factors; and (ii) apply the EMtree algorithm (Momal et al., 2020), which uses the fitted PLN models to create seasonal species interaction networks, using tree structured graphical models. We then quantified species turnover and rewiring using a measure of β-diversity (Poisot et al., 2012a) across the two seasonal networks. Finally, we investigated (using linear regressions) how species-specific traits could be used to explain the total number of interactions classified as rewiring, and species turnover.

2.3.2   Fish data

Stream fish abundances were obtained from the "Fish electrofishing, gill netting, and fyke netting counts" dataset provided by NEON (2020). This dataset contains fall and spring stream fish abundances made via electrofishing under strict sampling protocols [see Jensen (2019)]. Additionally, this dataset included abiotic data such as environmental, geographic, and sampling design factors (e.g., date of sampling, water temperature, dissolved oxygen, latitude), and fish length and fish weight data for each fish caught, for 28 aquatic monitoring locations across the United States.

To reduce yearly variation across seasons when pooling data into seasons, we only included sites that had consecutive seasonal measurements within a year, i.e., both fall and spring abundance measures made per year. Thus, our analysis used abundance samples from 9 sites spanning the United States between 2017–2019 (Figure 2.1).

The abundance dataset contained taxonomic information, but samples varied on the level of identification. Hence, we restricted our analyses to species with species-level identification as we were concerned that a higher taxonomic grouping would obscure key biological interactions. We excluded samples from the analysis if environmental conditions were not recorded.

For our trait analysis, we obtained species-specific traits from FishTraits (Frimpong and Angermeier, 2009) and obtained species' maximum length and maximum weight from the NEON dataset containing the samples used to construct our networks. FishTraits is an extensive database that contained traits for our species except for *Etheostoma lachneri*, which we supplemented with those of *Etheostoma raneyi*, a close relative (Ross, 2012). Furthermore, we obtained feeding behaviour information from NatureServe (NatureServe, 2020) where fish were classified as belonging to at least one of the following non-exclusive categories: (*i*) non-feeder (non-parasitic lamprey species), (*ii*) herbivore, (*iii*) invertivore, and (*iv*) piscivore; see Table 2.1.

2.3.3   Testing for yearly abundance trends

We tested for yearly trends in each pooled seasonal dataset using LASSO Poisson regression models (Friedman et al., 2010) on each species data. LASSO Poisson models are a type of penalized generalized linear model for count data that forces less contributive coefficients to be zero. Generally, for each species we compared the predictive ability of (*i*) `Site name`, and (*ii*) `Site name + Year`, to test for yearly trends and to determine if pooling data across years into seasons was appropriate. `Site name` was included in both models to capture site-specific abiotic measurements as well as account for the variability of species presence/absence across sites. The withheld seasonal datasets used for predictive purposes included each site's most recent abundance sample for that season. We determined the "best" model by calculating their predictive performance on the withheld dataset. We used two metrics for predictive performance: the cumulative root mean squared error (RMSE) and the cumulative RMSE for species with abundances greater than 0 in the prediction dataset ("RMSE obs>0"). All LASSO Poisson regression models were implemented using glmnet package (Friedman et al., 2010).

2.3.4   Constructing and testing Poisson lognormal (PLN) models

To model joint species abundances, required for inferring seasonal interaction networks, we first fitted, and tested a suite of PLN models (Chiquet et al., 2018, 2019) on the pooled seasonal dataset. PLN models are joint species distribution models that can be used to infer joint species abundances and interactions using environmental factors and species' abundance data. Here, we built models that included different combinations of (*i*) `water temperature` during sampling, (*ii*) `dissolved oxygen` during sampling, (*iii*) `specific conductivity` during sampling, (*iv*) `elevation` at sampling site, (*v*) `date` of abundance sampling, (*vi*) `latitude` at abundance sampling, and (*vii*) `site name`. We also included sampling effort in our models as excluding this effort reduces the comparability of abundance samples measured at different places and

times (Chiquet et al., 2019). Sampling effort was included for each abundance sample and was pre-calculated as a sum of the total counts of fish caught, a common approach for including sampling effort in models (Paulson et al., 2010). Altogether, the nine PLN models built for each season accounted for the following environmental variable(s): `Site name`, `Water temperature`, `Dissolved oxygen`, `Elevation`, `Specific conductivity`, `Site name + Water temperature`, `Site name + Dissolved oxygen`, `Site name + Elevation`, and `Site name + Specific conductivity`.

We evaluated our seasonal PLN models by using non-traditional Bayesian Information Criterion (BIC), an information-theoretic approach; and by calculating their predictive performance on withheld future abundance data. Note the non-traditional BIC scores represent the variational lower bound of the BIC, which account for the model's variational log-likelihood and its number of parameters [see Momal et al. (2020) for more details]. Overall, higher scores indicate better fitting models. To assess predictive performance, we predicted species abundances and compared the RMSE and RMSE obs>0. The models with the best BIC score and lowest RMSE scores were the models selected. As we use both an in-sample and out-of-sample measurement (i.e., information-theoretic techniques and RMSE on withheld data), the models should have higher accuracy and lower uncertainty (Bodner et al., 2020). All construction and testing of PLN models were done through the PLNmodels package (Chiquet et al., 2018, 2019).

2.3.5   Species interaction networks from EMtree

Separate Fall and Spring species interaction networks were inferred using the EMtree method proposed by Momal et al. (2020). Generally, EMtree combines both (i) PLN models to represent the joint distribution of species abundances and (ii) spanning tree graphical models to create undirected species interaction networks, where a spanning tree is defined as a subgraph of a network that connects all nodes with the minimum number of possible connections (Dale and Fortin, 2014). Note that while the number of interactions between all nodes is minimized and the minimum bound on the number of interactions a node may have in a tree is one, a node may have more than one or two interactions.

Network inference can be challenging due to the huge number of possible graphs for a given set of nodes (e.g., 1013 undirected graphs given 10 nodes). All network inference approaches try to infer the underlying true network configuration but are impeded by this vast number of configurations (Momal et al., 2020). To overcome this issue, EMtree employs a spanning tree-based approach, which is a technique designed to reduce the possible number of configurations given by the PLN model's joint distribution of abundances, to make inference tractable in the graph space (Momal et al., 2020). The links in the spanning tree represent possible interactions between species. EMtree constructs fitted species interaction networks by averaging across all spanning trees and employs an advanced tree-based algorithm to maximize the likelihood of the inferred species interactions from the PLN models. The EMtree approach combines both pairwise potential direct (e.g., predator-prey interactions) and indirect (e.g., indirect competition) interactions, represented as a single undirected connection between species' nodes. In the resulting networks, each connection was weighted with a value between zero and one, representing the conditional probability of each connection being part of the "true" underlying network. We assumed that if an interaction had a non-zero weight, i.e., it is suspected to be part of the network, it existed in the network.

To create the network, it was necessary to select a minimum threshold as a cut-off for

inferring species connections. This threshold can be used as a metric for assessing the reliability of connections with higher thresholds indicating higher reliability. Nonetheless, a guideline is to use the highest threshold before a node (i.e., species) loses all connections (Bassett et al., 2006). From a biological perspective, a connected network can emerge when just a few generalist species are present (Martín González et al., 2010). Hence, we created networks using thresholds between 0; the minimum possible threshold assuming virtually all connections, and 1; the maximum possible threshold producing no connections, and chose the network built with the highest threshold that remained connected. We increased network robustness by iteratively resampling the network 100 times. The EMtree approach was implemented using the EMtree package (Momal et al., 2020), and network visualization was accomplished through the igraph package (Csárdi and Nepusz, 2006).

2.3.6 Beta-diversity

To estimate species turnover and rewiring in our seasonal networks, we quantified the β-diversity across Fall and Spring. We adopted a β-diversity metric, β_{WN}, which measured the interaction turnover between two networks, with $0 \leq \beta_{WN} \leq 1$ (Poisot et al., 2012a). This metric can be represented by the following equation:

$$\beta_{WN} = \frac{a + b + c}{(2a + b + c)/2} - 1 \tag{2.1}$$

where a was the number of interactions shared between networks (Fall and Spring), and b and c were the number of interactions unique to each network, respectively. Hence, larger values of β_{WN} indicated a greater difference between the two networks. We further isolated the effects of species turnover, β_{ST}, and rewiring, β_{RW}, from β_{WN} using the equation $\beta_{WN} = \beta_{ST} + \beta_{RW}$. β_{RW} was evaluated by considering only the two subsets of networks—one in the Fall and one in the Spring—where species have interactions in both, and its numerical value was calculated using eq. (2.1). Additionally, we assessed total species dissimilarity between seasons (β_S) using eq. (2.1), where a, b, and c were the appropriate species identities.

2.3.7 Total species turnover, total rewiring, and species traits

To calculate the total number of species turnover and rewiring connections for each species, we identified each changing connection in each seasonal network as being one of the following: (i) "rewiring", where two species present in both seasons were linked in one season but not in the other; or (ii) "species turnover", where one or both species were present only in a single season, and the connection existed only for a single season. All connections preserved across seasons were classified as "maintained".

Using linear models, we examined the relationships between the total number of rewiring (i.e., sum of the connections classified as rewiring), and the total number of species turnover connections (i.e., sum of the connections classified as species turnover), with species traits, abundances, feeding preferences/trophic-level, and habitat preferences.

All analyses conducted were done in R version 4.0.2 (R Core Team, 2021).

2.4 Results

2.4.1 Data

We restricted our analysis to species that appeared in a seasonal dataset at least five times as fewer than five occurrences resulted in convergence issues when using the EMtree algorithm. This restriction resulted in 32 species in the Fall, 34 species in the Spring, with 29 species common to both seasons (Table 2.1), which contributed to a seasonal species dissimilarity score of $\beta_S \approx 0.13$.

2.4.2 Testing for yearly abundance

In the Fall, the LASSO Poisson regression of `Site name` (RMSE: 10.35, RMSE obs>0: 27.14) performed better than `Site name + Year` (RMSE: 17.94, RMSE obs>0: 34.02) (Table 2.2). Furthermore, in the Spring, the LASSO Poisson regression model of `Site name` (RMSE: 7.35, RMSE obs>0: 19.72) performed equally well as `Site name + Year` (RMSE: 7.11, RMSE obs>0: 19.28) (Table 2.2). Hence, Year did not contribute significantly to predicting Fall or Spring abundances and thus yearly variation was not deemed as a significant factor for either season.

2.4.3 PLN models

Using each respective pooled seasonal datasets, the three PLN models with highest BIC scores for both seasons were `Site name` (Fall BIC: −6419, Spring BIC: −8159), `Site name + Water temperature` (Fall BIC: −6473, Spring BIC: −8237), and `Site name + Dissolved Oxygen` (Fall BIC: −6456, Spring BIC: −8219) (Table 2.2). `Site name` also had the best BIC score and predictive performance in both the Fall (RMSE: 4.2, RMSE obs>0: 11.1) and Spring (RMSE: 5.0, RMSE obs>0: 12.4). Hence, the `Site name` PLN models, representing the inherent abiotic and spatial factors not measured at each site, were selected as best for both seasons.

2.4.4 Inferred seasonal networks from EMtree

We inferred each seasonal species interaction networks using EMtree paired with the Fall and Spring `Site name` PLN models (Figure 2.2). We tested potential threshold cut-offs for each network and determined the highest appropriate threshold to be 0.6, since above this value the network became disconnected. Furthermore, as many species in our community were generalists, we expected that the underlying network to be connected (Martín González et al., 2010). Thus, all network metrics presented correspond to seasonal networks constructed with a threshold of 0.6.

2.4.5 Beta-diversity

The topological changes across seasons were apparent when quantifying topological change using β-diversity metrics. Specifically, interaction turnover was $\beta_{WN} \approx 0.62$. In other words, there was a relatively large difference in the topology of the Fall and Spring networks. This seasonal topological change was largely driven by interaction rewiring (β_{RW}) rather than species turnover (β_{ST}). In particular, we found that $\beta_{RW}/\beta_{WN} \approx 81\%$, whereas $\beta_{ST}/\beta_{WN} \approx 19\%$.

2.4.6 Total species turnover, total rewiring, and species traits

Using linear regression models, we investigated how different species traits and abundances influenced the total number of rewiring (blue bars of Figure 2.3). While we did not find any meaningful models regarding key life history traits or species' abundances, we found that species traits related to maximum length and feeding helped explain around 41% of the total number of rewiring. Specifically, total number of rewiring had a significant and negative relationship with a species' piscivore status and a significant positive relationship with the interaction between maximum length of a species and its piscivore status, Figure 2.4 ($\beta_{\text{Max length}} = -0.03$, $p > 0.1$; $\beta_{Piscivore} = -6.10$, $p < 0.01$; $\beta_{\text{Max length·Piscivore}} = 0.04$, $p < 0.01$; adjusted $R^2 = 0.41$). The negative relationship between piscivore status and the total number of rewiring suggested that non-piscivores have a greater number of rewiring than piscivores when controlling for the maximum length of a species. Interestingly, despite maximum length not being significant, its interaction with piscivore status is significant indicating that for piscivores, there is a strong positive relationship between the total size and the number of rewiring that does not exist for the non-piscivores.

We also note that while no specific traits or species abundances explained the total number of species turnover connections (purple bars of Figure 2.3), approximately 80% of fish present for only a single season had preferences for large rivers. This percent is significantly higher than the approximately 45% of the non-turnover fish that shared this preference.

2.5 Discussion

The role of seasonality in shaping species interaction networks requires better assessment for understanding the stability and function of community assemblages. So far, most studies analyze seasonality in small-size organismal bipartite networks (e.g., plant-pollinator networks), yet limited evidence exists on how seasonality shapes multi-trophic networks across communities of larger species. Despite increasing evidence that topological changes arise due to rewiring and species turnover (Alarcón et al., 2008; Petanidou et al., 2008; Rasmussen et al., 2013; Lopez et al., 2017; Schwarz et al., 2020), as of yet, identifying which process is dominant and more critically, quantifying the contributions of each process, is rarely done across seasons for multi-trophic networks. Here, we provide a study on inferred seasonal multi-trophic networks that provides evidence of seasonal change using interaction turnover, and that seasonal rewiring may be a driving process of community changes in stream fish communities.

Given the strong evidence of seasonality in stream fish networks (Thompson and Townsend, 1999; Peterson et al., 2017), unsurprisingly, we found evidence that seasonality influenced our network structure. Indeed, the reported seasonal consumption of the most abundant aquatic invertebrates (Pinto and Uieda, 2007), and the seasonal dietary shifts of ominvirous and carnivorous fish (Akin and Winemiller, 2006) highlight the seasonal opportunistic feeding behaviour of many fish species. The differences in network structure we found between seasons are exemplified by the degree of its interaction turnover across seasons. As a score of zero indicates networks are identical and a score of one indicates that networks have no common interactions, our score of $\beta_{WN} = 0.62$, indicates a relatively high differentiation between our seasonal networks.

Beyond classifying network change, identifying the primary drivers of species interactions is essential for predicting community structure. In our study, we found that seasonal topological

changes to our inferred network were primarily driven by interaction rewiring (81%) with a small contribution by species turnover (19%). Consequently, the level of rewiring and turnover we found in our study mirrors results from other systems. In particular, the amount of seasonal rewiring and seasonal turnover in our study is comparable to the weekly and mean yearly interactions found in the rewiring-dominated plant-pollinator networks studied by CaraDonna et al. (2017). While the ratio of seasonal species to those present in both seasons in our study is lower, this difference in species dissimilarity is likely in part the result of our requirement that species need to be sampled at least five times. The inclusion of these rare species would likely increase our species dissimilarity measure but would not have changed our overall network structure since they need to be abundant enough to warrant interactions (Poisot et al., 2015). Thus, our study contributes to the growing literature of the potential ubiquity of rewiring across different systems. However, we recognize that high levels of rewiring may be more common in some systems. Therefore, we hope future studies continue to quantify rewiring across study systems to further test its ubiquity and to identify cases and species where it may not be as dominant.

Despite highlighting the need to resolve networks along a temporal dimension, our results provide a general prediction for how these seasonal communities may respond to disturbances. If species subject to seasonality are more strongly driven by rewiring, we may also expect these species to be more robust when subject to other types of disturbances (CaraDonna et al., 2017). For example, Kaiser-Bunbury et al. (2010) found that in plant-pollinator networks, rewiring increased community robustness when faced with community species loss, Saavedra et al. (2016a) found that seasonal interactions play a key role in maintaining the homeostatic state of ecological communities, and Vizentin-Bugoni et al. (2020) found that rewiring increased estimated robustness in plant-humming bird networks. Indeed, it would be of interest to conservation managers to determine if their systems are robust to future perturbations, given that their system also undergoes seasonal rewiring. However, while in general we expect rewiring to have a stabilizing effect, rewiring has been shown in some cases to have a negative effect on the persistence of both natural and computer-generated food webs (Gilljam et al., 2015). Hence, future studies should explore whether stability due to rewiring holds for different disturbance types, different ecosystems/organisms, and under which conditions it switches from a stabilizing to a destabilizing effect.

2.5.1 Total rewiring, total turnover, and species traits

As fish species' traits may have high plasticity (Frimpong and Angermeier, 2010), detecting relationships between traits and fish interaction dynamics can be an especially arduous task. Furthermore, given that rewiring can be both an active and/or passive process, it is perhaps especially difficult to identify key traits describing their ability to rewire. For example, a predator will actively rewire when it switches a prey item, whereas its prey passively rewires in response. In this case, we do not expect the predator and prey to exhibit the same traits. As traits related to the passive and active process of rewiring likely differ, we do not expect to find an all-encompassing relationship between any single trait and the total number of rewiring.

Nevertheless, the significant relationship we found between the total number of rewiring and the interaction between the maximum length of a species and its piscivore status $\left(R^2 = 0.41\right)$ likely captures traits associated with active rewiring. Indeed, larger species of piscivores generally do consume a larger range of prey size than their smaller counterparts (Gaeta et al., 2018). This active

rewiring may also capture the stabilizing ability of piscivores. Since these large mobile predators are able to track and exploit multiple abundant prey across multiple trophic levels, piscivorous fish can promote food web stability through reduced interaction strength and reduced predation pressure when prey density is low (Kondoh, 2003; McCann et al., 2005). In addition, when maximum length was held constant, we also captured a significant negative relationship between piscivore status and the total number of rewiring. This negative relationship indicates that overall, non-piscivores have a higher total number of rewiring which may be in part due to many smaller non-piscivores passively rewiring with a few larger key predators. Additionally, as our network captures more than food web dynamics, this negative relationship may also be capturing rewiring due to competition and other biological interactions. If this is the case, lower trophic levels may be more heavily competing with different species for space and food across seasons whereas piscivores may maintain competitive interactions with the same species year-round.

We were unable to find any significant traits related to species turnover. This is not particularly surprising as unlike rewiring interactions, turnover interactions are dependent upon the arrival and departure of only nine species in our system. We expect that an increased species turnover rate would allow for relevant traits to be more easily detected. Despite not finding any significant traits related to the total turnover interactions, interestingly, all turnover species were those that preferred large rivers. Given this, we suspect that these turnover fish species may be seasonally migratory.

2.5.2 Limitations

The main limitation of our study is the dependence on inferred interactions from abundance data. As there are no direct observations of the interactions, there is always the possibility that these interactions do not exist. However, the benefits of approaches like the one used here, should not be overlooked. Despite there being no direct observations in our system, the inferred network approach allowed us to hypothesize seasonal networks for a previously unexplored community. In general, inferred network approaches not only allow us to reduce the resources required to infer species interactions but can propose interactions when observation is difficult (Faisal et al., 2010). Indeed, in our inferred seasonal network, we detected an interaction between $S.\,trutta$ and $S.\,fontinalis$ which had been hypothesized and only captured through experimental manipulation (Fausch and White, 1981). Given that $S.\,trutta$ and $S.\,fontinalis$ are heavily monitored, we could validate our proposed interaction. However, most fish species are allocated fewer resources so there is little information available, particularly on their interactions. Ultimately, the inferred network approach allows us to generate new hypotheses about how these unobserved species may be interacting. The next steps forward could be to validate some of these key inferred interactions using experiments or in the case of predator-prey interactions, gut content analysis.

Another potential limitation in our study is the pooling together of yearly data (Jordán and Osváth, 2009). Ideally, we would have constructed networks for each season per year without pooling data, allowing us to accommodate both yearly and seasonal variation in our networks. However, given the data available, this was not possible due to convergence issues. To address the potential for yearly variation, we limited sites to those that had every seasonal abundance measurement between 2017–2019 and also ensured there were no substantial yearly trends in the abundance data using LASSO Poisson regression. In future, data collection efforts for these types of analyses should seek to collect greater abundance data per year such that both seasonal and yearly networks can easily be created.

2.5.3 Applications

Given the increasing availability of temporal abundance measurements, the robust EMtree approach we use here will likely be a valuable tool in the future to further disentangle species interaction networks. In particular, since it has been suggested that food webs rewire in predictable ways due to climate change (Bartley et al., 2019), this method may be used to investigate how interaction networks rewire in response to climate change where species interaction information is not available. Moreover, since it is widely recognized that interactions are the architecture of biodiversity (Bascompte and Jordano, 2007), the maintenance of these interactions, even those that are seasonal, is a necessity to maintain ecosystem stability. In this regard, the approach we adopted for our analysis could be valuable for conservation as it can be used to hypothesize key biological relationships that must be retained for species to avoid extinction (Heinen et al., 2020).

2.6 Conclusion

The approach we take for network inference highlights the utility of non-traditional methods (e.g., species abundance data) to infer interactions and thus community structure. Although our network inference is not without its uncertainties, we demonstrate how EMtree methods can be used to elucidate network structure. Overall, we find evidence that differences in our seasonal networks appear to be driven mainly by rewiring as compared to species turnover. Additionally, while there is recognition that traits are important factors of community assembly, our findings that maximum length and piscivore status contributes to a species' number of rewiring provide evidence that traits may influence how temporal interaction networks change. Finally, our study highlights the need to consider communities as evolving through time. Since seasonal change is capable of dramatically altering network topology, failing to capture temporal heterogeneities may cause us to mischaracterize community structure and functions.

2.7 Figures

2017 2018 2019

	2017	2018	2019
Arik	3 3	3 2	2 3
Hopb	4 2 2	1 3 4	4 4
King	4 4	2 1 1	3 4
Lewi	4 4	3 3	4 2 1
Mayf	5 1	4 3	4 4
Mcdi	1 3	3 3	3 1 2
Pose	3 1	3 3	4 3
Prin	2 3 4	4 3	4 1 3
Walk	3 3	4 3	3 3
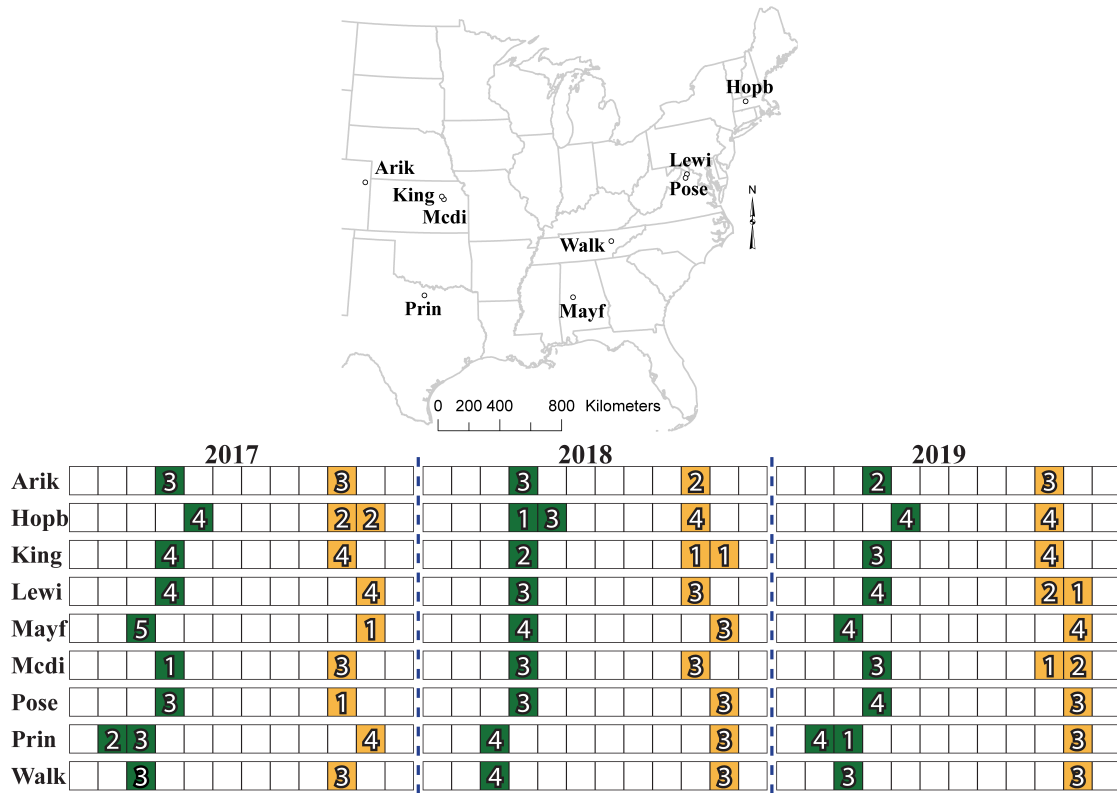
Figure 2.1. (Top) The nine NEON stream sampling locations across the United States used in this study; (Bottom) monthly dates of freshwater fish abundance sampling for each of the nine sites used, where green boxes indicate Spring month dates, yellow boxes indicate Fall month dates, and the numbers inside the boxes are the number of days in which that month was sampled. Each day sampled represents multiple reaches sampled for abundances at that site.
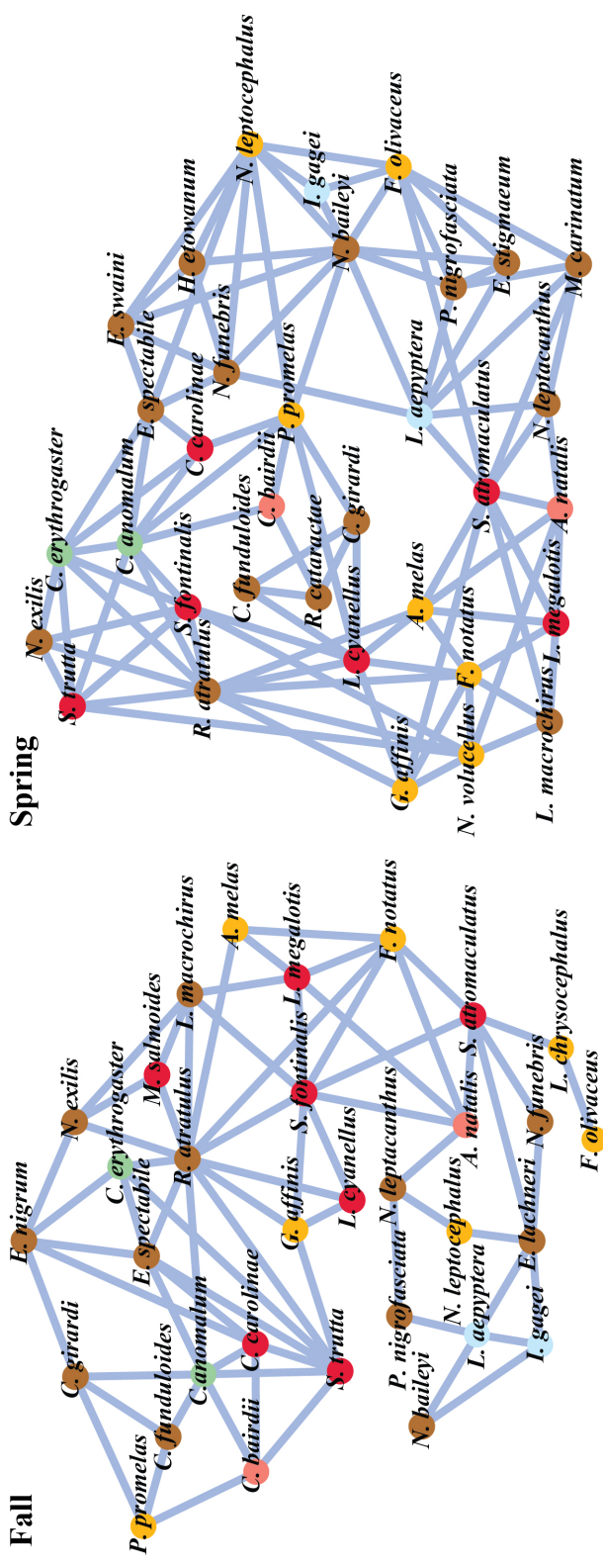
Figure 2.2. Threshold 0.6 of the Fall interaction network ($n = 32$ species) and the Spring interaction network ($n = 34$ species) of a freshwater fish stream community across nine sampling locations in the United States. Node colour corresponds to species feeding behavior: (1) light blue: non-feeding adults, (2) red: invertivore, and piscivore, (3) light green: herbivore, (4) dark yellow: herbivore, and invertivore, (5) dark yellow: herbivore, invertivore, and piscivore.
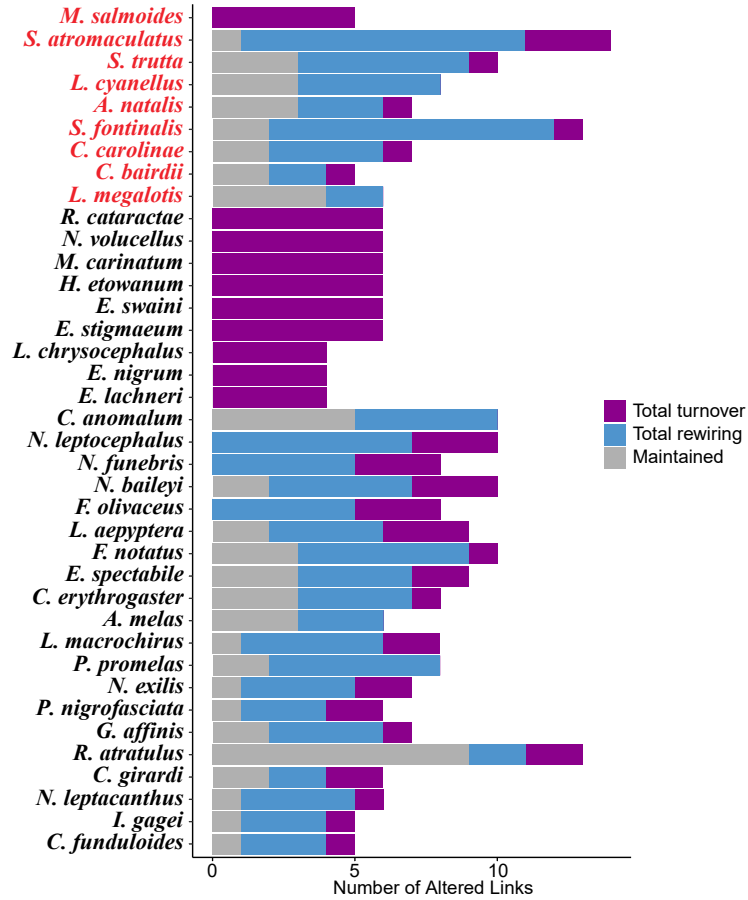
Figure 2.3. Number of maintained interactions and altered interactions for piscivores (red text) and non-piscivores (black text), including total number of rewiring (blue) and total number of species turnover interactions (purple), in each season using a network threshold of 0.6.
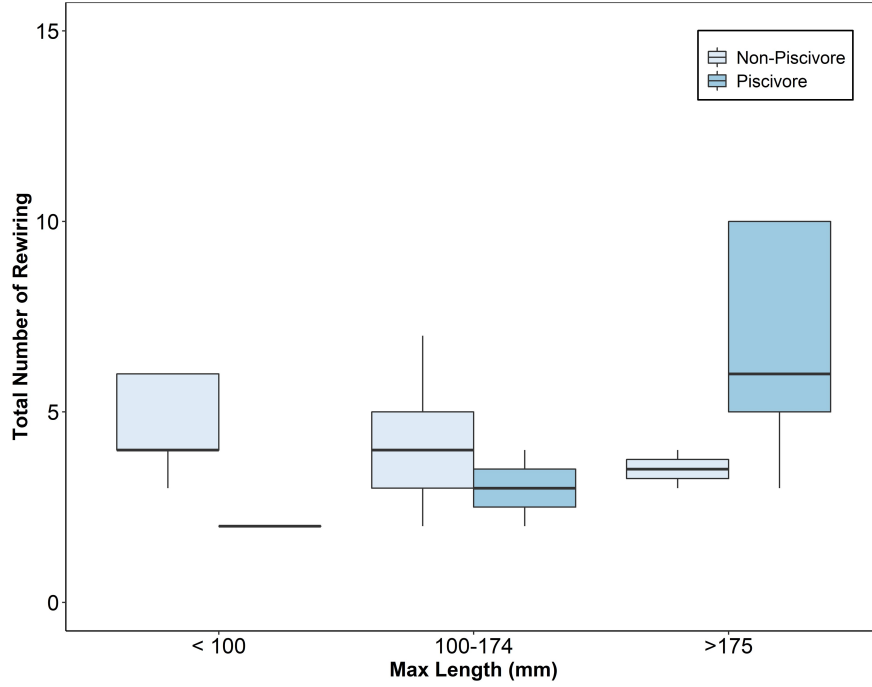
Figure 2.4. Regression between the maximum length of the fish species (in mm) and its status as a piscivore against the total number of inferred rewiring for each species, using a network threshold of 0.6. For non-piscivores, the maximum length of the species appears to have a negligible effect on the total number of rewiring, however for piscivores, there appears to be a strong positive relationship indicating that the greater the maximum length of the species, the greater the total number of rewiring for that species (non-piscivore: $n = 20$, with $n = 5$, $n = 13$, and $n = 2$ for max length levels, respectively, and piscivore: $n = 8$, with $n = 1$, $n = 2$, and $n = 5$ for max length levels, respectively).

2.8 Tables

Table 2.1. Fish feeding behaviours and total abundances for Fall and Spring in years 2017—2019. Feeding behaviours correspond to (*i*) Non-Feed: non-feeding adults correspond to non-parasitic lamprey species, (*ii*) Herb: herbivore, (*iii*) Invert: invertivore, and (*iv*) Pisc: piscovore.

Species	Feeding behaviours	Total abundance Fall	Spring	Species	Feeding behaviours	Total abundance Fall	Spring
Ameiurus melas	Herb, Invert	11	22	*Lepomis cyanellus*	Invert, Pisc	349	354
Ameiurus natalis	Herb, Invert, Pisc	64	53	*Lepomis macrochirus*	Invert	55	44
Campostoma anomalum	Herb	880	792	*Lepomis megalotis*	Invert, Pisc	32	52
Chrosomus erythrogaster	Herb	446	439	*Luxilus chrysocephalus*	Herb, Invert	31	
Clinostomus funduloides	Invert	65	200	*Micropterus salmoides*	Invert, Pisc		5
Cottus bairdii	Herb, Invert, Pisc	533	642	*Moxostoma carinatum*	Invert		15
Cottus carolinae	Invert, Pisc	134	193	*Nocomis leptocephalus*	Herb, Invert	86	35
Cottus girardi	Invert	796	953	*Notropis baileyi*	Invert	816	704
Etheostoma lachneri	Invert	73	301	*Notropis volucellus*	Herb, Invert		71
Etheostoma nigrum	Invert	301		*Noturus exilis*	Invert	98	98
Etheostoma spectabile	Invert	668	780	*Noturus funebris*	Invert	37	39
Etheostoma stigmaeum	Invert		38	*Noturus leptacanthus*	Invert	23	13
Etheostoma swaini	Invert		8	*Percina nigrofasciata*	Invert	69	37
Fundulus notatus	Herb, Invert	467	528	*Pimephales promelas*	Herb, Invert	150	163
Fundulus olivaceus	Herb, Invert	70	85	*Rhinichthys atratulus*	Invert	3559	3087
Gambusia affinis	Herb, Invert	1154	466	*Rhinichthys cataractae*	Invert		417
Hypentelium etowanum	Invert		13	*Salmo trutta*	Invert, Pisc	41	16
Ichthyomyzon gagei	Non-Feed	142	125	*Salvelinus fontinalis*	Invert, Pisc	84	53
Lampetra aepyptera	Non-Feed	131	170	*Semotilus atromaculatus*	Invert, Pisc	1328	938

Table 2.2. Model fit (BIC scores, pseudo-R^2), and prediction error (RMSE, RMSE obs>0) for each Poisson lognormal (PLNmodels) and Poisson regression model (glmnet) using $n = 32$ species for Fall data, and $n = 34$ for Spring data. Models were constructed using 74 (Fall) and 94 (Spring) observations where a single observation is a single sampling abundance measure for multiple species made at a specific point in a stream at one of the nine NEON sampling locations at a specific day. "RMSE" (root mean square error) indicates the predictive ability of each model and predicts for $n = 32$ (Fall) and $n = 34$ (Spring) species based on the most recent observations for each of the nine NEON sites [$n = 288$ (Fall) and $n = 306$ (Spring)]. "RMSE obs>0" indicates the predictive ability (root mean squared error) of each model for presence-only abundances (i.e., observations> 0) [$n = 38$ (Fall) and $n = 36$ (Spring)].

	Model type	Variables	BIC scores	RMSE	RMSE obs>0	R^2
Fall	PLN	Site name	−6418.47	4.23	11.11	0.93
		Site name + Water temperature	−6472.50	6.09	16.29	0.93
		Site name + Dissolved oxygen	−6456.43	6.14	16.55	0.92
	glmnet	Site name		10.35	27.14	
		Site name + Year		17.94	34.02	
Spring	PLN	Site name	−8158.60	5.00	12.37	0.94
		Site name + Water temperature	−8236.97	6.66	18.04	0.94
		Site name + Dissolved oxygen	−8219.05	4.90	12.90	0.94
	glmnet	Site name		7.35	19.72	
		Site name + Year		7.11	19.28	

Chapter 3

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

3.1 Abstract

<u>Aim:</u> 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.

<u>Location:</u> Trying to approach global.

<u>Time period:</u> Contemporary.

<u>Major taxa studied:</u> Plants and animals.

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

<u>Results:</u> 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.

<u>Main conclusions</u>: 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.

3.2 Introduction

Representation of ecological communities as networks has increased dramatically in the past few decades (Poisot et al., 2016b; Tylianakis and Morris, 2017; Delmas et al., 2019; Fortin et al., 2021). 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 and 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 and Saavedra, 2020).

While ecologists have long understood that temporal periodicity, in particular seasonality, are important components of ecological systems (Tonkin et al., 2017; Firkowski et al., 2022), few studies have actually investigated the relationship between community strucutre and seasonality in empirical communities (White and Hastings, 2020). Increasingly, studies are finding that seasonality plays an important role in shaping empirical ecological communities and their species interactions (McMeans et al., 2015; Tonkin et al., 2017; Rudolf, 2019; Brimacombe et al., 2021), 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 (Schleuning et al., 2014; Liu et al., 2021).

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 3.1a]. Modularity captures the degree to which species interact more strongly with a specific subset of species in a community (Dalsgaard et al., 2017) [Figure 3.1b]. 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 3.1c].

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 (MacArthur, 1984; Xing and Fayle, 2021; Brimacombe et al., 2022a), which may be in part due to less seasonality. Similarly, modularity may also increase toward tropical regions since selection may favor 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 subsets of species (Welti and 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., 2016b).

Current empirical findings do not always support these theoretical expectations (Xing and Fayle, 2021) [see Table 3.1 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 (Schleuning et al., 2012; Dalsgaard et al., 2017). 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 and 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 and Olesen, 2013; Welti and Joern, 2015) whereas others find modularity increases with seasonality and latitude (Schleuning et al., 2014; Dalsgaard et al., 2017). Other studies have also found no relationships between these measures and climatic variability or latitude (Ollerton and Cranmer, 2002; Morris et al., 2014; Doré et al., 2021).

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 and Saavedra, 2020; Zvereva and Kozlov, 2021). Since antagonistic and mutualistic interactions can lead to different dynamics (Allesina and Tang, 2012) and can have distinct fitness outcomes for interacting species (Guimarães Jr., 2020), it had been hypothesized that antagonistic and mutualistic networks could be structured differently (Lewinsohn et al., 2006; Thébault and 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 and Saavedra, 2020). Therefore, evaluating how 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 (Poisot 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, e.g., $n < 30$ [e.g., Olesen and Jordano (2002); Schleuning et al. (2014); Dalsgaard et al. (2017)]. 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, e.g., 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 (Jordano, 2016; de Aguiar et al., 2019), can all influence the depiction of a community as a network. Altogether, we may 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, e.g., 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., 2022a).

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 3.1), 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 3.1d). 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, e.g., consistency in the amount of time spent sampling and geographical area used to characterize the community. Second, we test if temperature and 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 and Legendre (2012)] (Figure 3.1e). 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.

3.3   Methods

3.3.1   Data: Bipartite networks and climatic seasonality

A total of 723 ecological bipartite networks and their sampling locations were collected (Figure 3.2). This dataset was made up of 298 plant-pollinator, 10 ant-plant, 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). Networks were obtained from open databases (e.g., `www.datadryad.org` and `www.web-of-life.es`) and from other studies' supplementary material (e.g., Michalska-Smith and Allesina (2019); Fricke and Svenning (2020) [see S3.10 Appendix: Table S3.7 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 and 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 and Fortin, 2014)] since all ecological networks used in this study are typically connected (Guimarães Jr., 2020) when sampled correctly.

Temperature and precipitation seasonality were obtained from WorldClim (Fick and Hijmans, 2017), specifically BIO4 and BIO15, respectively. Temperature seasonality (in units of °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.

3.3.2 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, e.g., 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 et al., 2007; Blüthgen, 2010; 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.

3.3.2.1 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 $\Delta Q = Q_{empirical} - \overline{Q}_{50:Vaznull}$, the difference between the empirical weighted modularity of a given network ($Q_{empirical}$), and the mean weighted modularity of an ensemble of 50 null models based on the empirical network ($\overline{Q}_{50:Vaznull}$). 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.

3.3.2.2 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 $\Delta H_2' = H_{2,empirical}' - \overline{H}_{2,50:Vaznull}'$, the difference between the empirical weighted specialization of a given network $\left(H_{2,empirical}'\right)$, and the mean weighted specialization of an ensemble of 50 Vaznull models based on the empirical network $\left(\overline{H}_{2:50,Vaznull}'\right)$.

3.3.2.3 Weighted nestedness (ΔN)

Weighted nestedness (N) for each weighted network was quantified using the *wnodf* function (Almeida-Neto and 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 $\Delta N = N_{empirical} - \overline{N}_{50:Vaznull}$, the difference between the empirical weighted nestedness of a given network ($N_{empirical}$), and the mean weighted specialization of an ensemble of 50 Vaznull models based on the empirical network $\left(\overline{N}_{50:Vaznull}\right)$.

3.3.3 Weighted network linear models

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

Linear mixed models [LMM(s)] 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; eq. (S3.1)], normalized weighted specialization [$\Delta H_{2,n}'$; eq. (S3.2)], and normalized weighted nestedness [ΔN_n; eq. (S3.2)], 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 (see S3.10 Appendix: Subsection S3.10.3).

Separate sets of LMMs were constructed: one set for plant-pollinators networks and one set for seed-dispersal networks. In each LMM, combinations of temperature and precipitation seasonality, as well as sampling intensity [eq. (3.1)], 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 less 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 (Barton, 2020).

Sampling intensity (network$_i$)

$$= \frac{\sqrt{\text{number of interactions in network}_i}}{\sqrt{\text{number of rows}\,(n)\,\text{in network}_i \cdot \text{number of columns}\,(m)\,\text{in network}_i}} \quad (3.1)$$

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` · `precipitation seasonality` + (1|`publication`). When the random effect of publication was important, we further investigated which 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 our 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 $R^2 < 0.15$, 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, 2018)]. 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 (see S3.10 Appendix: Subsection S3.10.4).

3.3.3.2 Plant-pollinator, seed-dispersal, and host-parasite linear regressions (LMs)

When linear mixed models 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 ($\Delta Q, \Delta Q_n$), weighted specialization ($\Delta H_2', \Delta H_{2,n}'$), and weighted nestedness ($\Delta N, \Delta N_n$). LMs were tested with all possible combinations of terms involving `sampling intensity` [eq. (3.1)], `temperature`, and `precipitation seasonality` given by the equation: `sampling intensity` + `temperature seasonality` · `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 $\left(\Delta H'_{2,>Samp.int.}\right)$, 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 · precipitation seasonality`). We did not perform these analyses using linear mixed models since there would not have been enough random effect groups to warrant their use.

LM configurations of `temperature seasonality`, `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.

3.3.3.3 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 ($\Delta Q, \Delta Q_n, \Delta Q_{>Samp.int.}$), weighted specialization $\left(\Delta H'_2, \Delta H'_{2,n}, \Delta H'_{2,>Samp.int.}\right)$, and weighted nestedness ($\Delta N, \Delta N_n, \Delta N_{>Samp.int.}$) 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 (see S3.10 Appendix: Subsection S3.10.1), we did not include a term for autocorrelation in any of our models.

3.3.4   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 and 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: (i) the Erdős-Rényi (λ_1^{er}) random bipartite graph (Erdős and Rényi, 1959) in which the numbers of nodes and connections were preserved, but nodes were connected at random, and (ii) a configuration model [λ_1^{cm}] (Bender and 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. As well, 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 Marčhenko-Pastur (Marčenko and Pastur, 1967). See Michalska-Smith and Allesina (2019)'s supporting information for a more thorough derivation of all eigenvalue metrics.

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

$$1 - \frac{\lambda_1^{cm}}{\lambda_1} \,, \tag{3.2}$$

$$1 - \frac{\lambda_1^{er}}{\lambda_1} \,, \tag{3.3}$$

$$1 - \frac{\lambda_2^{mp}}{\lambda_2} \,. \tag{3.4}$$

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.

3.3.4.1 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 eqs. (3.2)–(3.4)]. `Temperature seasonality` and `precipitation seasonality` as well as a binary variable to identify networks as either antagonistic or mutualistic were included as explanatory variables.

3.4 Results

3.4.1 Weighted network linear models

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

For plant-pollinator networks, the complete configuration linear mixed model (LMM) with all the fixed effects of `sampling intensity` (Samp.int.), `temperature seasonality` (Temp.) and `precipitation seasonality` (Precip.) (i.e., `Samp.int. + Temp. · Precip.`) only minimally contributed to explaining variations in weighted modularity (ΔQ) and weighted specialization [$\Delta H_2'$] (marginal $R^2 = 0.055$ and 0.116, respectively; Table 3.2). In both cases, the random effect of publication (which consisted of 6 categories) contributed to explaining most of the accounted variation (conditional $R^2 \approx 0.33$). 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 Subsubsection 3.4.1.2). 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.` (S3.10 Appendix: Table S3.3). We did not investigate models to explain the variation in normalized weighted modularity (ΔQ_n), or in normalized weighted specialization $\left(\Delta H_{2,n}'\right)$ since residuals violated model assumptions.

For seed-dispersal networks, the complete configuration LMM with all the

fixed effects of `temperature seasonality`, `precipitation seasonality` (and their interaction), and `sampling intensity` only explained a minimal amount of the variation for weighted modularity $\left(\Delta Q; \text{marginal } R^2 = 0.082\right)$ and weighted nestedness $\left[\Delta N; \text{marginal } R^2 = 0.051\right]$ (Table 3.2). For both weighted modularity and weighted nestedness, the random effect of publication (which consisted of 9 categories) contributed most to explaining the accounted variation of both metrics $\left(\text{conditional } R^2 = 0.232 \text{ and } 0.293, \text{ respectively}\right)$. 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 $\left(\text{marginal } R^2 = 0.279, \text{ conditional } R^2 = 0.357; \text{ Table 3.2 and S3.10 Appendix: Table S3.1}\right)$. Regarding the normalized metrics, we only explored seasonality's influence on normalized structural metrics using LMs (Subsubsection 3.4.1.2) as the inclusion of random effects did not improve the models.

3.4.1.2 Plant-pollinator, seed-dispersal, and host-parasite linear models (LMs)

As the marginal and condition R^2 were equal for weighted nestedness (ΔN) in plant-pollinator linear mixed models, linear models (LMs) were instead adopted to evaluate the relationship between temperature seasonality 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.`, $R^2_{adj} = 0.206$, Table 3.3 and S3.10 Appendix: Table S3.2). 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 $\left(\text{i.e., } R^2_{adj} = 0.117\right)$.

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 $\left(\Delta H'_{2,n}\right)$. We found that seasonality only weakly explained the variation in ΔN_n $\left(R^2_{adj} = 0.044; \text{ S3.10 Appendix: Table S3.4}\right)$, 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 3.3 and S3.10 Appendix: Table S3.2). Specifically, the chosen models for both weighted specialization $(\Delta H'_2)$ and weighted nestedness (ΔN) only included `sampling intensity` as an explanatory variable $\left(R^2_{adj} = 0.144, \text{ and } R^2_{adj} = 0.467, \text{ respectively}\right)$. While the chosen model for weighted modularity (ΔQ) was the complete model of `Samp.int. + Temp. · Precip.` $\left(R^2_{adj} = 0.175; \text{ S3.10 Appendix: Table S3.2 and Figure 3.3}\right)$, 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 $\left(\text{i.e., Temp.} \cdot \text{Precip.}, R^2_{adj} = 0.136, \text{ S3.10 Appendix: Table S3.2}\right)$. Additionally, since model assumptions for both normalized weighted modularity (ΔQ_n), and normalized weighted specialization $\left(\Delta H'_{2,n}\right)$ violated model assumptions, we only explored LMs for normalized weighted nestedness (ΔN_n) in host-parasite networks (S3.10 Appendix: Table S3.4). Although we found that the chosen model for normalized weighted nestedness (ΔN_n) included both `sampling intensity` and `precipitation seasonality` as explanatory variables $\left(R^2_{adj} = 0.619\right)$, most of the

variation explained was via sampling intensity since a model with only `sampling intensity` had an R^2_{adj} of 0.572.

3.4.1.3 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 (S3.10 Appendix: Table S3.6). 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` $\left(\text{i.e., } \mathtt{Samp.int.} + \mathtt{Temp.} \cdot \mathtt{Precip.}, R^2_{adj} = 0.323\right)$, while the chosen model for explaining the variation in weighted specialization $(\Delta H'_{2,>Samp.int.})$ was $\mathtt{Temp.} \cdot \mathtt{Precip.}$ $\left(R^2_{adj} = 0.326\right)$. Yet, when explaining the variation in weighted nestedness $(\Delta N_{>Samp.int.})$ in plant-pollinator networks, we found a much weaker relationship with seasonality $\left(R^2_{adj} = 0.146\right)$ as the chosen model included only `temperature seasonality` as an explanatory variable. Conversely for seed-dispersal networks, the only noteworthy relationships we found $\left(\text{i.e., } R^2_{adj} > 0.15\right)$ to suggest that seasonality explained any of the three network metrics were the models for weighted specialization $(\Delta H'_{2,>Samp.int.})$ wherein the chosen model contained all explanatory variables $\left(\text{i.e., } \mathtt{Samp.int.} + \mathtt{Temp.} \cdot \mathtt{Precip.}, R^2_{adj} = 0.246\right)$. However, most of the variation in $\Delta H'_{2,>Samp.int.}$ was explained by sampling intensity alone as a model with only `sampling intensity` had a moderate relationship with $\Delta H'_{2,>Samp.int.}$ $\left(R^2_{adj} = 0.199; \text{S3.10 Appendix: Table S3.6}\right)$.

3.4.2 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 seasonality` and `precipitation seasonality`, and `network type` (i.e., antagonistic/mutualistic) only explained about 5% $\left(R^2_{adj} = 0.052\right)$ of the total variation in unweighted nestedness [eqs. (3.2) and (3.3)] and unweighted modularity [eq. (3.4)] metrics. When projecting these results in an RDA triplot (Figure 3.4), antagonistic and mutualistic systems did not show evidence of having different structures as they overlapped in RDA space.

3.5 Discussion

The representation and analyses of ecological communities using networks have increased dramatically over the last few decades (Poisot et al., 2016*b*; Tylianakis and Morris, 2017; Delmas et al., 2019; Fortin et al., 2021). 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 (Pellissier et al., 2018; Poisot et al., 2021; Brimacombe et al., 2022*a*). In our large-scale analyses using the largest open dataset of bipartite networks yet compiled, we find (1) only weak evidence that temperature and/or precipitation seasonality

explains the variation in the weighted metrics of modularity, specialization, or nestedness in plant-pollinator, seed-dispersal, or host-parasite systems and (2) 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 (S3.10 Appendix: Table S3.3)] and about 5% of unweighted metrics (RDA; Figure 3.4). Importantly, the results for 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 (Schwarz et al., 2020; CaraDonna et al., 2021), 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 $\left(\text{i.e., } R^2_{adj} \approx 0.325\right)$ 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 (S3.10 Appendix: Table S3.6).

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: (*i*) the ways interactions are recorded, (*ii*) the time and area allotted for observing interactions, and (*iii*) 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 (Clegg et al., 2018; Bodner et al., 2022). For example, separate nodes are likely required to represent different life stages of species for those in which life stages act and behave entirely different from one another, e.g., tadpole and frog, resulting in even greater difficulties when comparing with networks without such variations between ontogenetic stages.

3.6 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.

3.7 Data and code availability

All data and code to reproduce our results are available at: `www.osf.io/h2m7j/`.

3.8 Figures
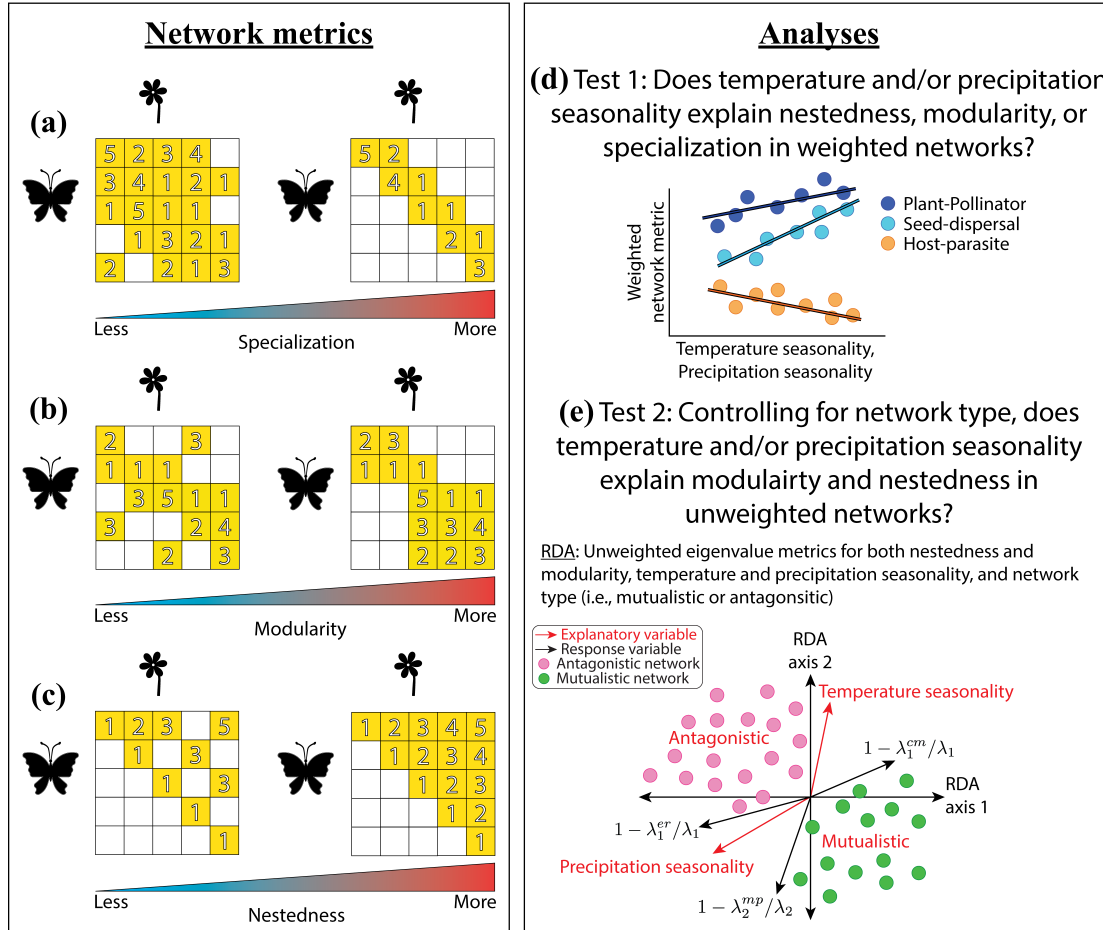
Figure 3.1. Left: Illustration of specialization, modularity, and nestedness in connected weighted plant-pollinator systems, where white boxes indicate a lack of pairwise species interaction, and yellow numbered boxes indicate a weighted interaction between plant (columns) and pollinator (rows) species. 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 (c) nestedness 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 $(1-\lambda_1^{cm}/\lambda_1, 1-\lambda_1^{er}/\lambda_1)$ and modularity $(1-\lambda_2^{mp}/\lambda_2)$ 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).
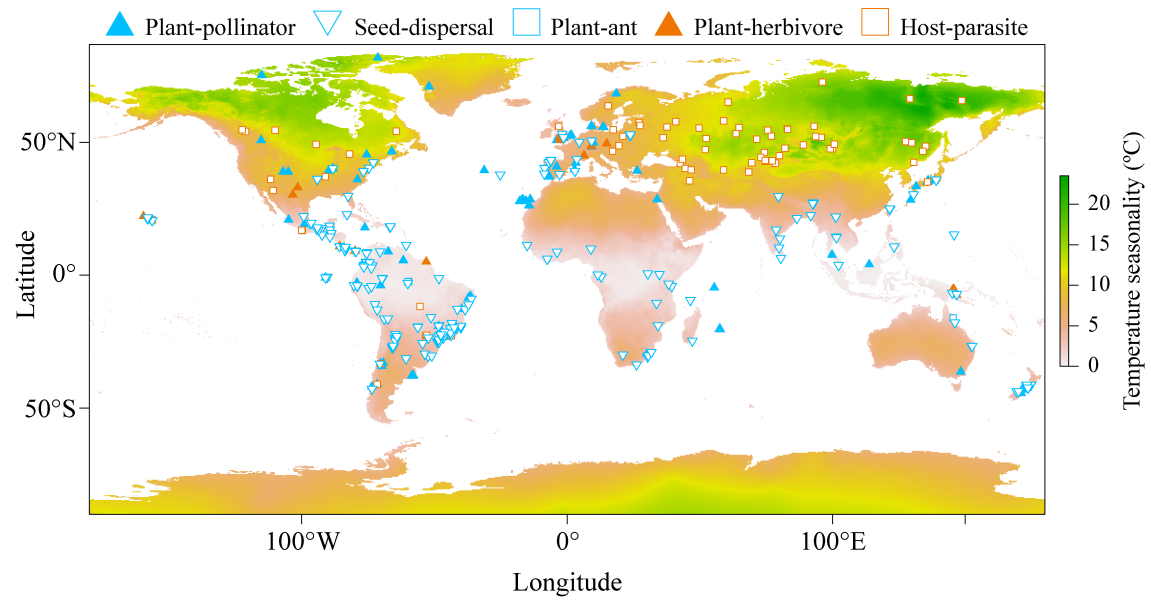
Figure 3.2. The location of the empirical bipartite networks ($n = 723$) used in this study, and their corresponding temperature seasonality (°C) from Fick and Hijmans (2017) where blue symbols indicate mutualistic networks (plant-pollinator, seed-dispersal, and plant-ant) and orange symbols indicate antagonistic networks (plant-herbivore, and host-parasite).
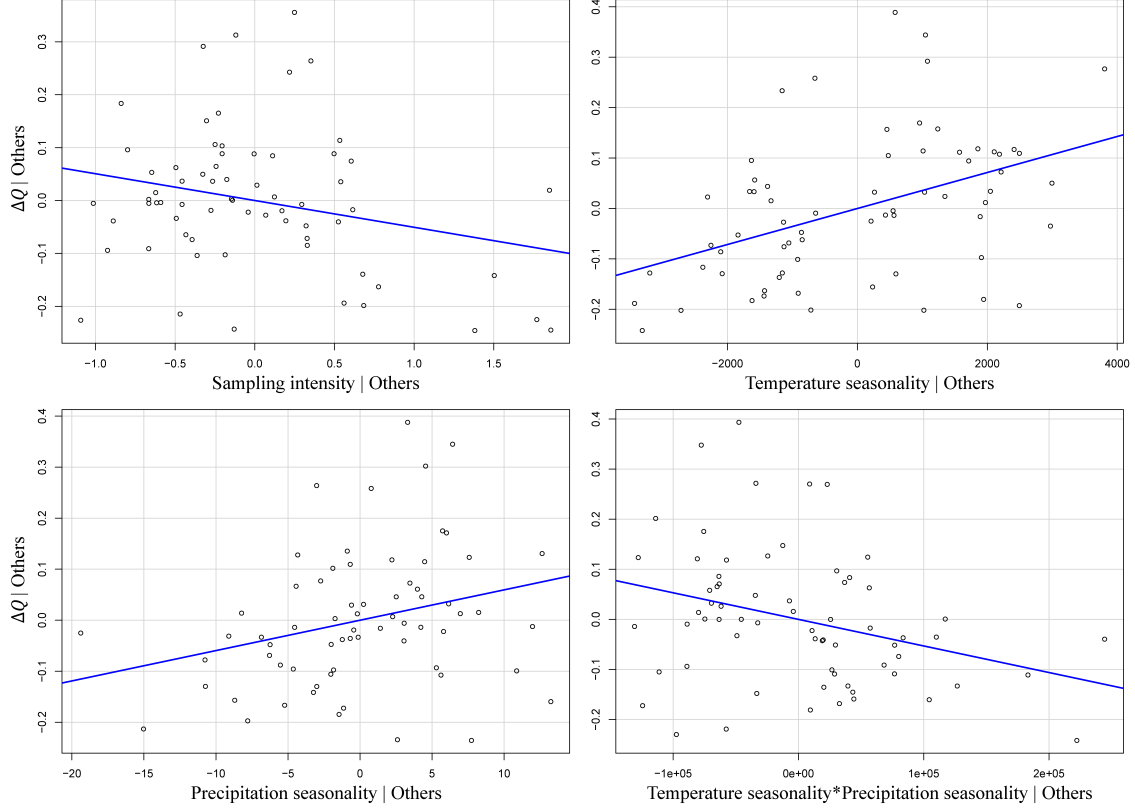
Figure 3.3. Added variable plot for the chosen linear model explaining the variation in weighted modularity (ΔQ) using the explanatory variables `sampling intensity` + `temperature seasonality` · `precipitation seasonality` ($R^2_{adj} = 0.178$) for host-parasite ($n = 67$) networks. A single outlier was removed from the analyses presented here, but see S3.10 Appendix: Figure S3.19 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.
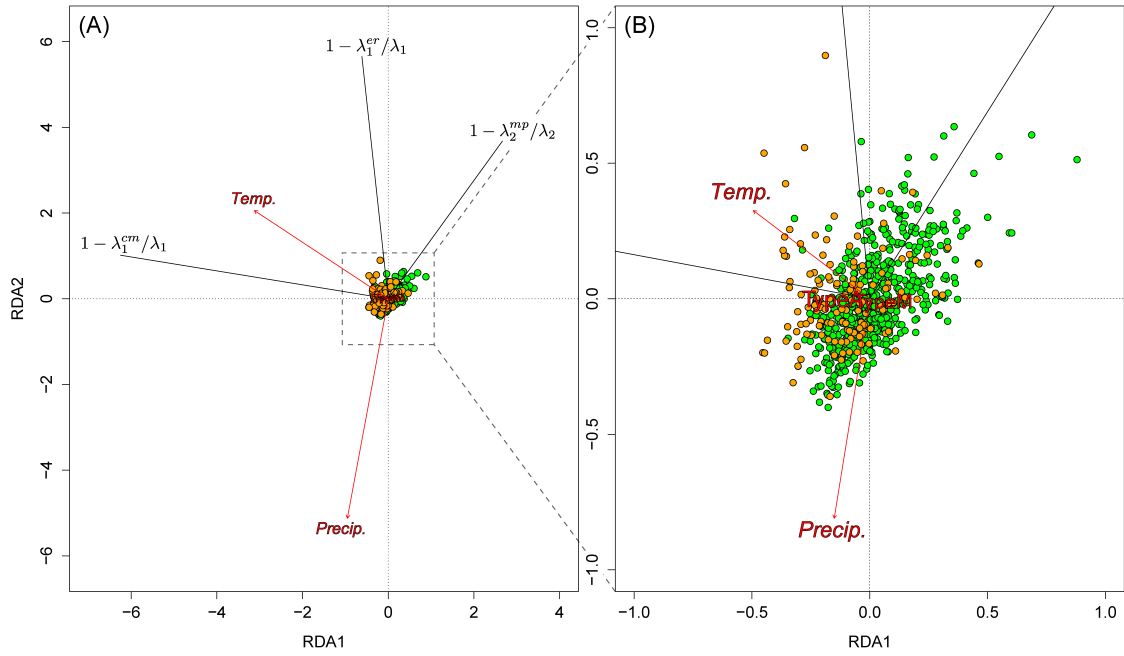
Figure 3.4. Redundancy analysis (RDA) distance triplot explaining metrics of unweighted nestedness ($1 - \lambda_1^{cm}/\lambda_1$, $1 - \lambda_1^{er}/\lambda_1$) and unweighted modularity ($1 - \lambda_2^{mp}/\lambda_2$) using `precipitation seasonality` (`Precip.`) and `temperature seasonality` (`Temp.`) 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 ($R^2_{adj} = 0.052$).

3.9 Tables

Table 3.1. 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 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 mutualisitic 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.

Table 3.2. Linear mixed models (LMMs) for explaining the variation in weighted modularity (ΔQ), weighted specialization ($\Delta H'_2$), and weighted nestedness (ΔN). 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 $R^2 < 0.15$, we did not investigate which combinations of fixed effects were chosen. See S3.10 Appendix: Table S3.1 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 3.3).

Network type	Dependent variable	Fixed effect(s)	Marginal R^2	Conditional R^2
Plant-pollinator ($n = 164$)	ΔQ	`Samp.int.`+`Temp.`·`Precip.`	0.055	0.332
	$\Delta H'_2$	`Samp.int.`+`Temp.`·`Precip.`	0.116	0.323
	ΔN	`Samp.int.`+`Temp.`·`Precip.`	0.218	0.218
Seed-dispersal ($n = 166$)	ΔQ	`Samp.int.`+`Temp.`·`Precip.`	0.082	0.232
	$\Delta H'_2$	`Samp.int.`+`Temp.`·`Precip.`	0.293	0.377
		`Samp.int.`	0.279	0.357
	ΔN	`Samp.int.`+`Temp.`·`Precip.`	0.051	0.293

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Table 3.3. Linear models (LMs) for explaining the variation in weighted modularity (ΔQ), weighted specialization ($\Delta H'_2$), and weighted nestedness (ΔN). `Temp.` is temperature seasonality, `Precip.` is precipitation seasonality, `Samp.int.` is the log-transformed sampling intensity for each network, coeff. is the coefficient's value, R^2_{adj} is the adjusted R^2 of the model, and ΔAIC is the difference between the AIC of a given model and the model with lowest AIC value. When `Samp.int.` alone is not the chosen model, we also provide the model with lowest AIC value. See S3.10 Appendix: Table S3.2 for all possible model configurations using the independent variables for explaining weighted metrics.

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^{***}	$4.0e^{-2}$	—	0.206	0.00
		Samp.int.	-7.3^{***}	—	-4.1^{***}	—	—	0.117	15.52
	ΔQ	Samp.int.+Temp.·Precip.	$-3.4e^{-2}$	$3.4e^{-5***}$	$-4.8e^{-2*}$	$5.1e^{-3*}$	$-4.7e^{-7**}$	0.175	0.00
		Samp.int.	$2.3e^{-1***}$	—	$4.1e^{-3}$	—	—	-0.015	11.19
Host-parasite ($n=68$)	$\Delta H'_2$	Samp.int.	$2.9e^{-1***}$	—	$9.2e^{-2***}$	—	—	0.144	0.00
	ΔN	Samp.int.	$-1.3e^{1***}$	—	$-1.1e^{1***}$	—	—	0.467	0.00

$^{***}p<0.001$, $^{**}p<0.01$, $^{*}p<0.05$

S3.10 Appendix

S3.10.1 Tests for spatial auto-correlation

Tests for positive autocorrelation using global Moran's I of the scaled residuals for each chosen model that explains the variation in network metrics [i.e., weighted modularity (ΔQ), weighted specialization ($\Delta H_2'$), weighted nestedness (ΔN), normalized weighted nestedness (ΔN_n), weighted modularity for networks whose sampling intensity is greater than the median sampling intensity of their respective system ($\Delta Q_{>Samp.int.}$), weighted specialization for networks whose sampling intensity is greater than the median sampling intensity of their respective system ($\Delta H_{2,>Samp.int.}'$), weighted nestedness for networks whose sampling intensity is greater than the median sampling intensity of their respective system ($\Delta N_{>Samp.int.}$)] in each system (i.e., host-parasite, plant-pollinator, and seed-dispersal). Autocorrelation tests were performed using the DHARMa package (Hartig, 2021) in R (R Core Team, 2021). In cases where multiple networks occurred at the same location, scaled residuals were recalculated using the *simulateResiduals* function.

All residuals were calculated via a simulation approach (similar to the Bayesian p-value or the parametric bootstrap). Simulated residuals were scaled between 0 and 1, where a value of 0 indicated that all simulated residuals were larger than the observed value, and 1 indicated that no residuals were larger than the observed value.

In three out of the eighteen models, we did find statistically significant positive autocorrelation [global Moran's I, (see autocorrelation.R to rerun all analyses)] but the autocorrelations were weak. Specifically, the weak but statistically significant autocorrelations occurred in a single plant-pollinator network model (Figure S3.3—global Moran's I for $\Delta N = 0.208$) as well as in two seed-dispersal network models (Figure S3.8—global Moran's I for $\Delta Q = 0.133$ and Figure S3.9—global Moran's I for $\Delta H_2' = 0.095$). Hence, there was no strong evidence of positive autocorrelation in the scaled residuals of our models for weighted modularity ($\Delta Q, \Delta Q_{>Samp.int.}$), weighted specialization $\left(\Delta H_2', \Delta H_{2,>Samp.int.}'\right)$, or weighted nestedness ($\Delta N, \Delta N_n, \Delta N_{>Samp.int.}$).

S3.10.1.1 Global Moran's *I* for plant-pollinator networks
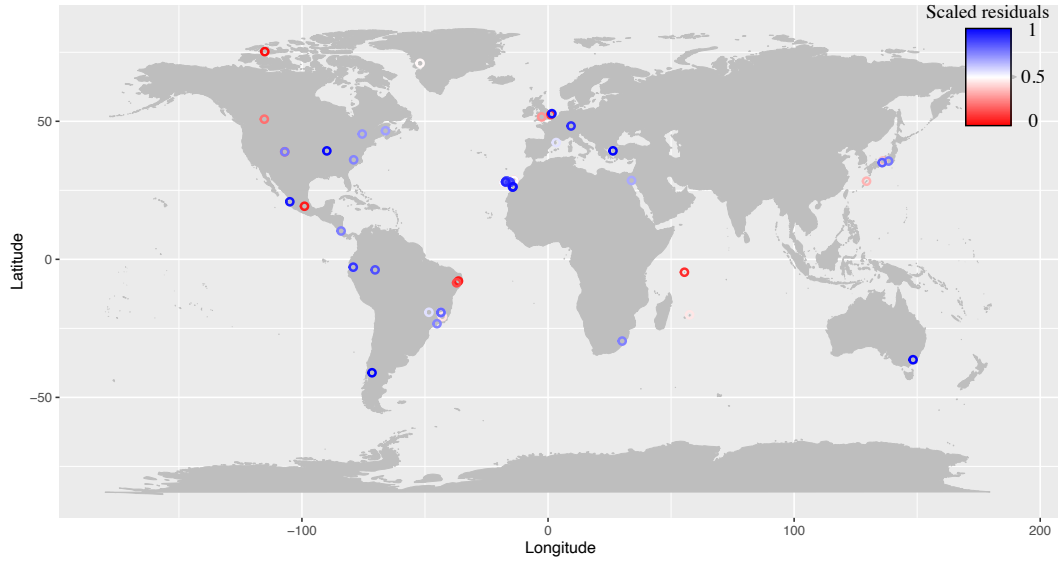
Figure S3.1. Global Moran's *I* (observed = 0.096, *p*-value = 0.125) using the scaled residuals (between 0 and 1) from the chosen linear mixed model (i.e., the model with the lowest AIC) explaining the variation in weighted modularity (ΔQ) using the fixed effects of `sampling intensity`, `temperature seasonality`, and `precipitation seasonality` ($\mathtt{Samp.int.} + \mathtt{Temp.} \cdot \mathtt{Precip.}$) and the random effect of publication for ($n = 62$) plant-pollinator networks. Location of coloured rings on map correspond to network locations, where colour corresponds to the value of the scaled residual for the location's network(s).
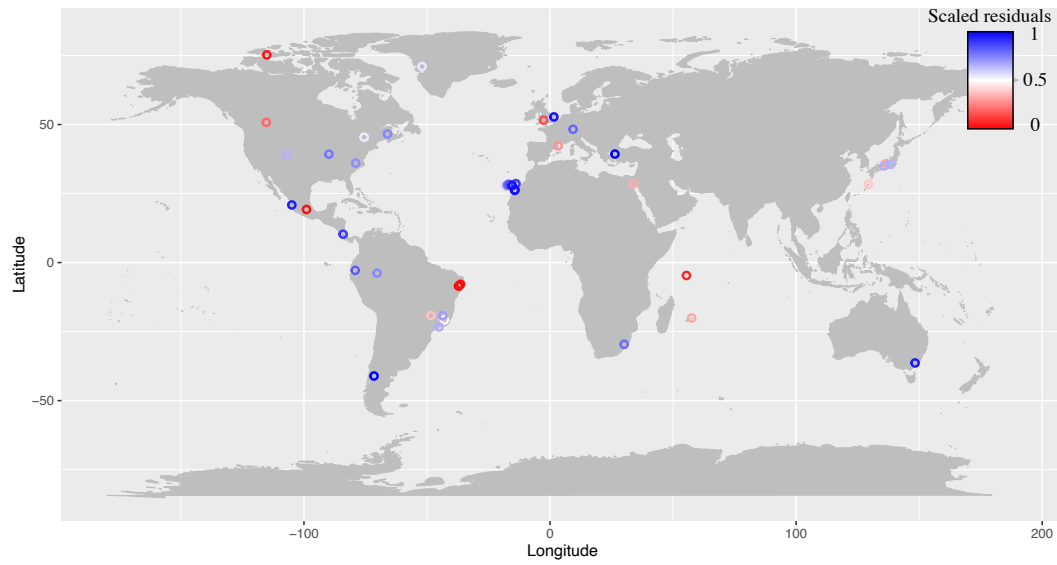
Figure S3.2. Global Moran's I (observed $= 0.127$, p-value $= 0.070$) using the scaled residuals (between 0 and 1) from the chosen linear mixed model (i.e., the model with the lowest AIC) explaining the variation in weighted specialization $(\Delta H_2')$ using the fixed effects of `sampling intensity`, `temperature seasonality`, and `precipitation seasonality` (`Samp.int. + Temp. · Precip.`) and the random effect of publication for $(n = 62)$ plant-pollinator networks. Location of coloured rings on map correspond to network locations, where colour corresponds to the value of the scaled residual for the location's network(s).

48
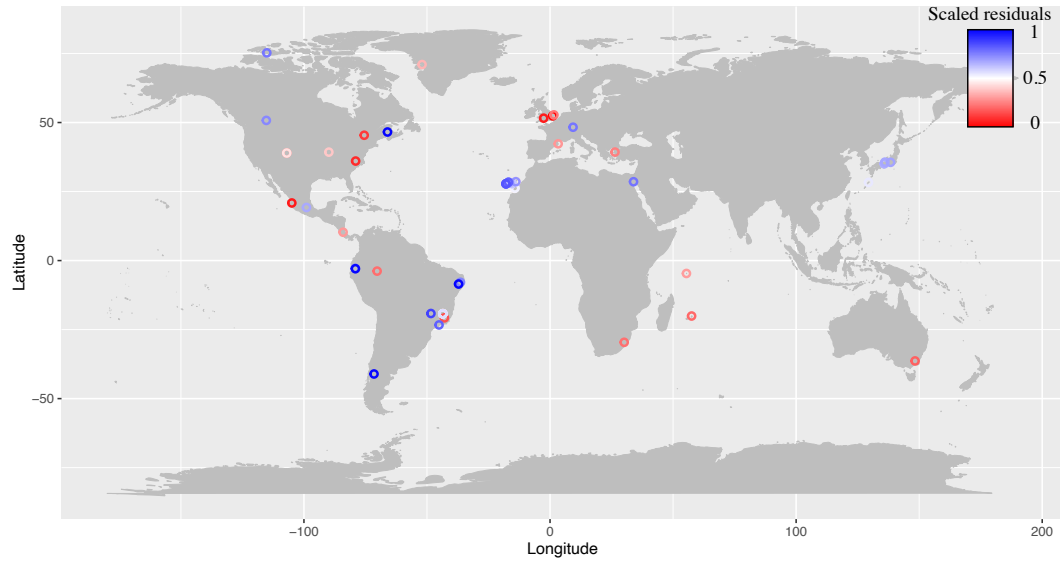
Figure S3.3. Global Moran's I (observed $= 0.208$, p-value $= 0.010$) using the scaled residuals (between 0 and 1) from the chosen linear model (i.e., the model with the lowest AIC) explaining the variation in weighted nestedness (ΔN) using `sampling intensity`, and `temperature seasonality` (`Samp.int. + Temp.`) for ($n = 62$) plant-pollinator networks. Location of coloured rings on map correspond to network locations, where colour corresponds to the value of the scaled residual for the location's network(s).
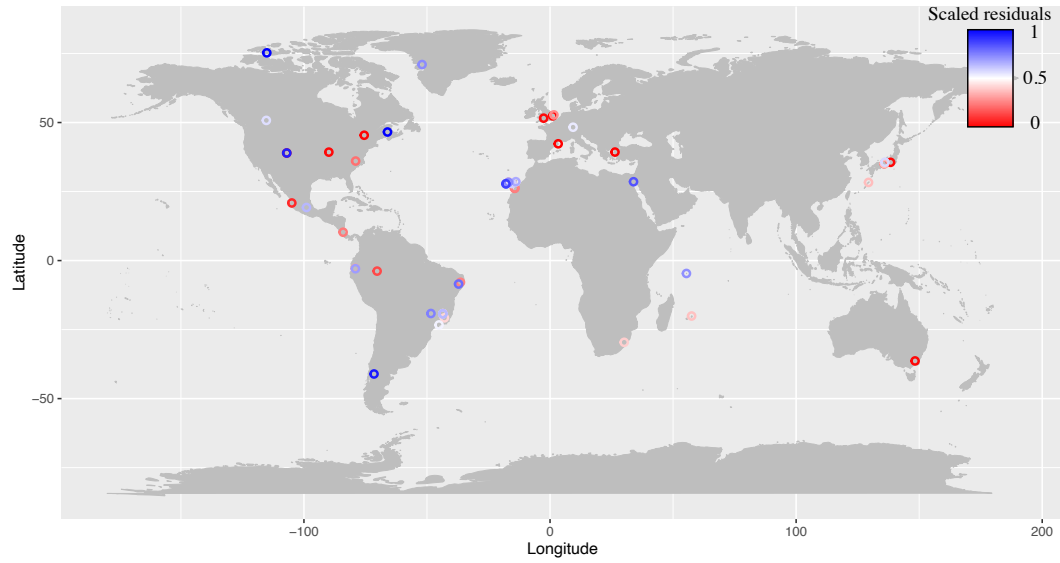
Figure S3.4. Global Moran's I (observed = −0.034, p-value = 0.573) using the scaled residuals (between 0 and 1) from the chosen linear mixed model (i.e., the model with the lowest AIC) explaining the variation in normalized weighted nestedness (ΔN_n) using the fixed effect of `temperature seasonality` and the random effect of publication for ($n = 62$) plant-pollinator networks. Location of coloured rings on map correspond to network locations, where colour corresponds to the value of the scaled residual for the location's network(s).

50
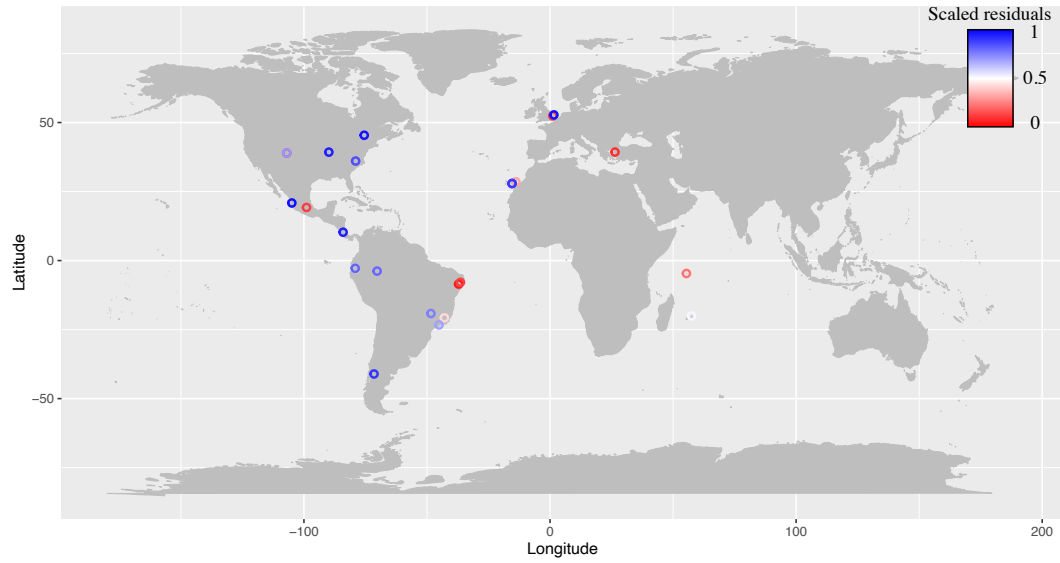
Figure S3.5. Global Moran's I (observed $= -0.010$, p-value $= 0.424$) using the scaled residuals (between 0 and 1) from the chosen linear model (i.e., the model with the lowest AIC) explaining the variation in weighted modularity ($\Delta Q_{>Samp.int.}$) using `sampling intensity`, `temperature seasonality`, and `precipitation seasonality` (Samp.int. + Temp. · Precip.) for ($n = 25$) plant-pollinator networks whose sampling intensity is greater than the median sampling intensity of all plant-pollinator. Location of coloured rings on map correspond to network locations, where colour corresponds to the value of the scaled residual for the location's network(s).
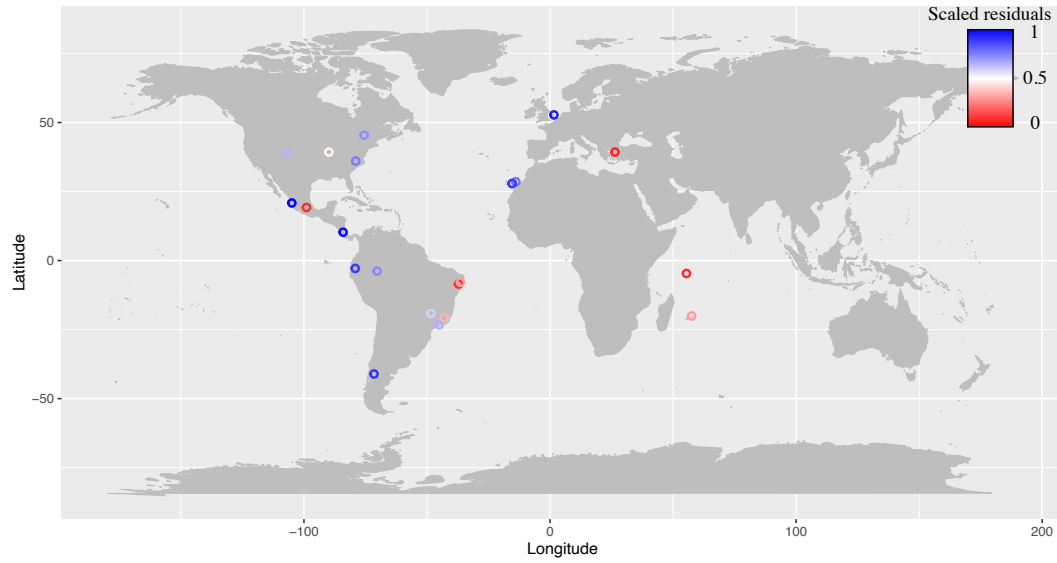
Figure S3.6. Global Moran's I (observed $=$ 0.100, p-value $=$ 0.195) using the scaled residuals (between 0 and 1) from the chosen linear model (i.e., the model with the lowest AIC) explaining the variation in weighted specialization $\left(\Delta H'_{2,>Samp.\,int.}\right)$ using `temperature seasonality`, and `precipitation seasonality` (Temp. $+$ Precip.) for $(n=25)$ plant-pollinator networks whose sampling intensity is greater than the median sampling intensity of all plant-pollinator networks. Location of coloured rings on map correspond to network locations, where colour corresponds to the value of the scaled residual for the location's network(s).
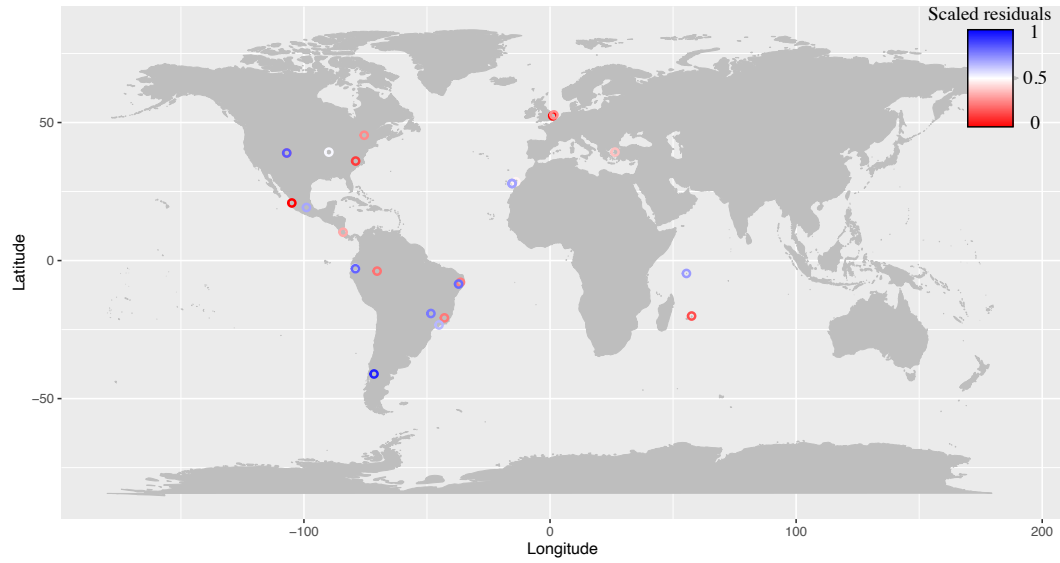
Figure S3.7. Global Moran's I (observed = –0.037, p-value = 0.488) using the scaled residuals (between 0 and 1) from the chosen linear model (i.e., the model with the lowest AIC) explaining the variation in weighted nestedness ($\Delta N_{>Samp.int.}$) using `temperature seasonality` for ($n = 25$) plant-pollinator networks whose sampling intensity is greater than the median sampling intensity of all plant-pollinator networks. Location of coloured rings on map correspond to network locations, where colour corresponds to the value of the scaled residual for the location's network(s).

S3.10.1.2   Global Moran's _I_ for seed-dispersal networks
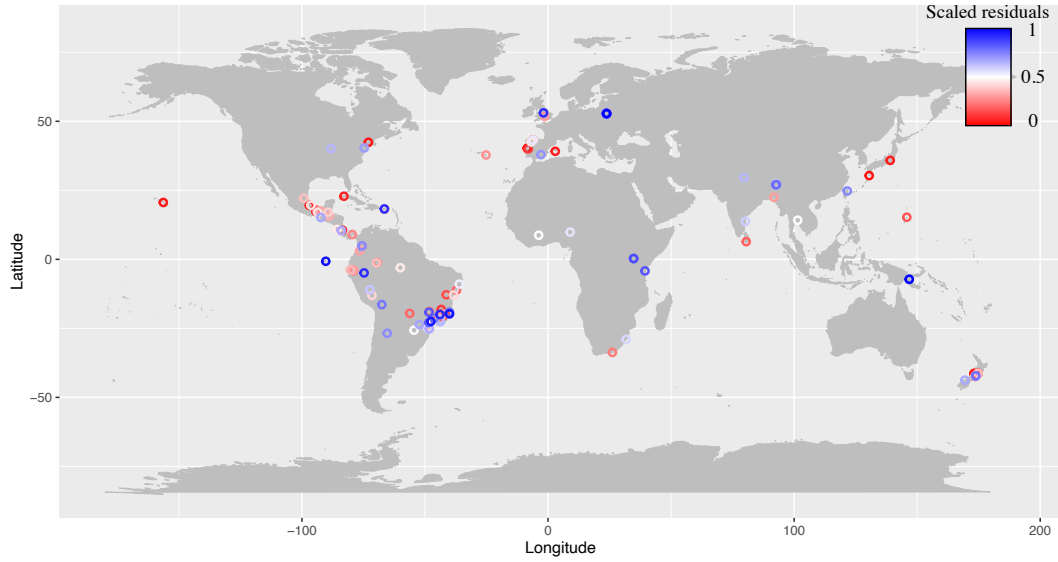
Figure S3.8. Global Moran's _I_ (observed = 0.133, _p_-value = 0.002) using the scaled residuals (between 0 and 1) from the chosen linear mixed model (i.e., the model with the lowest AIC) explaining the variation in weighted modularity (ΔQ) using the fixed effects of `sampling intensity`, `temperature seasonality`, and `precipitation seasonality` (`Samp.int.` + `Temp.·Precip.`) and the random effect of publication for ($n = 132$) seed-dispersal networks. Location of the coloured rings on map correspond to network locations, where colour corresponds to the value of the scaled residual for the location's network(s).
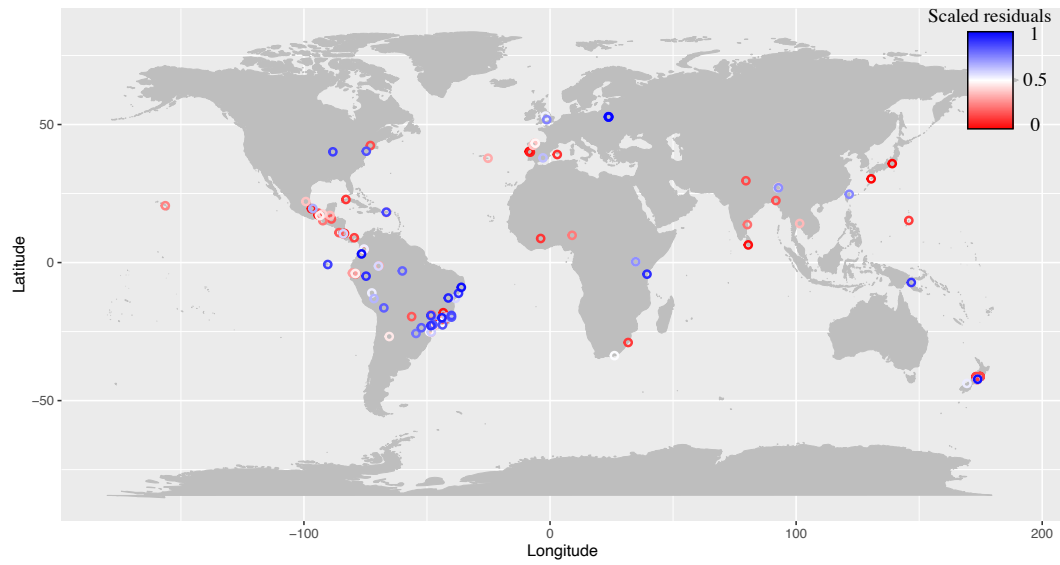
Figure S3.9. Global Moran's I (observed $= 0.095$, p-value $= 0.018$) using the scaled residuals (between 0 and 1) from the chosen linear mixed model (i.e., the model with the lowest AIC) explaining the variation in weighted specialization ($\Delta H_2'$) using the fixed effect of `sampling intensity` and the random effect of publication for ($n = 132$) seed-dispersal networks. Location of coloured rings on map correspond to network locations, where colour corresponds to the value of the scaled residual for the location's network(s).
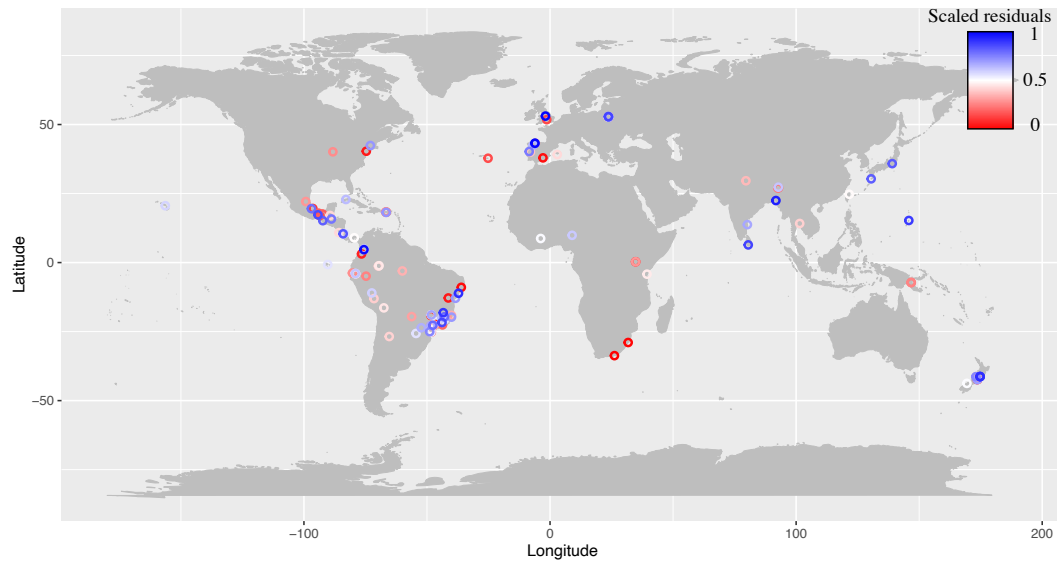
Figure S3.10. Global Moran's I (observed $= 0.040$, p-value $= 0.164$) using the scaled residuals (between 0 and 1) from the chosen linear mixed model (i.e., the model with the lowest AIC) explaining the variation in weighted nestedness (ΔN) using the fixed effects of `sampling intensity`, `temperature seasonality`, and `precipitation seasonality` (`Samp.int. + Temp.·Precip.`) and the random effect of publication for $(n = 132)$ seed-dispersal networks. Location of coloured rings on map correspond to network locations, where colour corresponds to the value of the scaled residual for the location's network(s).
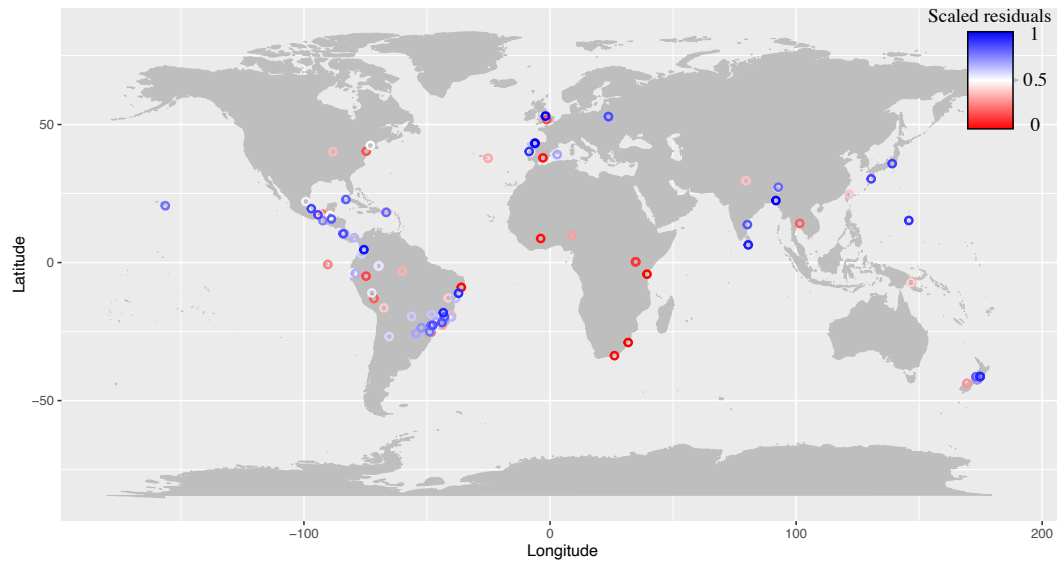
Figure S3.11. Global Moran's I (observed $= 0.045$, p-value $= 0.141$) using the scaled residuals (between 0 and 1) from the chosen linear model (i.e., the model with the lowest AIC) explaining the variation in normalized weighted nestedness (ΔN_n) using `sampling intensity`, and `temperature seasonality` (`Samp.int.` $+$ `Temp.`) for ($n = 132$) seed-dispersal networks. Location of coloured rings on map correspond to network locations, where colour corresponds to the value of the scaled residual for the location's network(s).
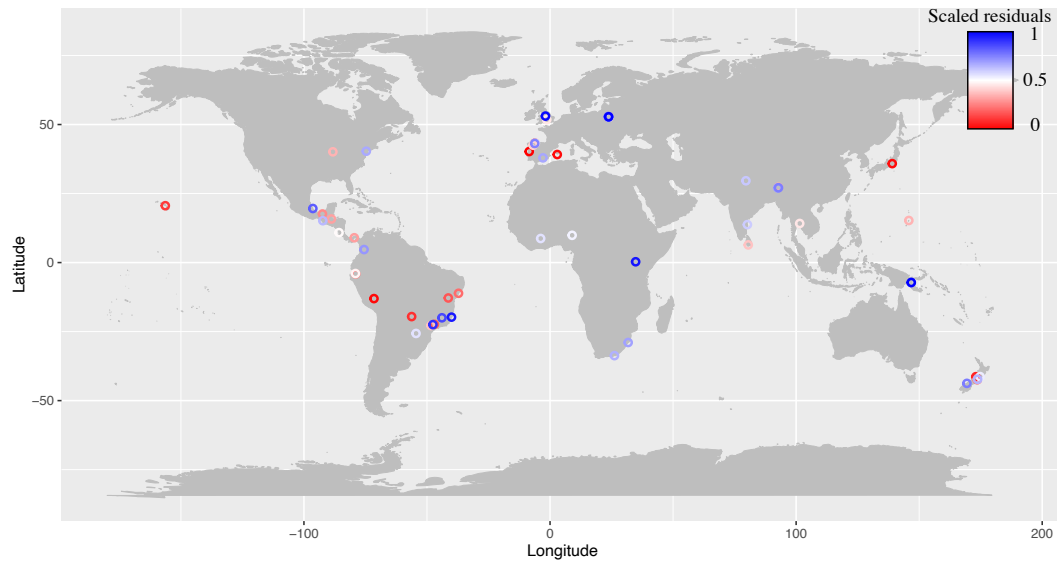
Figure S3.12. Global Moran's I (observed $= -0.009$, p-value $= 0.465$) using the scaled residuals (between 0 and 1) from the chosen linear model (i.e., the model with the lowest AIC) explaining the variation in weighted modularity ($\Delta Q_{>Samp.int.}$) using `temperature seasonality` for ($n = 68$) seed-dispersal networks whose sampling intensity is greater than the median sampling intensity of all seed-dispersal networks. Location of coloured rings on map correspond to network locations, where colour corresponds to the value of the scaled residual for the location's network(s).
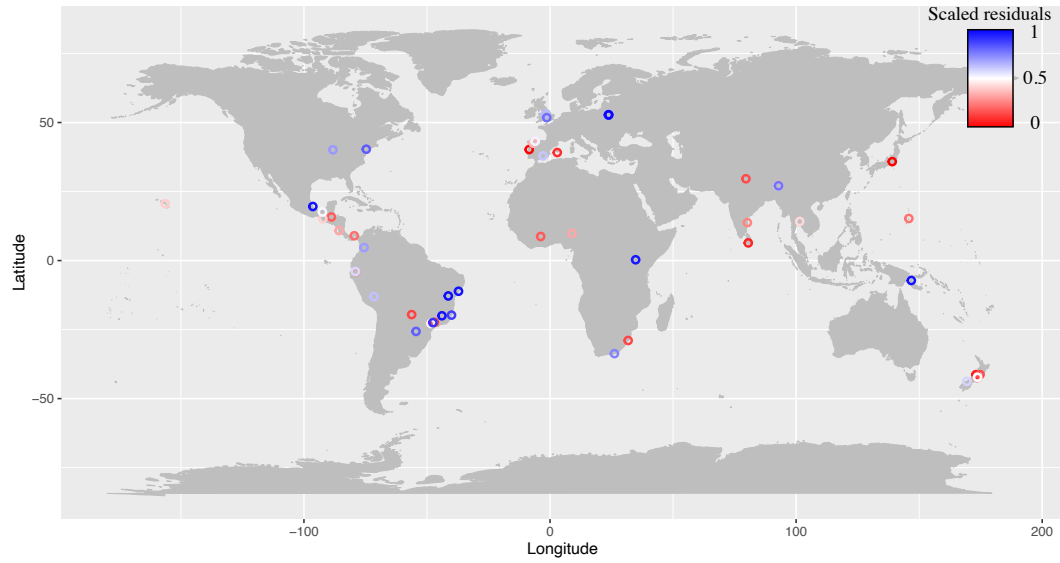
Figure S3.13. Global Moran's I (observed $= 0.014$, p-value $= 0.334$) using the scaled residuals (between 0 and 1) from the chosen linear model (i.e., the model with the lowest AIC) explaining the variation in weighted specialization $\left(\Delta H'_{2,>Samp.\,int.}\right)$ using `sampling intensity`, and `temperature seasonality` (`Samp.int. + Temp.`) for $(n = 68)$ seed-dispersal networks whose sampling intensity is greater than the median sampling intensity of all seed-dispersal networks. Location of the coloured rings on map correspond to network locations, where colour corresponds to the value of the scaled residual for the location's network(s).
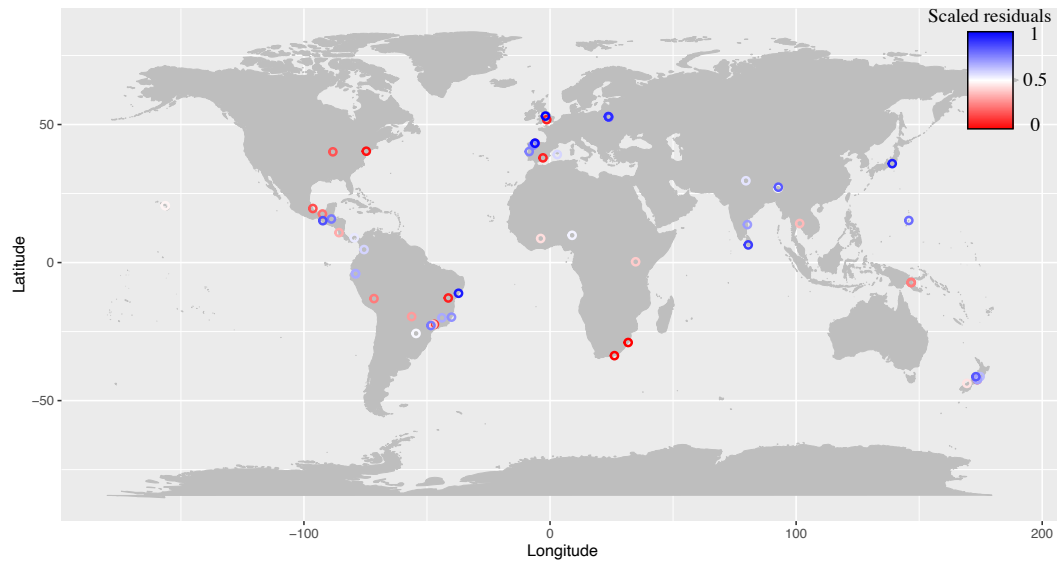
Figure S3.14. Global Moran's I (observed $= -0.021$, p-value $= 0.537$) using the scaled residuals (between 0 and 1) from the chosen linear model (i.e., the model with the lowest AIC) explaining the variation in weighted nestedness ($\Delta N_{>Samp.int.}$) using `temperature seasonality` for ($n = 68$) seed-dispersal networks whose sampling intensity is greater than the median sampling intensity of all seed-dispersal networks. Location of the coloured rings on map correspond to network locations, where colour corresponds to the value of the scaled residual for the location's network(s).

S3.10.1.3 Global Moran's *I* for host-parasite networks
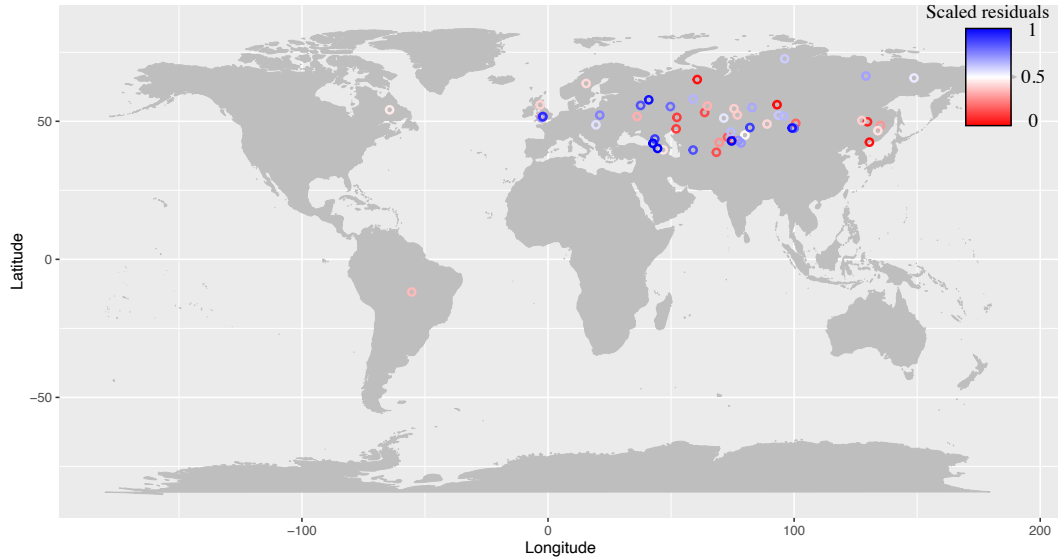
Figure S3.15. Global Moran's *I* (observed = 0.081; *p*-value = 0.129) using the scaled residuals (between 0 and 1) from the chosen linear model (i.e., the model with the lowest AIC) explaining the variation in weighted modularity (ΔQ) using `sampling intensity`, `temperature seasonality`, and `precipitation seasonality` ($\mathtt{Samp.int.} + \mathtt{Temp.} \cdot \mathtt{Precip.}$) for ($n = 68$) host-parasite networks. Location of coloured rings on map correspond to network locations, where colour corresponds to the value of the scaled residual for the location's network(s).
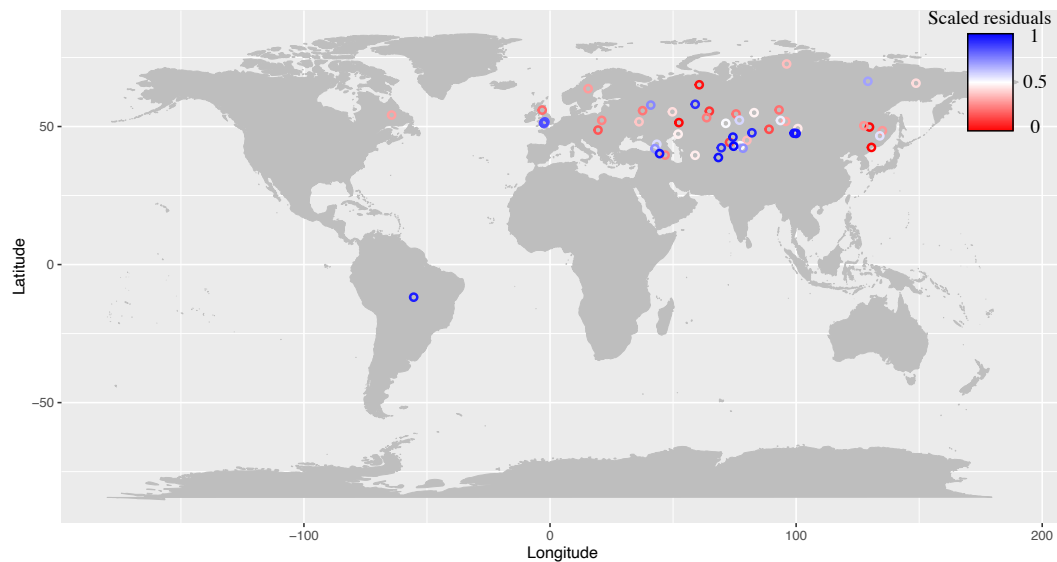
Figure S3.16. Global Moran's I (observed $= 0.120$, p-value $= 0.055$) using the scaled residuals (between 0 and 1) from the chosen linear model (i.e., the model with the lowest AIC) explaining the variation in weighted specialization $(\Delta H_2')$ using `sampling intensity` for $(n = 68)$ host-parasite networks. Location of coloured rings on map correspond to network locations, where colour corresponds to the value of the scaled residual for the location's network(s).
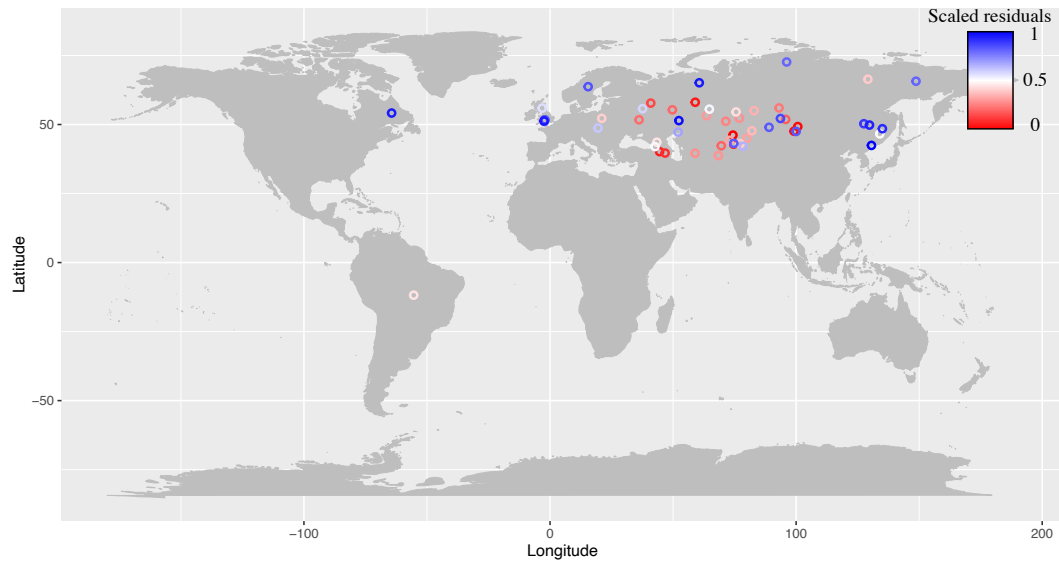
Figure S3.17. Global Moran's I (observed $= 0.067$, p-value $= 0.168$) using the scaled residuals (between 0 and 1) from the chosen linear model (i.e., the model with the lowest AIC) explaining the variation in weighted nestedness (ΔN) using `sampling intensity` for ($n = 68$) host-parasite networks. Location of coloured rings on map correspond to network locations, where colour corresponds to the value of the scaled residual for the location's network(s).
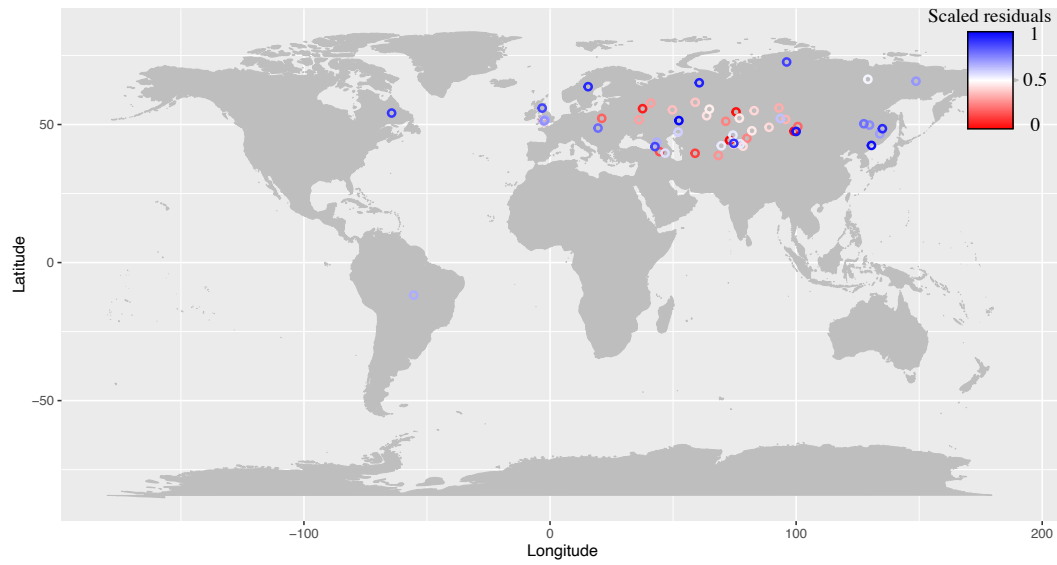
Figure S3.18. Global Moran's I (observed $= 0.041$, p-value $= 0.253$) using the scaled residuals (between 0 and 1) from the chosen linear model (i.e., the model with the lowest AIC) explaining the variation in normalized weighted nestedness (ΔN_n) using `sampling intensity`, and `precipitation seasonality` (`Samp.int.+Precip.`) for $(n = 68)$ host-parasite networks. Location of coloured rings on map correspond to network locations, where colour corresponds to the value of the scaled residual for the location's network(s).

S3.10.2 Extension of Table 3.2, Table 3.3, and Figure 3.3

Table S3.1. Extension from Table 3.2 of linear mixed models (LMMs) for explaining the variation in weighted specialization ($\Delta H_2'$). Marginal R^2 is the proportion of variation explained by the fixed effects, conditional R^2 is the proportion of variation explained by both the fixed and random effects, and ΔAIC is the difference between the AIC of a given model and the model with lowest AIC value. 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.

Network type	Dependent variable	Fixed effect(s)	Marginal R^2	Conditional R^2	ΔAIC
Seed-dispersal ($n = 166$)	$\Delta H_2'$	`Samp.int.`	0.279	0.357	0.00
		`Samp.int.+Precip.`	0.283	0.372	0.68
		`Samp.int.+Temp.·Precip.`	0.293	0.377	1.65
		`Samp.int.+Temp.`	0.279	0.356	1.92
		`Samp.int.+Temp.+Precip.`	0.280	0.374	2.67
		`Temp.·Precip.`	0.094	0.193	44.77
		`Temp.+Precip.`	0.081	0.192	45.18
		`Temp.`	0.063	0.157	46.77
		`Precip.`	0.036	0.252	48.37

Table S3.2. Extension from Table 3.3 of linear regression models (LMs) for explaining the variation in weighted modularity (ΔQ), weighted specialization ($\Delta H'_2$), and weighted nestedness (ΔN). Temp. is the temperature variability, Precip. is the precipitation variability, Samp.int. is the log-transformed sampling intensity for each network, coeff. is the coefficient's value, R^2_{adj} is the adjusted R^2 of the model, and ΔAIC is the difference between the AIC of a given model and the model with lowest AIC value.

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.	$-7.6e^{-2}$	$-4.6e^{-4*}$	-3.9^{***}	$4.0e^{-2}$	—	0.206	0.00
		Samp.int.+Temp.	$-5.0e^{-2**}$	$-6.4e^{-4***}$	-4.2^{***}	—	—	0.197	0.93
		Samp.int.+Temp.·Precip.	$-6.7e^{-2**}$	$-6.3e^{-4}$	-3.8^{***}	$2.1e^{-2}$	$4.9e^{-6}$	0.202	1.77
		Samp.int.+Precip.	$-1.1e^{1***}$	—	-3.5^{***}	$7.3e^{-2***}$	—	0.180	4.28
		Samp.int.	$-7.3e^{-2***}$	—	-4.1^{***}	—	—	0.117	15.52
		Temp.+Precip.	$-9.6e^{-2***}$	$-3.1e^{-4}$	—	$6.6e^{-2**}$	—	0.102	19.19
		Temp.·Precip.	$-7.1e^{-2**}$	$-7.8e^{-4}$	—	$1.2e^{-2}$	$1.4e^{-5}$	0.106	19.59
		Precip.	$-1.2e^{1***}$	—	—	$8.7e^{-2***}$	—	0.094	19.75
		Temp.	$-5.4e^{-2***}$	$-5.9e^{-4***}$	—	—	—	0.067	24.49
Host-parasite ($n = 68$)	ΔQ	Samp.int.+Temp.·Precip.	$-3.4e^{-2}$	$3.4e^{-5***}$	$-4.8e^{-2*}$	$5.1e^{-3*}$	$-4.7e^{-7**}$	0.175	0.00
		Temp.·Precip.	$1.0e^{-3}$	$2.7e^{-5**}$	—	$3.2e^{-3}$	$-3.4e^{-7*}$	0.136	2.19
		Temp.	$1.3e^{-1**}$	$1.1e^{-5**}$	—	—	—	0.100	3.07
		Samp.int.+Temp.	$1.4e^{-1**}$	$1.3e^{-5***}$	$-2.2e^{-2}$	—	—	0.100	4.01
		Temp.+Precip.	$1.3e^{-1**}$	$1.3e^{-5}$	—	$-3.3e^{-4}$	—	0.088	4.87
		Samp.int.+Temp.+Precip.	$1.4e^{-1**}$	$1.3e^{-5***}$	$-2.1e^{-2}$	$-9.8e^{-5}$	—	0.086	6.00
		Precip.	$2.0e^{-1***}$	—	—	$8.2e^{-4}$	—	0.010	9.54
		Samp.int.	$2.3e^{-1***}$	—	$4.1e^{-3}$	—	—	-0.015	11.19
		Samp.int.+Precip.	$2.1e^{-1***}$	—	$-1.1e^{-2}$	$9.7e^{-4}$	—	-0.003	11.34

Table continued ...

... Continuation of Table S3.2.

Network type	Metric	Independent variable(s)	Intercept	Temp. coeff.	Samp.int. coeff.	Precip. coeff.	Temp.·Precip. coeff.	R^2_{adj}	ΔAIC
	$\Delta H'_2$	Samp.int.	$2.9e^{-1}$***	—	$9.2e^{-2}$***	—	—	0.144	0.00
		Samp.int.+Temp.	$3.4e^{-1}$***	$-6.8e^{-6}$	$1.1e^{-1}$***	—	—	0.150	0.46
		Samp.int.+Temp.+Precip.	$3.4e^{-1}$***	$-1.1e^{-5}$	$9.3e^{-2}$**	$1.4e^{-3}$	—	0.160	0.60
		Samp.int.+Temp.·Precip.	$2.3e^{-1}$*	$1.6e^{-6}$	$7.7e^{-2}$*	$4.4e^{-3}$	$-2.8e^{-7}$	0.167	1.00
		Samp.int.+Precip.	$2.8e^{-1}$***	—	$8.4e^{-2}$**	$4.9e^{-4}$	—	0.135	1.70
		Temp.·Precip.	$1.8e^{-1}$	$1.4e^{-5}$	—	$7.5e^{-3}$**	$-5.0e^{-7}$*	0.105	4.91
		Precip.	$3.2e^{-1}$***	—	—	$1.7e^{-3}$	—	0.042	7.67
Host-		Temp.+Precip.	$3.7e^{-1}$***	$-7.6e^{-6}$	—	$2.4e^{-3}$*	—	0.046	8.31
parasite		Temp.	$3.8e^{-1}$***	$1.3e^{-6}$	—	—	—	-0.014	11.53
($n = 68$)		Samp.int.	$-1.3e^{1}$***	—	$-1.1e^{1}$***	—	—	0.467	0.00
		Samp.int.+Precip.	$-1.3e^{1}$***	—	$-1.1e^{1}$***	$-2.8e^{-2}$	—	0.462	1.67
		Samp.int.+Temp.	$-1.4e^{1}$***	$2.8e^{-5}$	$-1.1e^{1}$***	—	—	0.459	1.99
		Samp.int.+Temp.+Precip.	$-1.3e^{1}$***	$1.5e^{-4}$	$-1.1e^{1}$***	$-4.0e^{-2}$	—	0.455	3.48
	ΔN	Samp.int.+Temp.·Precip.	-7.6	$-5.6e^{-4}$	9.9***	$-2.1e^{-1}$	$1.6e^{-5}$	0.459	3.85
		Temp.·Precip.	$-2.4e^{-1}$	$-2.1e^{-3}$**	—	$-6.1e^{-1}$***	$4.4e^{-5}$**	0.213	28.42
		Precip.	$-1.8e^{1}$***	—	—	$-1.8e^{-1}$**	—	0.118	34.26
		Temp.+Precip.	$-1.7e^{1}$***	$-2.4e^{-4}$	—	$-1.6e^{-1}$*	—	0.108	35.97
		Temp.	$-1.8e^{1}$***	$-8.2e^{-4}$*	—	—	—	0.054	39.02

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

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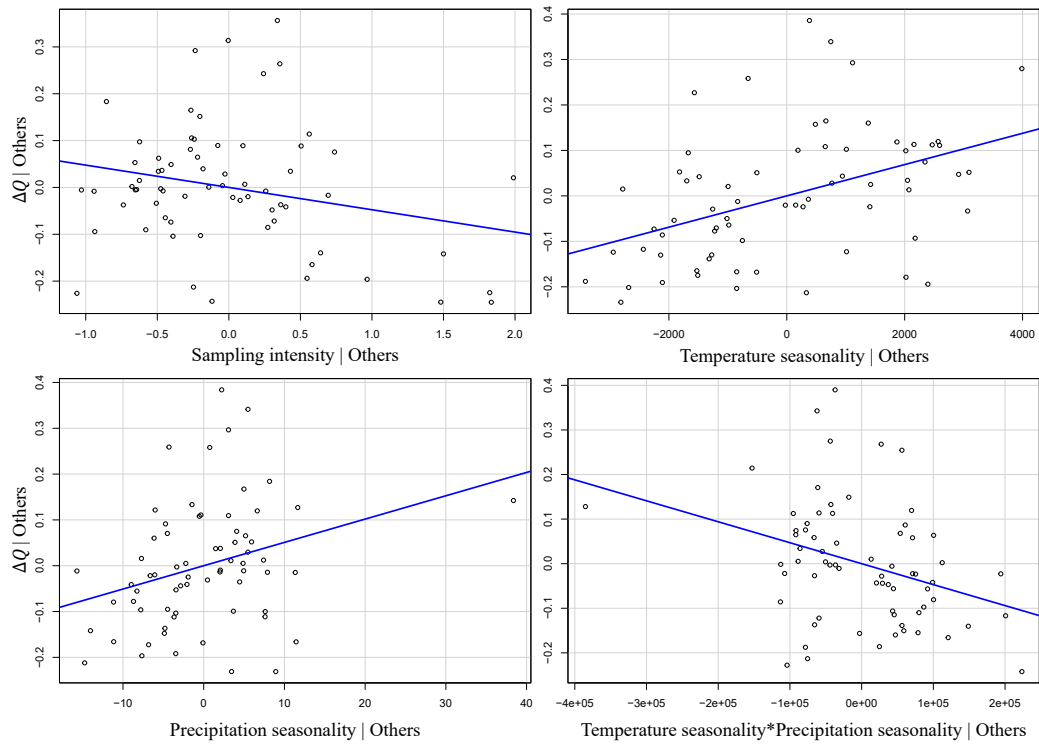
Figure S3.19. Added variable plot for the chosen linear model (without outlier removed, see Figure 3.3 with outlier removed) explaining the variation in weighted modularity (ΔQ) using the explanatory variables `sampling intensity` + `temperature seasonality` · `precipitation seasonality` $\left(R^2_{adj} = 0.175\right)$ for host-parasite $(n = 68)$ networks. Each panel represents the relationship between ΔQ and each explanatory variable in the model while controlling for all other variables in the model.

S3.10.3 Linear mixed models and linear regression models for explaining normalized weighted metrics ΔQ_n, $\Delta H'_{2,n}$, and ΔN_n

To verify whether our conclusions that there exists no strong evidence for relationships between seasonality (i.e., temperature and precipitation variability) and weighted network metrics still held when using normalized metrics, we reran our analyses using normalized weighted modularity [ΔQ_n; eq. (S3.1)], normalized weighted specialization $\left[\Delta H'_{2,n}; \text{eq. (S3.2)}\right]$, and normalized weighted nestedness [ΔN_n; eq. (S3.3)] for plant-pollinator, seed-dispersal, and host-parasite networks.

In plant-pollinator networks, we attempted to construct linear mixed models for normalized weighted metrics, but the residuals violated the assumption of homoscedasticity except when explaining the variation in normalized weighted nestedness (ΔN_n). In this case, the chosen linear mixed model for ΔN_n (i.e., had lowest AIC) contained only `temperature seasonality` as a fixed effect with publication as a random effect, and had a marginal R^2 of 0.156 and a condition R^2 of 0.253 (Table S3.3).

In seed-dispersal networks, since the random effect of publication rarely contributed to explaining the variation in normalized weighted metrics of ΔQ_n, $\Delta H'_{2,n}$, and ΔN_n, we instead only constructed linear models. Moreover, we only report the results for ΔN_n (Table S3.4) since assumptions were violated when attempting to explain ΔQ_n and $\Delta H'_{2,n}$. Altogether, we found that our models for explaining the variation in ΔN_n for seed-dispersal networks had low adjusted R^2 $\left(R^2_{adj} \leq 0.046\right)$.

Like the analyses in the main manuscript, we only constructed linear models for host-parasite networks when explaining normalized weighted metrics since the host-parasite system did not have the requisite number of publication categories (e.g., > 5) to warrant the construction of linear mixed models. We also only report the results for ΔN_n (Table S3.4) since the assumptions of linear regression were violated when attempting to explain the variation in ΔQ_n and $\Delta H'_{2,n}$. We found that the chosen model for ΔN_n in host-parasite networks had an R^2_{adj} of 0.619 and included both `sampling intensity` and `precipitation seasonality` as explanatory variables. However, a model that only included `sampling intensity` as an explanatory variable for ΔN_n had an R^2_{adj} of 0.572 meaning that the inclusion of `precipitation seasonality` only minimally improved the model by about 5

Given that the best evidence for explaining any normalized weighted metrics using seasonality was from plant-pollinator networks where the variation in normalized weighted nestedness (ΔN_n) was only weakly explained by `temperature seasonality` $\left(\text{conditional } R^2 = 0.156\right)$, we re-confirm our hypothesis that there is no strong evidence that seasonality explains network metrics.

$$\Delta Q_n = \frac{Q_{empirical} - \overline{Q}_{50:Vaznull}}{\sigma_{Q_{50:Vaznull}}} \; , \tag{S3.1}$$

where $Q_{empirical}$ is the empirical weighted modularity of a given network as evaluated using the $DIRT\_LPA\_wb\_plus$ function from the bipartite package (Dormann et al., 2008), $\overline{Q}_{50:Vaznull}$ is the mean weighted modularity of an ensemble of 50 Vaznull models based on the empirical network, and $\sigma_{Q_{50:Vaznull}}$ is the standard deviation of weighted modularity from the 50 Vaznull models.

$$\Delta H'_{2,n} = \frac{H'_{2,empirical} - \overline{H}'_{2,50:Vaznull}}{\sigma_{H'_{2,50:Vaznull}}} \; , \tag{S3.2}$$

where $H'_{2,empirical}$ is the empirical weighted specialization of a given network as evaluated using the $H2fun$ function in the bipartite package, $\overline{H}'_{2,50:Vaznull}$ is the mean weighted specialization of an ensemble of 50 Vaznull models based on the empirical network, and $\sigma_{H'_{2,50:Vaznull}}$ is the standard deviation of weighted specialization from the 50 Vaznull models.

$$\Delta N_n = \frac{N_{empirical} - \overline{N}_{50:Vaznull}}{\sigma_{N_{50:Vaznull}}} \; , \tag{S3.3}$$

where $N_{empirical}$ is the empirical weighted nestedness of a given network as evaluated using the $wnodf$ function (Almeida-Neto and Ulrich, 2011) in the MBI package (Chen, 2013), $\overline{N}_{50:Vaznull}$ is the mean weighted nestedness of an ensemble of 50 Vaznull models based on the empirical network, and $\sigma_{N_{50:Vaznull}}$ is the standard deviation of weighted nestedness from the 50 Vaznull models.

Table S3.3. Linear mixed models (LMMs) for explaining the variation in normalized weighted nestedness (ΔN_n). Marginal R^2 is the proportion of variation explained by the fixed effects, conditional R^2 is the proportion of variation explained by both the fixed and random effects, and ΔAIC is the difference between the AIC of a given model and the model with lowest AIC value. 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.

Network type	Dependent variable	Fixed effect(s)	Marginal R^2	Conditional R^2	ΔAIC
Plant-pollinator ($n = 164$)	ΔN_n	`Temp.`	0.156	0.253	0.00
		`Samp.int.+Temp.`	0.175	0.284	1.50
		`Temp.+Precip.`	0.168	0.290	1.66
		`Samp.int.+Temp.+Precip.`	0.196	0.340	3.16
		`Temp.·Precip.`	0.178	0.314	3.34
		`Samp.int.+Temp.·Precip.`	0.202	0.355	4.94
		`Precip.`	0.055	0.220	9.57
		`Samp.int.+Precip.`	0.053	0.218	11.52
		`Samp.int.`	0.001	0.158	13.88

Table S3.4. Linear regression models (LMs) for explaining the variation in normalized weighted nestedness (ΔN_n). Temp. is the temperature seasonality, Precip. is the precipitation seasonality, Samp.int. is the log-transformed sampling intensity for each network, coeff. is the coefficient's value, R^2_{adj} is the adjusted R^2 of the model, and ΔAIC is the difference between the AIC of a given model and the model with lowest AIC value.

Network type	Metric	Independent variable(s)	Intercept	Temp. coeff.	Samp. int. coeff.	Precip. coeff.	Temp.· Precip. coeff.	R^2_{adj}	ΔAIC
Host-parasite ($n=68$)	ΔN_n	Samp.int.+Precip.	-2.5**	—	-5.9***	$5.3e^{-2**}$	—	0.619	0.00
		Samp.int.+Temp.+Precip.	-2.8*	$5.9e^{-5}$	-5.9***	$4.8e^{-2*}$	—	0.615	1.76
		Samp.int.+Temp.·Precip.	-2.9	$7.5e^{-5}$	-6.0***	$5.2e^{-2}$	$-3.6e^{-7}$	0.609	3.76
		Samp.int.+Temp.	-2.6*	$2.1e^{-4}$	-5.5***	—	—	0.587	5.57
		Samp.int.	-1.1	—	-5.1***	—	—	0.572	7.04
		Temp.·Precip.	1.5	$-8.6e^{-4*}$	—	$-1.9e^{-1*}$	$1.7e^{-5*}$	0.083	60.76
		Temp.	-4.9**	$-2.1e^{-4}$	—	—	—	0.012	63.90
		Precip.	-5.6***	—	—	$-3.0e^{-2}$	—	0.007	64.25
		Temp.+Precip.	-4.8**	$-1.5e^{-4}$	—	$-1.6e^{-2}$	—	0.001	65.62
Seed-dispersal ($n=166$)	ΔN_n	Samp.int.+Temp.	-2.1***	$1.8e^{-4**}$	$-6.6e^{-1**}$	—	—	0.044	0.00
		Samp.int.+Temp.+Precip.	-2.5***	$1.9e^{-4**}$	$-6.1e^{-1*}$	$7.3e^{-3}$	—	0.046	0.75
		Samp.int.+Temp.·Precip.	-2.4***	$1.3e^{-4}$	$-6.1e^{-1*}$	$2.1e^{-3}$	$2.0e^{-6}$	0.041	2.52
		Temp.+Precip.	-2.7***	$1.2e^{-4}$	—	$9.9e^{-3}$	—	0.017	4.70
		Temp.	-2.2***	$9.7e^{-5}$	—	—	—	0.010	4.96
		Samp.int.	-1.7***	—	$-3.5e^{-1}$	—	—	0.009	5.09
		Temp.·Precip.	-2.5***	$5.7e^{-5}$	—	$4.6e^{-3}$	$2.0e^{-6}$	0.012	6.47
		Precip.	-2.2***	—	—	$6.2e^{-3}$	—	$-4.4e^{-4}$	6.62
		Samp.int.+Precip.	-1.9***	—	$-3.2e^{-1}$	$3.8e^{-3}$	—	0.005	6.77

*** $p<0.001$, ** $p<0.01$, * $p<0.05$

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S3.10.4 Linear regressions alternatives to the linear mixed models used in the manuscript (i.e., Table 3.2)

It is possible that the linear mixed models with publication as a random intercept removed the importance of seasonality (i.e., temperature, and precipitation variability) for explaining the variation in weighted modularity (ΔQ), weighted specialization ($\Delta H_2'$), and weighted nestedness (ΔN) in plant-pollinator, and seed-dispersal networks shown in Table 3.2. To overcome this issue, we revaluated these relationships by instead using linear models (LMs; Table S3.5). We reconfirm our conclusion that there is no strong evidence for which seasonality appears to explain network structure. More specifically, the best evidence that seasonality explains the variation in network structure using LMs is the plant-pollinator network's chosen model for weighted nestedness (ΔN) which included `sampling intensity` (`Samp.int.`), `temperature seasonality` (`Temp.`), and `precipitation seasonality` (`Precip.`) as explanatory variables $\left(R_{adj}^2 = 0.206 \right)$. However, `temperature seasonality`, and `precipitation seasonality` only contributed about 10% to this (i.e., a model of only `temperature seasonality`, and `precipitation seasonality` for explaining the variation in ΔN had $R_{adj}^2 = 0.102$).

Table S3.5. Linear regression models (LMs) for explaining the variation in weighted modularity (ΔQ), weighted specialization ($\Delta H'_2$), and weighted nestedness (ΔN). ΔN for plant-pollinator networks is provided here but it is the same as in Table S3.2. Temp. is the temperature variability, Precip. is the precipitation variability, Samp. int. is the log-transformed sampling intensity for each network, coeff. is the coefficient's value, R^2_{adj} is the adjusted R^2 of the model, and ΔAIC is the difference between the AIC of a given model and the model with lowest AIC value.

Network type	Metric	Independent variable(s)	Intercept	Temp. coeff.	Samp. int. coeff.	Precip. coeff.	Temp.· Precip. coeff.	R^2_{adj}	ΔAIC
		Temp.	$1.9e^{-1}$***	$6.3e^{-6}$**	—	—	—	0.046	0.00
		Temp.+Precip.	$1.6e^{-1}$***	$8.1e^{-6}$**	—	$4.4e^{-4}$	—	0.051	0.03
		Samp.int.+Temp.+Precip.	$1.5e^{-1}$***	$8.6e^{-6}$***	$1.2e^{-2}$	$5.2e^{-4}$	—	0.052	0.84
		Samp.int.+Temp.	$1.9e^{-1}$***	$6.3e^{-6}$**	$8.0e^{-3}$	—	—	0.043	1.48
	ΔQ	Temp.·Precip.	$1.7e^{-1}$***	$6.3e^{-6}$	—	$2.2e^{-4}$	$5.5e^{-8}$	0.046	1.88
		Samp.int.+Temp.·Precip.	$1.7e^{-1}$***	$5.7e^{-6}$	$1.4e^{-2}$	$1.9e^{-4}$	$8.5e^{-8}$	0.048	2.47
		Samp.int.	$2.1e^{-1}$***	—	$6.1e^{-3}$	—	—	-0.004	8.37
Plant-pollinator ($n = 164$)		Precip.	$2.1e^{-1}$***	—	—	$-1.2e^{-4}$	—	-0.005	8.48
		Samp.int.+Precip.	$2.1e^{-1}$***	—	$5.5e^{-3}$	$-9.4e^{-5}$	—	-0.010	10.25
		Samp.int.+Temp.	$2.0e^{-1}$***	$1.1e^{-5}$***	$4.4e^{-2}$**	—	—	0.135	0.00
		Samp.int.+Temp.+Precip.	$1.7e^{-1}$***	$1.3e^{-5}$***	$4.8e^{-2}$***	$4.8e^{-4}$	—	0.137	0.43
		Samp.int.+Temp.·Precip.	$1.6e^{-1}$***	$1.4e^{-5}$*	$4.7e^{-2}$***	$6.3e^{-4}$	$-4.1e^{-8}$	0.132	2.38
		Temp.	$2.0e^{-1}$***	$1.0e^{-5}$***	—	—	—	0.082	8.77
	$\Delta H'_2$	Temp.+Precip.	$1.9e^{-1}$***	$1.1e^{-5}$***	—	$1.6e^{-4}$	—	0.077	10.59
		Temp.·Precip.	$1.7e^{-1}$***	$1.6e^{-5}$*	—	$7.4e^{-4}$	$-1.5e^{-7}$	0.075	11.86
		Samp.int.	$2.4e^{-1}$***	—	$4.1e^{-2}$**	—	—	0.044	15.31
		Samp.int.+Precip.	$2.6e^{-1}$***	—	$3.8e^{-2}$**	$-4.3e^{-4}$	—	0.048	15.64
		Precip.	$2.7e^{-1}$***	—	—	$-5.8e^{-4}$	—	0.012	20.77

Table continued . . .

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Network type	Metric	Independent variable(s)	Intercept	Temp. coeff.	Samp. int. coeff.	Precip. coeff.	Temp.·Precip. coeff.	R^2_{adj}	ΔAIC
		Samp.int.+Temp.+Precip.	-7.6***	$-4.6e^{-4}$*	-3.9***	$4.0e^{-2}$	—	0.206	0.00
		Samp.int.+Temp.	-5.0***	$-6.4e^{-4}$***	-4.2***	—	—	0.197	0.93
		Samp.int.+Temp.·Precip.	-6.7**	$-6.3e^{-4}$	-3.8***	$2.1e^{-2}$	$4.9e^{-6}$	0.202	1.77
Plant-		Samp.int.+Precip.	$-1.1e^{1}$***	—	-3.5***	$7.3e^{-2}$***	—	0.180	4.28
pollinator	ΔN	Samp.int.	-7.3***	—	-4.1***	—	—	0.117	15.52
($n = 164$)		Temp.+Precip.	-9.6***	$-3.1e^{-4}$	—	$6.6e^{-2}$**	—	0.102	19.19
		Temp.·Precip.	-7.1**	$-7.8e^{-4}$	—	$1.2e^{-2}$	$1.4e^{-5}$	0.106	19.59
		Precip.	$-1.2e^{1}$***	—	—	$8.7e^{-2}$***	—	0.094	19.75
		Temp.	-5.4***	$-5.9e^{-4}$***	—	—	—	0.067	24.49
		Samp.int.+Precip.	$1.8e^{-1}$***	—	$4.1e^{-2}$***	$-5.0e^{-4}$	—	0.121	0.00
		Samp.int.	$1.6e^{-1}$***	—	$4.6e^{-2}$***	—	—	0.110	1.05
		Samp.int.+Temp.+Precip.	$1.8e^{-1}$***	$1.6e^{-6}$	$3.8e^{-2}$***	$-4.7e^{-4}$	—	0.117	1.72
Seed-		Samp.int.+Temp.	$1.5e^{-1}$***	$2.5e^{-6}$	$4.1e^{-2}$***	—	—	0.108	2.34
dispersal	ΔQ	Samp.int.+Temp.·Precip.	$1.7e^{-1}$***	$2.8e^{-6}$	$3.8e^{-2}$***	$-3.8e^{-4}$	$-3.6e^{-8}$	0.112	3.69
($n = 166$)		Temp.+Precip.	$1.9e^{-1}$***	$5.9e^{-6}$*	—	$-6.4e^{-4}$*	—	0.059	11.33
		Temp.·Precip.	$1.9e^{-1}$***	$7.1e^{-6}$	—	$-5.4e^{-4}$	$-3.7e^{-8}$	0.053	13.29
		Precip.	$2.2e^{-1}$***	—	—	$-8.1e^{-4}$**	—	0.040	13.63
		Temp.	$1.5e^{-1}$***	$7.6e^{-6}$**	—	—	—	0.039	13.83

... Continuation of Table S3.5.

Network type	Metric	Independent variable(s)	Intercept	Temp. coeff.	Samp. int. coeff.	Precip. coeff.	Temp.· Precip. coeff.	R^2_{adj}	ΔAIC
		Samp.int.+Temp.·Precip.	$1.4e^{-1***}$	$1.7e^{-5*}$	$8.8e^{-2***}$	$6.8e^{-4}$	$-4.0e^{-7}$	0.323	0.00
		Samp.int.	$1.7e^{-1***}$	—	$9.7e^{-2***}$	—	—	0.310	0.14
		Samp.int.+Precip.	$1.9e^{-1***}$	—	$9.3e^{-2***}$	$-4.3e^{-4}$	—	0.313	0.47
		Samp.int.+Temp.	$1.6e^{-1***}$	$4.1e^{-6}$	$9.0e^{-2***}$	—	—	0.312	0.66
	$\Delta H'_2$	Samp.int.+Temp.+Precip.	$1.8e^{-1***}$	$3.4e^{-6}$	$8.8e^{-2***}$	$-3.6e^{-4}$	—	0.313	1.49
		Temp.·Precip.	$1.7e^{-1***}$	$2.7e^{-5**}$	—	$3.2e^{-4}$	$-4.0e^{-7}$	0.126	41.35
		Temp.+Precip.	$2.1e^{-1***}$	$1.3e^{-5***}$	—	$-7.4e^{-4}$	—	0.117	42.11
		Temp.	$1.7e^{-1***}$	$1.5e^{-5***}$	—	—	—	0.102	43.93
		Precip.	$2.7e^{-1***}$	—	—	$-1.1e^{-3**}$	—	0.047	53.69
Seed-dispersal ($n=166$)		Samp.int.	$-5.3***$	—	-1.1	—	—	0.010	0.00
		Samp.int.+Temp.	$-5.9***$	$2.4e^{-4}$	$-1.5*$	—	—	0.012	0.59
		Samp.int.+Precip.	$-5.3***$	—	-1.1	$5.1e^{-4}$	—	0.004	2.00
		Samp.int.+Temp.·Precip.	$-4.3*$	$-3.8e^{-4}$	-1.5	$-4.5e^{-2}$	$1.9e^{-5}$	0.014	2.24
	ΔN	Precip.	$-6.2***$	—	—	$9.0e^{-3}$	—	-0.005	2.44
		Samp.int.+Temp.+Precip.	$-6.1***$	$2.5e^{-4}$	-1.5	$5.1e^{-3}$	—	0.007	2.52
		Temp.	$-6.0***$	$5.4e^{-5}$	—	—	—	-0.006	2.57
		Temp.·Precip.	$-4.7*$	$-5.5e^{-4}$	—	$-3.9e^{-2}$	$1.9e^{-5}$	-0.002	4.00
		Temp.+Precip.	$-6.6***$	$8.4e^{-5}$	—	$1.1e^{-2}$	—	-0.010	4.24

$***p<0.001$, $**p<0.01$, $*p<0.05$

S3.10.5 $\Delta Q_{>Samp.int.}$, $\Delta H'_{2,>Samp.int.}$, and $\Delta N_{>Samp.int.}$ in plant-pollinator, and seed-dispersal networks

Table S3.6. Linear regression models (LMs) for explaining the variation in weighted modularity ($\Delta Q_{>Samp.int.}$), weighted specialization ($\Delta H'_{2,>Samp.int.}$), and weighted nestedness ($\Delta N_{>Samp.int.}$) for networks whose sampling intensity is greater than the median sampling intensity of their respective system. Temp. is the temperature variability, Precip. is the precipitation variability, Samp.int. is the log-transformed sampling intensity for each network, coeff. is the coefficient's value, R^2_{adj} is the adjusted R^2 of the model, and ΔAIC is the difference between the AIC of a given model and the model with lowest AIC value.

Network type	Metric	Independent variable(s)	Intercept	Temp. coeff.	Samp.int. coeff.	Precip. coeff.	Temp.· Precip. coeff.	R^2_{adj}	ΔAIC
	$\Delta Q_{>Samp.int.}$	Samp.int.+Temp.·Precip.	$3.5e^{-1}$***	$-3.3e^{-5}$***	$4.3e^{-2}$*	$5.0e^{-3}$***	$1.6e^{-6}$***	0.323	0.00
		Temp.·Precip.	$3.5e^{-1}$***	$-3.0e^{-5}$**	—	$-4.5e^{-3}$***	$1.6e^{-6}$***	0.293	2.54
		Samp.int.+Temp.	$1.6e^{-1}$***	$9.6e^{-6}$**	$3.6e^{-2}$	—	—	0.110	20.51
		Temp.	$1.7e^{-1}$***	$9.6e^{-6}$**	—	—	—	0.094	20.95
		Samp.int.+Temp.+Precip.	$1.4e^{-1}$***	$1.1e^{-5}$*	$3.4e^{-2}$	$2.5e^{-4}$	—	0.100	22.34
		Temp.+Precip.	$1.5e^{-1}$***	$1.2e^{-5}$**	—	$4.5e^{-4}$	—	0.089	22.43
		Samp.int.+Precip.	$2.2e^{-1}$***	—	$4.3e^{-2}$	$-8.4e^{-4}$	—	0.038	26.90
Plant-pollinator ($n = 82$)		Samp.int.	$1.9e^{-1}$***	—	$3.7e^{-2}$	—	—	0.015	27.80
		Precip.	$2.4e^{-1}$***	—	—	$7.0e^{-4}$	—	0.012	28.07
	$\Delta H'_{2,>Samp.int.}$	Temp.·Precip.	$4.0e^{-1}$***	$-2.9e^{-5}$*	—	$-5.0e^{-3}$***	$1.8e^{-6}$***	0.326	0.00
		Samp.int.+Temp.·Precip.	$4.0e^{-1}$***	$-3.1e^{-5}$**	$3.2e^{-2}$	$-5.3e^{-3}$***	$1.8e^{-6}$***	0.331	0.38
		Temp.	$2.0e^{-1}$***	$1.6e^{-5}$***	—	—	—	0.168	15.39
		Samp.int.+Temp.	$1.9e^{-1}$***	$1.6e^{-5}$***	$2.6e^{-2}$	—	—	0.166	16.55
		Temp.+Precip.	$1.7e^{-1}$***	$1.9e^{-5}$***	—	$6.3e^{-4}$	—	0.165	16.69
		Samp.int.+Temp.+Precip.	$1.7e^{-1}$***	$1.8e^{-5}$***	$2.2e^{-2}$	$5.1e^{-4}$	—	0.160	18.11
		Precip.	$3.1e^{-1}$***	—	—	$-1.2e^{-3}$	—	0.034	27.65
		Samp.int.+Precip.	$3.0e^{-1}$***	—	$3.7e^{-2}$	$-1.3e^{-3}$*	—	0.039	28.15
		Samp.int.	$2.5e^{-1}$***	—	$2.7e^{-2}$	—	—	-0.003	30.71

Table continued ...

... Continuation of Table S3.6.

Network type	Metric	Independent variable(s)	Intercept	Temp. coeff.	Samp. int. coeff.	Precip. coeff.	Temp.· Precip. coeff.	R^2_{adj}	ΔAIC
Plant-pollinator ($n = 82$)	$\Delta N_{>Samp.int.}$	Temp.	-6.4^{***}	$-9.1e^{-4***}$	—	—	—	0.146	0.00
		Samp.int.+Temp.	-5.5^{***}	$-9.1e^{-4***}$	-1.9	—	—	0.147	0.84
		Temp.+Precip.	-5.5	$-9.7e^{-4**}$	—	$-1.5e^{-2}$	—	0.136	1.89
		Samp.int.+Temp.+Precip.	-5.2	$-9.3e^{-4**}$	-1.8	$-4.7e^{-3}$	—	0.137	2.83
		Temp.·Precip.	-4.5	$-1.2e^{-3}$	—	$-4.0e^{-2}$	$7.8e^{-6}$	0.126	3.81
		Samp.int.+Temp.·Precip.	-4.6	$-1.1e^{-3}$	-1.8	$-2.2e^{-2}$	$5.3e^{-6}$	0.126	4.80
		Samp.int.+Precip.	$-1.2e^{1***}$	—	-2.6	$9.0e^{-2}$	—	0.055	9.31
		Precip.	$-1.3e^{1***}$	—	—	$8.2e^{-2*}$	—	0.043	9.32
		Samp.int.	-8.7^{***}	—	-1.9	—	—	0.001	12.90
Seed-dispersal ($n = 83$)	$\Delta Q_{>Samp.int.}$	Temp.	$1.8e^{-1***}$	$6.8e^{-6}$	—	—	—	0.034	0.00
		Samp.int.+Temp.	$1.7e^{-1***}$	$6.1e^{-6}$	$1.4e^{-2}$	—	—	0.028	1.47
		Temp.+Precip.	$2.0e^{-1***}$	$5.9e^{-6}$	—	$-3.1e^{-4}$	—	0.027	1.54
		Precip.	$2.4e^{-1***}$	—	—	$-5.7e^{-4}$	—	0.008	2.16
		Samp.int.	$1.9e^{-1***}$	—	$2.3e^{-2}$	—	—	0.005	2.42
		Temp.·Precip.	$1.8e^{-1***}$	$1.3e^{-5}$	—	$2.6e^{-4}$	$-1.9e^{-7}$	0.021	3.00
		Samp.int.+Temp.+Precip.	$1.9e^{-1***}$	$5.4e^{-6}$	$1.3e^{-2}$	$-2.7e^{-4}$	—	0.020	3.13
		Samp.int.+Precip.	$2.1e^{-1***}$	—	$1.8e^{-2}$	$-4.8e^{-4}$	—	0.007	3.27
		Samp.int.+Temp.·Precip.	$1.7e^{-1***}$	$1.2e^{-5}$	$1.2e^{-2}$	$2.9e^{-4}$	$-1.9e^{-7}$	0.013	4.62

Table continued ...

... Continuation of Table S3.6.

Network type	Metric	Independent variable(s)	Intercept	Temp. coeff.	Samp. int. coeff.	Precip. coeff.	Temp.· Precip. coeff.	R^2_{adj}	ΔAIC
		`Samp.int.+Temp.·Precip.`	$9.3e^{-2}$	$2.8e^{-5}$**	$8.1e^{-2}$***	$1.5e^{-3}$	$-5.6e^{-7}$*	0.267	0.00
		`Samp.int.+Temp.`	$1.5e^{-1}$***	$9.5e^{-6}$*	$8.3e^{-2}$***	—	—	0.247	0.33
		`Samp.int.+Temp.+Precip.`	$1.6e^{-1}$***	$8.9e^{-6}$*	$8.2e^{-2}$***	$-2.3e^{-4}$	—	0.239	2.13
		`Samp.int.`	$1.7e^{-1}$***	—	$9.7e^{-2}$***	—	—	0.199	4.46
	$\Delta H'_{2,>Samp.int.}$	`Samp.int.+Precip.`	$2.0e^{-1}$***	—	$9.2e^{-2}$***	$-5.7e^{-4}$	—	0.202	5.08
		`Temp.·Precip.`	$1.7e^{-1}$**	$3.2e^{-5}$**	—	$1.3e^{-3}$	$-5.9e^{-7}$	0.140	12.24
		`Temp.`	$2.1e^{-1}$***	$1.3e^{-5}$**	—	—	—	0.112	13.05
		`Temp.+Precip.`	$2.4e^{-1}$***	$1.2e^{-5}$**	—	$-5.1e^{-4}$	—	0.110	14.15
Seed-dispersal ($n=83$)		`Precip.`	$3.1e^{-1}$***	—	—	$-1.0e^{-3}$	—	0.034	20.01
		`Temp.`	-6.9***	$9.7e^{-5}$	—	—	—	-0.010	0.00
		`Precip.`	-6.5***	—	—	$7.6e^{-4}$	—	-0.012	0.17
		`Samp.int.`	-6.4***	—	$-4.8e^{-3}$	—	—	-0.012	0.17
		`Temp.+Precip.`	-7.2**	$1.1e^{-4}$	—	$5.8e^{-3}$	—	-0.022	1.97
	$\Delta N_{>Samp.int.}$	`Samp.int.+Temp.`	-6.7***	$1.0e^{-4}$	$-1.6e^{-1}$	—	—	-0.023	1.99
		`Samp.int.+Precip.`	-6.5**	—	$2.8e^{-3}$	$7.7e^{-4}$	—	-0.025	2.17
		`Temp.·Precip.`	-5.2	$-4.7e^{-4}$	—	$-4.5e^{-2}$	$1.7e^{-5}$	-0.024	3.06
		`Samp.int.+Temp.+Precip.`	-7.0**	$1.2e^{-4}$	$-1.3e^{-1}$	$5.4e^{-3}$	—	-0.035	3.96
		`Samp.int.+Temp.·Precip.`	-5.1	$-4.6e^{-4}$	$-8.6e^{-2}$	$-4.5e^{-2}$	$1.7e^{-5}$	-0.037	5.06

*** $p<0.001$, ** $p<0.01$, * $p<0.05$

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S3.10.6 Network references

Table S3.7. Networks (and their citations) used in *No strong evidence that modularity, specialization or nestedness are linked to seasonal climatic variability in bipartite networks*. Host-parasite networks are "HP", plant-herbivore networks are "PH", ant-plant networks are "AP", plant-pollinator networks are "PP", and seed-dispersal networks are "SD".

#	Type	Network name	Reference	Weighted
1.	HP	A_HP_Arai_mcgregor	Arai and Mudry (1983)	
2.	HP	A_HP_Arai_parsnip	Arai and Mudry (1983)	
3.	HP	A_HP_Arthur1976	Arthur et al. (1976)	
4.	HP	A_HP_Bangham1955	Bangham (1955)	
5.	HP	A_HP_Belay10	Choudhury et al. (2004)	
6.	HP	A_HP_Belay13	Muzzall and Whelan (2011)	
7.	HP	A_HP_Belay14	Morozińska-Gogol (2007)	
8.	HP	A_HP_Belay15	Jalali and Barzegar (2006)	
9.	HP	A_HP_Belay2	Takemoto et al. (2009); Lima Jr. et al. (2012)	
10.	HP	A_HP_Belay23	Székely and Molnár (1997)	
11.	HP	A_HP_Belay25	Kirjušina and Vismanis (2007)	
12.	HP	A_HP_Belay26	Kirjušina and Vismanis (2007)	
13.	HP	A_HP_Belay27	Violante-González et al. (2007)	
14.	HP	A_HP_Belay30	Violante-González et al. (2007)	
15.	HP	A_HP_Carvalheiro2008	Carvalheiro et al. (2008)	
16.	HP	A_HP_Chinniah1978	Chinniah and Threlfall (1978)	Yes
17.	HP	A_HP_daGraça	da Graça et al. (2017)	
18.	HP	A_HP_Dechtiar1972	Dechtiar (1972)	
19.	HP	A_HP_Font	Font (1998)	
20.	HP	A_HP_Hadfield_2013_001	Hadfield et al. (2014)	Yes
21.	HP	A_HP_Hadfield_2013_002	Hadfield et al. (2014)	Yes

Table continued ...

... Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
22.	HP	A_HP_Hadfield_2013_003	Hadfield et al. (2014)	Yes
23.	HP	A_HP_Hadfield_2013_004	Hadfield et al. (2014)	Yes
24.	HP	A_HP_Hadfield_2013_005	Hadfield et al. (2014)	Yes
25.	HP	A_HP_Hadfield_2013_006	Hadfield et al. (2014)	Yes
26.	HP	A_HP_Hadfield_2013_007	Hadfield et al. (2014)	Yes
27.	HP	A_HP_Hadfield_2013_008	Hadfield et al. (2014)	Yes
28.	HP	A_HP_Hadfield_2013_009	Hadfield et al. (2014)	Yes
29.	HP	A_HP_Hadfield_2013_010	Hadfield et al. (2014)	Yes
30.	HP	A_HP_Hadfield_2013_012	Hadfield et al. (2014)	Yes
31.	HP	A_HP_Hadfield_2013_013	Hadfield et al. (2014)	Yes
32.	HP	A_HP_Hadfield_2013_014	Hadfield et al. (2014)	Yes
33.	HP	A_HP_Hadfield_2013_016	Hadfield et al. (2014)	Yes
34.	HP	A_HP_Hadfield_2013_017	Hadfield et al. (2014)	Yes
35.	HP	A_HP_Hadfield_2013_018	Hadfield et al. (2014)	Yes
36.	HP	A_HP_Hadfield_2013_019	Hadfield et al. (2014)	Yes
37.	HP	A_HP_Hadfield_2013_020	Hadfield et al. (2014)	Yes
38.	HP	A_HP_Hadfield_2013_021	Hadfield et al. (2014)	Yes
39.	HP	A_HP_Hadfield_2013_022	Hadfield et al. (2014)	Yes
40.	HP	A_HP_Hadfield_2013_023	Hadfield et al. (2014)	Yes
41.	HP	A_HP_Hadfield_2013_024	Hadfield et al. (2014)	Yes
42.	HP	A_HP_Hadfield_2013_025	Hadfield et al. (2014)	Yes
43.	HP	A_HP_Hadfield_2013_026	Hadfield et al. (2014)	Yes
44.	HP	A_HP_Hadfield_2013_027	Hadfield et al. (2014)	Yes
45.	HP	A_HP_Hadfield_2013_029	Hadfield et al. (2014)	Yes
46.	HP	A_HP_Hadfield_2013_030	Hadfield et al. (2014)	Yes

Table continued ...

...Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
47.	HP	A_HP_Hadfield_2013_031	Hadfield et al. (2014)	Yes
48.	HP	A_HP_Hadfield_2013_032	Hadfield et al. (2014)	Yes
49.	HP	A_HP_Hadfield_2013_033	Hadfield et al. (2014)	Yes
50.	HP	A_HP_Hadfield_2013_034	Hadfield et al. (2014)	Yes
51.	HP	A_HP_Hadfield_2013_035	Hadfield et al. (2014)	Yes
52.	HP	A_HP_Hadfield_2013_036	Hadfield et al. (2014)	Yes
53.	HP	A_HP_Hadfield_2013_037	Hadfield et al. (2014)	Yes
54.	HP	A_HP_Hadfield_2013_038	Hadfield et al. (2014)	Yes
55.	HP	A_HP_Hadfield_2013_039	Hadfield et al. (2014)	Yes
56.	HP	A_HP_Hadfield_2013_040	Hadfield et al. (2014)	Yes
57.	HP	A_HP_Hadfield_2013_041	Hadfield et al. (2014)	Yes
58.	HP	A_HP_Hadfield_2013_042	Hadfield et al. (2014)	Yes
59.	HP	A_HP_Hadfield_2013_043	Hadfield et al. (2014)	Yes
60.	HP	A_HP_Hadfield_2013_044	Hadfield et al. (2014)	Yes
61.	HP	A_HP_Hadfield_2013_045	Hadfield et al. (2014)	Yes
62.	HP	A_HP_Hadfield_2013_046	Hadfield et al. (2014)	Yes
63.	HP	A_HP_Hadfield_2013_047	Hadfield et al. (2014)	Yes
64.	HP	A_HP_Hadfield_2013_048	Hadfield et al. (2014)	Yes
65.	HP	A_HP_Hadfield_2013_049	Hadfield et al. (2014)	Yes
66.	HP	A_HP_Hadfield_2013_050	Hadfield et al. (2014)	Yes
67.	HP	A_HP_Hadfield_2013_051	Hadfield et al. (2014)	Yes
68.	HP	A_HP_Lecorff2000	Le Corff et al. (2000)	
69.	HP	A_HP_Leong1981	Leong and Holmest (1981)	
70.	HP	A_HP_Macfadyen2009_paras-herb_A1	Macfadyen et al. (2009)	Yes
71.	HP	A_HP_Macfadyen2009_paras-herb_A10	Macfadyen et al. (2009)	Yes

Table continued ...

#	Type	Network name	Reference	Weighted
72.	HP	A_HP_Macfadyen2009_paras-herb_A2	Macfadyen et al. (2009)	Yes
73.	HP	A_HP_Macfadyen2009_paras-herb_A3	Macfadyen et al. (2009)	Yes
74.	HP	A_HP_Macfadyen2009_paras-herb_A4	Macfadyen et al. (2009)	Yes
75.	HP	A_HP_Macfadyen2009_paras-herb_A5	Macfadyen et al. (2009)	Yes
76.	HP	A_HP_Macfadyen2009_paras-herb_A6	Macfadyen et al. (2009)	Yes
77.	HP	A_HP_Macfadyen2009_paras-herb_A7	Macfadyen et al. (2009)	Yes
78.	HP	A_HP_Macfadyen2009_paras-herb_A8	Macfadyen et al. (2009)	Yes
79.	HP	A_HP_Macfadyen2009_paras-herb_A9	Macfadyen et al. (2009)	Yes
80.	HP	A_HP_Macfadyen2009_paras-herb_B1	Macfadyen et al. (2009)	Yes
81.	HP	A_HP_Macfadyen2009_paras-herb_B2	Macfadyen et al. (2009)	Yes
82.	HP	A_HP_Macfadyen2009_paras-herb_B3	Macfadyen et al. (2009)	Yes
83.	HP	A_HP_Macfadyen2009_paras-herb_B4	Macfadyen et al. (2009)	Yes
84.	HP	A_HP_Macfadyen2009_paras-herb_B5	Macfadyen et al. (2009)	Yes
85.	HP	A_HP_Macfadyen2009_paras-herb_B6	Macfadyen et al. (2009)	Yes
86.	HP	A_HP_Macfadyen2009_paras-herb_B7	Macfadyen et al. (2009)	Yes
87.	HP	A_HP_Macfadyen2009_paras-herb_B8	Macfadyen et al. (2009)	Yes
88.	HP	A_HP_Mendonca	de Mendonça et al. (2020)	
89.	HP	A_HP_Pilosof2013_1982	Pilosof et al. (2013)	
90.	HP	A_HP_Pilosof2013_1983	Pilosof et al. (2013)	
91.	HP	A_HP_Pilosof2013_1984	Pilosof et al. (2013)	
92.	HP	A_HP_Pilosof2013_1985	Pilosof et al. (2013)	
93.	HP	A_HP_Pilosof2013_1986	Pilosof et al. (2013)	
94.	HP	A_HP_Pilosof2013_1987	Pilosof et al. (2013)	
95.	HP	A_HP_Rauque	Rauque et al. (2003)	
96.	HP	A_HP_Stireman2003	Stireman and Singer (2003)	

... Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
97.	HP	A_HP_Sugiura2007	Sugiura (2007)	
98.	PH	A_PH_Basset1996	Basset et al. (1996)	
99.	PH	A_PH_Bergamini	Bergamini et al. (2017)	Yes
100.	PH	A_PH_Coley2006	Coley et al. (2006)	
101.	PH	A_PH_HennemanXXXX-1	Henneman and Memmott (2001)	
102.	PH	A_PH_HennemanXXXX-2	Henneman and Memmott (2001)	
103.	PH	A_PH_Ibanez2013	Ibanez et al. (2013)	
104.	PH	A_PH_Janzen1980	Janzen et al. (1980)	
105.	PH	A_PH_Janzen2003	Janzen et al. (2003)	
106.	PH	A_PH_Joern-Altuda	Joern (1979)	
107.	PH	A_PH_Joern-Marathon	Joern (1979)	
108.	PH	A_PH_Lewis2002	Lewis et al. (2002)	
109.	PH	A_PH_Macfadyen2009_plant-herb_A1	Macfadyen et al. (2009)	Yes
110.	PH	A_PH_Macfadyen2009_plant-herb_A10	Macfadyen et al. (2009)	Yes
111.	PH	A_PH_Macfadyen2009_plant-herb_A2	Macfadyen et al. (2009)	Yes
112.	PH	A_PH_Macfadyen2009_plant-herb_A3	Macfadyen et al. (2009)	Yes
113.	PH	A_PH_Macfadyen2009_plant-herb_A4	Macfadyen et al. (2009)	Yes
114.	PH	A_PH_Macfadyen2009_plant-herb_A5	Macfadyen et al. (2009)	Yes
115.	PH	A_PH_Macfadyen2009_plant-herb_A6	Macfadyen et al. (2009)	Yes
116.	PH	A_PH_Macfadyen2009_plant-herb_A7	Macfadyen et al. (2009)	Yes
117.	PH	A_PH_Macfadyen2009_plant-herb_A8	Macfadyen et al. (2009)	Yes
118.	PH	A_PH_Macfadyen2009_plant-herb_B1	Macfadyen et al. (2009)	Yes
119.	PH	A_PH_Macfadyen2009_plant-herb_B2	Macfadyen et al. (2009)	Yes
120.	PH	A_PH_Macfadyen2009_plant-herb_B3	Macfadyen et al. (2009)	Yes
121.	PH	A_PH_Macfadyen2009_plant-herb_B4	Macfadyen et al. (2009)	Yes

Table continued ...

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...Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
122.	PH	A_PH_Macfadyen2009_plant-herb_B8	Macfadyen et al. (2009)	Yes
123.	PH	A_PH_Macfadyen2009_plant-herb_B9	Macfadyen et al. (2009)	Yes
124.	PH	A_PH_Novotny2005	Novotny et al. (2005)	
125.	PH	A_PH_Novotny2012	Novotny et al. (2012)	Yes
126.	PH	A_PH_Pearse2013	Pearse and Altermatt (2013)	
127.	PH	A_PH_site01_period01_Martins	Pereira Martins et al. (2020)	Yes
128.	PH	A_PH_site03_period01_Martins	Pereira Martins et al. (2020)	Yes
129.	PH	A_PH_site04_period01_Martins	Pereira Martins et al. (2020)	Yes
130.	PH	A_PH_site05_period01_Martins	Pereira Martins et al. (2020)	Yes
131.	PH	A_PH_site06_period01_Martins	Pereira Martins et al. (2020)	Yes
132.	PH	A_PH_site07_period01_Martins	Pereira Martins et al. (2020)	Yes
133.	PH	A_PH_site08_period01_Martins	Pereira Martins et al. (2020)	Yes
134.	PH	A_PH_site09_period01_Martins	Pereira Martins et al. (2020)	Yes
135.	PH	A_PH_site10_period01_Martins	Pereira Martins et al. (2020)	Yes
136.	PH	A_PH_Stary2008	Starý and Havelka (2008)	
137.	PH	A_PH_Tavakilian1997	Tavakilian et al. (1997)	
138.	PH	A_PH_Ueckert	Ueckert et al. (1976)	
139.	AP	M_AP_Bluthgen2004	Blüthgen et al. (2004)	Yes
140.	AP	M_AP_Fonseca1996	Fonseca and Ganade (1996)	Yes
141.	AP	M_AP_Passmore2012-2107-FF	Passmore et al. (2012)	
142.	AP	M_AP_Passmore2012-2108-FF	Passmore et al. (2012)	
143.	AP	M_AP_Passmore2012-Camp41-CF	Passmore et al. (2012)	
144.	AP	M_AP_Passmore2012-Colosso-FF	Passmore et al. (2012)	
145.	AP	M_AP_Passmore2012-Dimona-CF	Passmore et al. (2012)	
146.	AP	M_AP_Passmore2012-Florestal-CF	Passmore et al. (2012)	

Table continued ...

...Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
147.	AP	M_AP_Passmore2012-PortoAlegre-CF	Passmore et al. (2012)	
148.	AP	M_AP_Passmore2012-PortoAlegre-FF	Passmore et al. (2012)	
149.	PP	M_PL_Abreu	Abreu and Vieira (2004)	Yes
150.	PP	M_PL_Arizmendi	del Coro Arizmendi and Ornelas (1990)	Yes
151.	PP	M_PL_Arroyo1982-1	Arroyo et al. (1982)	
152.	PP	M_PL_Arroyo1982-2	Arroyo et al. (1982)	
153.	PP	M_PL_Arroyo1982-3	Arroyo et al. (1982)	
154.	PP	M_PL_Barrett1987	Barrett and Helenurm (1987)	Yes
155.	PP	M_PL_Bartomeus	Bartomeus et al. (2008)	Yes
156.	PP	M_PL_Bezerra2009	Bezerra et al. (2009)	Yes
157.	PP	M_PL_Brosi2017_Back_of_Baldy_Bend_2014_Control	Brosi et al. (2017)	Yes
158.	PP	M_PL_Brosi2017_Back_of_Baldy_Bend_2014_Manipulation	Brosi et al. (2017)	Yes
159.	PP	M_PL_Brosi2017_Belleview_Bench_2013_Control	Brosi et al. (2017)	Yes
160.	PP	M_PL_Brosi2017_Belleview_Bench_2013_Manipulation	Brosi et al. (2017)	Yes
161.	PP	M_PL_Brosi2017_Brush_Creek_Sign_2014_Control	Brosi et al. (2017)	Yes
162.	PP	M_PL_Brosi2017_Brush_Creek_Sign_2014_Manipulation	Brosi et al. (2017)	Yes
163.	PP	M_PL_Brosi2017_Brush_Creek_Steep_2013_Control	Brosi et al. (2017)	Yes
164.	PP	M_PL_Brosi2017_Brush_Creek_Steep_2013_Manipulation	Brosi et al. (2017)	Yes
165.	PP	M_PL_Brosi2017_Cold_Springs_Ranch_2014_Control	Brosi et al. (2017)	Yes
166.	PP	M_PL_Brosi2017_Cold_Springs_Ranch_2014_Manipulation	Brosi et al. (2017)	Yes
167.	PP	M_PL_Brosi2017_Gothic_CG_2014_Control	Brosi et al. (2017)	Yes
168.	PP	M_PL_Brosi2017_Gothic_CG_2014_Manipulation	Brosi et al. (2017)	Yes
169.	PP	M_PL_Brosi2017_Gothic_Road_2013_Control	Brosi et al. (2017)	Yes
170.	PP	M_PL_Brosi2017_Gothic_Road_2013_Manipulation	Brosi et al. (2017)	Yes
171.	PP	M_PL_Brosi2017_Gothic_Road_Grate_2014_Control	Brosi et al. (2017)	Yes

Table continued ...

... Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
172.	PP	M_PL_Brosi2017_Gothic_Road_Grate_2014_Manipulation	Brosi et al. (2017)	Yes
173.	PP	M_PL_Brosi2017_Gothic_Road_Steep_2013_Control	Brosi et al. (2017)	Yes
174.	PP	M_PL_Brosi2017_Gothic_Road_Steep_2013_Manipulation	Brosi et al. (2017)	Yes
175.	PP	M_PL_Brosi2017_Gothic_Road_Steep_2014_Control	Brosi et al. (2017)	Yes
176.	PP	M_PL_Brosi2017_Gothic_Road_Steep_2014_Manipulation	Brosi et al. (2017)	Yes
177.	PP	M_PL_Brosi2017_Gothic_Town_2014_Control	Brosi et al. (2017)	Yes
178.	PP	M_PL_Brosi2017_Gothic_Town_2014_Manipulation	Brosi et al. (2017)	Yes
179.	PP	M_PL_Brosi2017_Judd_Falls_TH_2013_Control	Brosi et al. (2017)	Yes
180.	PP	M_PL_Brosi2017_Judd_Falls_TH_2013_Manipulation	Brosi et al. (2017)	Yes
181.	PP	M_PL_Brosi2017_Judd_Falls_TH_2014_Control	Brosi et al. (2017)	Yes
182.	PP	M_PL_Brosi2017_Judd_Falls_TH_2014_Manipulation	Brosi et al. (2017)	Yes
183.	PP	M_PL_Brosi2017_Past_Rustlers_2013_Control	Brosi et al. (2017)	Yes
184.	PP	M_PL_Brosi2017_Past_Rustlers_2013_Manipulation	Brosi et al. (2017)	Yes
185.	PP	M_PL_Brosi2017_Rustlers_2013_Control	Brosi et al. (2017)	Yes
186.	PP	M_PL_Brosi2017_Rustlers_2013_Manipulation	Brosi et al. (2017)	Yes
187.	PP	M_PL_Burkle2013	Burkle et al. (2013)	Yes
188.	PP	M_PL_CaraDonna_rmbl_interaction_networks_data_EDI	CaraDonna (2020)	Yes
189.	PP	M_PL_Carstensen2017_Brazil_Cedro	Carstensen et al. (2018)	Yes
190.	PP	M_PL_Carstensen2017_Brazil_Elefante	Carstensen et al. (2018)	Yes
191.	PP	M_PL_Carstensen2017_Brazil_Gigante	Carstensen et al. (2018)	Yes
192.	PP	M_PL_Carstensen2017_Brazil_Midway	Carstensen et al. (2018)	Yes
193.	PP	M_PL_Carstensen2017_Brazil_Paulino	Carstensen et al. (2018)	Yes
194.	PP	M_PL_Carstensen2017_Brazil_Soizig	Carstensen et al. (2018)	Yes
195.	PP	M_PL_Carstensen2017_Brazil_Tinkerbell	Carstensen et al. (2018)	Yes
196.	PP	M_PL_Carstensen2017_ElHierro	Carstensen et al. (2018)	Yes

Table continued ...

... Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
197.	PP	M_PL_Carstensen2017_Fuerteventura	Carstensen et al. (2018)	Yes
198.	PP	M_PL_Carstensen2017_Gomera	Carstensen et al. (2018)	Yes
199.	PP	M_PL_Carstensen2017_GranCanaria	Carstensen et al. (2018)	Yes
200.	PP	M_PL_Carstensen2017_TenerifeSyd	Carstensen et al. (2018)	Yes
201.	PP	M_PL_Carstensen2017_Teno	Carstensen et al. (2018)	Yes
202.	PP	M_PL_Carstensen2017_WesternSahara	Carstensen et al. (2018)	Yes
203.	PP	M_PL_Clements1923	Clements and Long (1923)	
204.	PP	M_PL_Cotton	Cotton (1998)	Yes
205.	PP	M_PL_Dicks2002-1	Dicks et al. (2002)	Yes
206.	PP	M_PL_Dicks2002-2	Dicks et al. (2002)	Yes
207.	PP	M_PL_Dupont2003	Dupont et al. (2003)	
208.	PP	M_PL_Dupont2009-1	Dupont and Olesen (2009)	
209.	PP	M_PL_Dupont2009-2	Dupont and Olesen (2009)	
210.	PP	M_PL_Elberling1999	Elberling and Olesen (1999)	
211.	PP	M_PL_Gilarranz_2015_Amarante	Gilarranz et al. (2015)	
212.	PP	M_PL_Gilarranz_2015_Barrosa	Gilarranz et al. (2015)	
213.	PP	M_PL_Gilarranz_2015_CincoCerros	Gilarranz et al. (2015)	
214.	PP	M_PL_Gilarranz_2015_Difunito	Gilarranz et al. (2015)	
215.	PP	M_PL_Gilarranz_2015_Difuntos	Gilarranz et al. (2015)	
216.	PP	M_PL_Gilarranz_2015_ElMorro	Gilarranz et al. (2015)	
217.	PP	M_PL_Gilarranz_2015_LaBrava	Gilarranz et al. (2015)	
218.	PP	M_PL_Gilarranz_2015_LaChata	Gilarranz et al. (2015)	
219.	PP	M_PL_Gilarranz_2015_LaPaja	Gilarranz et al. (2015)	
220.	PP	M_PL_Gilarranz_2015_PiedraAlta	Gilarranz et al. (2015)	
221.	PP	M_PL_Gilarranz_2015_Vigilancia	Gilarranz et al. (2015)	

Table continued ...

... Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
222.	PP	M_PL_Gilarranz_2015_Volcan	Gilarranz et al. (2015)	
223.	PP	M_PL_Herrera1988	Herrera (1988)	
224.	PP	M_PL_High_mountain_matrix_Norfolk	Norfolk et al. (2018)	Yes
225.	PP	M_PL_Hocking1968	Hocking (1968)	
226.	PP	M_PL_Inoue1990	Inoue (1990)	Yes
227.	PP	M_PL_Inouye1988	Inouye and Pyke (1988)	Yes
228.	PP	M_PL_Kaiser-Bunbury_2010_060_01	Kaiser-Bunbury et al. (2010)	Yes
229.	PP	M_PL_Kaiser-Bunbury_2010_060_02	Kaiser-Bunbury et al. (2010)	Yes
230.	PP	M_PL_Kaiser-Bunbury_2010_060_03	Kaiser-Bunbury et al. (2010)	Yes
231.	PP	M_PL_Kaiser-Bunbury_2010_060_04	Kaiser-Bunbury et al. (2010)	Yes
232.	PP	M_PL_Kaiser-Bunbury_2010_060_05	Kaiser-Bunbury et al. (2010)	Yes
233.	PP	M_PL_Kaiser-Bunbury_2010_060_06	Kaiser-Bunbury et al. (2010)	Yes
234.	PP	M_PL_Kaiser-Bunbury_2010_060_07	Kaiser-Bunbury et al. (2010)	Yes
235.	PP	M_PL_Kaiser-Bunbury_2010_060_08	Kaiser-Bunbury et al. (2010)	Yes
236.	PP	M_PL_Kaiser-Bunbury_2010_060_09	Kaiser-Bunbury et al. (2010)	Yes
237.	PP	M_PL_Kaiser-Bunbury_2010_060_10	Kaiser-Bunbury et al. (2010)	Yes
238.	PP	M_PL_Kaiser-Bunbury_2010_060_11	Kaiser-Bunbury et al. (2010)	Yes
239.	PP	M_PL_Kaiser-Bunbury_2010_060_12	Kaiser-Bunbury et al. (2010)	Yes
240.	PP	M_PL_Kaiser-Bunbury_2010_060_13	Kaiser-Bunbury et al. (2010)	Yes
241.	PP	M_PL_Kaiser-Bunbury_2010_060_14	Kaiser-Bunbury et al. (2010)	Yes
242.	PP	M_PL_Kaiser-Bunbury_2010_060_15	Kaiser-Bunbury et al. (2010)	Yes
243.	PP	M_PL_Kaiser-Bunbury_2010_060_16	Kaiser-Bunbury et al. (2010)	Yes
244.	PP	M_PL_Kaiser-Bunbury_2010_060_17	Kaiser-Bunbury et al. (2010)	Yes
245.	PP	M_PL_Kaiser-Bunbury_2010_060_18	Kaiser-Bunbury et al. (2010)	Yes
246.	PP	M_PL_Kaiser-Bunbury_2010_060_19	Kaiser-Bunbury et al. (2010)	Yes

Table continued ...

... Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
247.	PP	M_PL_Kaiser-Bunbury_2010_060_20	Kaiser-Bunbury et al. (2010)	Yes
248.	PP	M_PL_Kaiser-Bunbury_2010_060_21	Kaiser-Bunbury et al. (2010)	Yes
249.	PP	M_PL_Kaiser-Bunbury_2010_060_22	Kaiser-Bunbury et al. (2010)	Yes
250.	PP	M_PL_Kaiser-Bunbury_2010_060_23	Kaiser-Bunbury et al. (2010)	Yes
251.	PP	M_PL_Kaiser-Bunbury_2010_060_24	Kaiser-Bunbury et al. (2010)	Yes
252.	PP	M_PL_Kaiser-Bunbury_2014_061_01	Kaiser-Bunbury et al. (2014)	Yes
253.	PP	M_PL_Kaiser-Bunbury_2014_061_02	Kaiser-Bunbury et al. (2014)	Yes
254.	PP	M_PL_Kaiser-Bunbury_2014_061_03	Kaiser-Bunbury et al. (2014)	Yes
255.	PP	M_PL_Kaiser-Bunbury_2014_061_04	Kaiser-Bunbury et al. (2014)	Yes
256.	PP	M_PL_Kaiser-Bunbury_2014_061_05	Kaiser-Bunbury et al. (2014)	Yes
257.	PP	M_PL_Kaiser-Bunbury_2014_061_06	Kaiser-Bunbury et al. (2014)	Yes
258.	PP	M_PL_Kaiser-Bunbury_2014_061_07	Kaiser-Bunbury et al. (2014)	Yes
259.	PP	M_PL_Kaiser-Bunbury_2014_061_08	Kaiser-Bunbury et al. (2014)	Yes
260.	PP	M_PL_Kaiser-Bunbury_2014_061_09	Kaiser-Bunbury et al. (2014)	Yes
261.	PP	M_PL_Kaiser-Bunbury_2014_061_10	Kaiser-Bunbury et al. (2014)	Yes
262.	PP	M_PL_Kaiser-Bunbury_2014_061_11	Kaiser-Bunbury et al. (2014)	Yes
263.	PP	M_PL_Kaiser-Bunbury_2014_061_12	Kaiser-Bunbury et al. (2014)	Yes
264.	PP	M_PL_Kaiser-Bunbury_2014_061_13	Kaiser-Bunbury et al. (2014)	Yes
265.	PP	M_PL_Kaiser-Bunbury_2014_061_14	Kaiser-Bunbury et al. (2014)	Yes
266.	PP	M_PL_Kaiser-Bunbury_2014_061_15	Kaiser-Bunbury et al. (2014)	Yes
267.	PP	M_PL_Kaiser-Bunbury_2014_061_16	Kaiser-Bunbury et al. (2014)	Yes
268.	PP	M_PL_Kaiser-Bunbury_2014_061_17	Kaiser-Bunbury et al. (2014)	Yes
269.	PP	M_PL_Kaiser-Bunbury_2014_061_18	Kaiser-Bunbury et al. (2014)	Yes
270.	PP	M_PL_Kaiser-Bunbury_2014_061_19	Kaiser-Bunbury et al. (2014)	Yes
271.	PP	M_PL_Kaiser-Bunbury_2014_061_20	Kaiser-Bunbury et al. (2014)	Yes

Table continued ...

... Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
272.	PP	M_PL_Kaiser-Bunbury_2014_061_21	Kaiser-Bunbury et al. (2014)	Yes
273.	PP	M_PL_Kaiser-Bunbury_2014_061_22	Kaiser-Bunbury et al. (2014)	Yes
274.	PP	M_PL_Kaiser-Bunbury_2014_061_23	Kaiser-Bunbury et al. (2014)	Yes
275.	PP	M_PL_Kaiser-Bunbury_2014_061_24	Kaiser-Bunbury et al. (2014)	Yes
276.	PP	M_PL_Kaiser-Bunbury_2014_061_25	Kaiser-Bunbury et al. (2014)	Yes
277.	PP	M_PL_Kaiser-Bunbury_2014_061_26	Kaiser-Bunbury et al. (2014)	Yes
278.	PP	M_PL_Kaiser-Bunbury_2014_061_27	Kaiser-Bunbury et al. (2014)	Yes
279.	PP	M_PL_Kaiser-Bunbury_2014_061_28	Kaiser-Bunbury et al. (2014)	Yes
280.	PP	M_PL_Kaiser-Bunbury_2014_061_29	Kaiser-Bunbury et al. (2014)	Yes
281.	PP	M_PL_Kaiser-Bunbury_2014_061_30	Kaiser-Bunbury et al. (2014)	Yes
282.	PP	M_PL_Kaiser-Bunbury_2014_061_31	Kaiser-Bunbury et al. (2014)	Yes
283.	PP	M_PL_Kaiser-Bunbury_2014_061_32	Kaiser-Bunbury et al. (2014)	Yes
284.	PP	M_PL_Kaiser-Bunbury_2014_061_35	Kaiser-Bunbury et al. (2014)	Yes
285.	PP	M_PL_Kaiser-Bunbury_2014_061_36	Kaiser-Bunbury et al. (2014)	Yes
286.	PP	M_PL_Kaiser-Bunbury_2014_061_37	Kaiser-Bunbury et al. (2014)	Yes
287.	PP	M_PL_Kaiser-Bunbury_2014_061_38	Kaiser-Bunbury et al. (2014)	Yes
288.	PP	M_PL_Kaiser-Bunbury_2014_061_39	Kaiser-Bunbury et al. (2014)	Yes
289.	PP	M_PL_Kaiser-Bunbury_2014_061_40	Kaiser-Bunbury et al. (2014)	Yes
290.	PP	M_PL_Kaiser-Bunbury_2014_061_43	Kaiser-Bunbury et al. (2014)	Yes
291.	PP	M_PL_Kaiser-Bunbury_2014_061_44	Kaiser-Bunbury et al. (2014)	Yes
292.	PP	M_PL_Kaiser-Bunbury_2014_061_45	Kaiser-Bunbury et al. (2014)	Yes
293.	PP	M_PL_Kaiser-Bunbury_2014_061_46	Kaiser-Bunbury et al. (2014)	Yes
294.	PP	M_PL_Kaiser-Bunbury_2014_061_47	Kaiser-Bunbury et al. (2014)	Yes
295.	PP	M_PL_Kaiser-Bunbury_2014_061_48	Kaiser-Bunbury et al. (2014)	Yes
296.	PP	M_PL_Kakutani1990	Kakutani et al. (1990)	Yes

Table continued ...

#	Type	Network name	Reference	Weighted
297.	PP	M_PL_Kantsa	Kantsa et al. (2018)	Yes
298.	PP	M_PL_Kato1990	Kato et al. (1990)	
299.	PP	M_PL_Kato1993	Kato et al. (1993)	Yes
300.	PP	M_PL_Kato1996	Kato (1996)	
301.	PP	M_PL_Kato1996b	Kato and Miura (1996)	Yes
302.	PP	M_PL_Kato2000	Kato (2000)	Yes
303.	PP	M_PL_LaraC	Lara (2006)	Yes
304.	PP	M_PL_Lara-Romero_2016_nevero-Encroachedpasture-1	Lara-Romero et al. (2016)	
305.	PP	M_PL_Lara-Romero_2016_nevero-Encroachedpasture-10	Lara-Romero et al. (2016)	
306.	PP	M_PL_Lara-Romero_2016_nevero-Encroachedpasture-2	Lara-Romero et al. (2016)	
307.	PP	M_PL_Lara-Romero_2016_nevero-Encroachedpasture-3	Lara-Romero et al. (2016)	
308.	PP	M_PL_Lara-Romero_2016_nevero-Encroachedpasture-4	Lara-Romero et al. (2016)	
309.	PP	M_PL_Lara-Romero_2016_nevero-Encroachedpasture-5	Lara-Romero et al. (2016)	
310.	PP	M_PL_Lara-Romero_2016_nevero-Encroachedpasture-6	Lara-Romero et al. (2016)	
311.	PP	M_PL_Lara-Romero_2016_nevero-Encroachedpasture-7	Lara-Romero et al. (2016)	
312.	PP	M_PL_Lara-Romero_2016_nevero-Encroachedpasture-8	Lara-Romero et al. (2016)	
313.	PP	M_PL_Lara-Romero_2016_nevero-Encroachedpasture-9	Lara-Romero et al. (2016)	
314.	PP	M_PL_Lara-Romero_2016_nevero-Pasture-1	Lara-Romero et al. (2016)	
315.	PP	M_PL_Lara-Romero_2016_nevero-Pasture-2	Lara-Romero et al. (2016)	
316.	PP	M_PL_Lara-Romero_2016_nevero-Pasture-3	Lara-Romero et al. (2016)	
317.	PP	M_PL_Lara-Romero_2016_nevero-Pasture-4	Lara-Romero et al. (2016)	
318.	PP	M_PL_Lara-Romero_2016_nevero-Pasture-5	Lara-Romero et al. (2016)	
319.	PP	M_PL_Lara-Romero_2016_nevero-Pasture-6	Lara-Romero et al. (2016)	
320.	PP	M_PL_Lara-Romero_2016_nevero-Pasture-8	Lara-Romero et al. (2016)	
321.	PP	M_PL_Lara-Romero_2016_nevero-Pasture-9	Lara-Romero et al. (2016)	

... Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
322.	PP	M_PL_Lara-Romero_2016_penalara-Encroachedpasture-1	Lara-Romero et al. (2016)	
323.	PP	M_PL_Lara-Romero_2016_penalara-Encroachedpasture-10	Lara-Romero et al. (2016)	
324.	PP	M_PL_Lara-Romero_2016_penalara-Encroachedpasture-2	Lara-Romero et al. (2016)	
325.	PP	M_PL_Lara-Romero_2016_penalara-Encroachedpasture-3	Lara-Romero et al. (2016)	
326.	PP	M_PL_Lara-Romero_2016_penalara-Encroachedpasture-4	Lara-Romero et al. (2016)	
327.	PP	M_PL_Lara-Romero_2016_penalara-Encroachedpasture-5	Lara-Romero et al. (2016)	
328.	PP	M_PL_Lara-Romero_2016_penalara-Encroachedpasture-6	Lara-Romero et al. (2016)	
329.	PP	M_PL_Lara-Romero_2016_penalara-Encroachedpasture-7	Lara-Romero et al. (2016)	
330.	PP	M_PL_Lara-Romero_2016_penalara-Encroachedpasture-8	Lara-Romero et al. (2016)	
331.	PP	M_PL_Lara-Romero_2016_penalara-Encroachedpasture-9	Lara-Romero et al. (2016)	
332.	PP	M_PL_Lara-Romero_2016_penalara-Pasture-1	Lara-Romero et al. (2016)	
333.	PP	M_PL_Lara-Romero_2016_penalara-Pasture-10	Lara-Romero et al. (2016)	
334.	PP	M_PL_Lara-Romero_2016_penalara-Pasture-2	Lara-Romero et al. (2016)	
335.	PP	M_PL_Lara-Romero_2016_penalara-Pasture-3	Lara-Romero et al. (2016)	
336.	PP	M_PL_Lara-Romero_2016_penalara-Pasture-4	Lara-Romero et al. (2016)	
337.	PP	M_PL_Lara-Romero_2016_penalara-Pasture-5	Lara-Romero et al. (2016)	
338.	PP	M_PL_Lara-Romero_2016_penalara-Pasture-6	Lara-Romero et al. (2016)	
339.	PP	M_PL_Lara-Romero_2016_penalara-Pasture-7	Lara-Romero et al. (2016)	
340.	PP	M_PL_Lara-Romero_2016_penalara-Pasture-8	Lara-Romero et al. (2016)	
341.	PP	M_PL_Lara-Romero_2016_penalara-Pasture-9	Lara-Romero et al. (2016)	
342.	PP	M_PL_LasCasas	Las-Casas et al. (2012)	Yes
343.	PP	M_PL_Low_mountain_matrix_Norfolk	Norfolk et al. (2018)	Yes
344.	PP	M_PL_Lundgren2005	Lundgren and Olesen (2005)	Yes
345.	PP	M_PL_Maglianesi_high	Maglianesi et al. (2014)	Yes
346.	PP	M_PL_Maglianesi_low	Maglianesi et al. (2014)	Yes

Table continued ...

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#	Type	Network name	Reference	Weighted
347.	PP	M_PL_Maglianesi_mid	Maglianesi et al. (2014)	Yes
348.	PP	M_PL_Magrach2017_Germany_2011_high	Magrach et al. (2018)	
349.	PP	M_PL_Magrach2017_Germany_2011_low	Magrach et al. (2018)	
350.	PP	M_PL_Magrach2017_Germany_2012_high	Magrach et al. (2018)	
351.	PP	M_PL_Magrach2017_Germany_2012_low	Magrach et al. (2018)	
352.	PP	M_PL_Magrach2017_Sweden_2011_high	Magrach et al. (2018)	
353.	PP	M_PL_Magrach2017_Sweden_2011_low	Magrach et al. (2018)	
354.	PP	M_PL_Magrach2017_Sweden_2012_high	Magrach et al. (2018)	
355.	PP	M_PL_Magrach2017_Sweden_2012_low	Magrach et al. (2018)	
356.	PP	M_PL_Magrach2017_UK_2011_high	Magrach et al. (2018)	
357.	PP	M_PL_Magrach2017_UK_2011_low	Magrach et al. (2018)	
358.	PP	M_PL_Magrach2017_UK_2012_high	Magrach et al. (2018)	
359.	PP	M_PL_Magrach2017_UK_2012_low	Magrach et al. (2018)	
360.	PP	M_PL_Maruyama	Simmons et al. (2019b)	Yes
361.	PP	M_PL_Mazan_Tinoco	Tinoco et al. (2017)	Yes
362.	PP	M_PL_Medan2002-1	Medan et al. (2002)	
363.	PP	M_PL_Medan2002-2	Medan et al. (2002)	
364.	PP	M_PL_Memmott1999	Memmott (1999)	Yes
365.	PP	M_PL_Mosquin1967	Mosquin and Martin (1967)	Yes
366.	PP	M_PL_Motten1982	Motten (1986)	Yes
367.	PP	M_PL_Olesen2002	Olesen et al. (2002)	
368.	PP	M_PL_Olesen-3	Olesen et al. (2002)	
369.	PP	M_PL_Olito	Olito and Fox (2015)	Yes
370.	PP	M_PL_Ollerton2003	Ollerton et al. (2003)	Yes
371.	PP	M_PL_Orford_2016_Farm-2012-A9	Orford et al. (2016)	

Table continued . . .

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#	Type	Network name	Reference	Weighted
372.	PP	M_PL_Orford_2016_Farm-2012-B1	Orford et al. (2016)	
373.	PP	M_PL_Orford_2016_Farm-2012-B2	Orford et al. (2016)	
374.	PP	M_PL_Orford_2016_Farm-2012-B4	Orford et al. (2016)	
375.	PP	M_PL_Orford_2016_Farm-2012-B5	Orford et al. (2016)	
376.	PP	M_PL_Orford_2016_Farm-2012-B6	Orford et al. (2016)	
377.	PP	M_PL_Orford_2016_Farm-2012-B7	Orford et al. (2016)	
378.	PP	M_PL_Orford_2016_Farm-2012-B8	Orford et al. (2016)	
379.	PP	M_PL_Orford_2016_Farm-2012-B9	Orford et al. (2016)	
380.	PP	M_PL_Orford_2016_Farm-2013-B1	Orford et al. (2016)	
381.	PP	M_PL_Orford_2016_Farm-2013-B2	Orford et al. (2016)	
382.	PP	M_PL_Orford_2016_Farm-2013-B4	Orford et al. (2016)	
383.	PP	M_PL_Orford_2016_Farm-2013-B7	Orford et al. (2016)	
384.	PP	M_PL_Orford_2016_Field-10	Orford et al. (2016)	
385.	PP	M_PL_Orford_2016_Field-13	Orford et al. (2016)	
386.	PP	M_PL_Orford_2016_Field-15	Orford et al. (2016)	
387.	PP	M_PL_Orford_2016_Field-19	Orford et al. (2016)	
388.	PP	M_PL_Orford_2016_Field-24	Orford et al. (2016)	
389.	PP	M_PL_Orford_2016_Field-27	Orford et al. (2016)	
390.	PP	M_PL_Orford_2016_Field-28	Orford et al. (2016)	
391.	PP	M_PL_Orford_2016_Field-33	Orford et al. (2016)	
392.	PP	M_PL_Orford_2016_Field-36	Orford et al. (2016)	
393.	PP	M_PL_Orford_2016_Field-4	Orford et al. (2016)	
394.	PP	M_PL_Orford_2016_Field-40	Orford et al. (2016)	
395.	PP	M_PL_Orford_2016_Field-42	Orford et al. (2016)	
396.	PP	M_PL_Orford_2016_Field-45	Orford et al. (2016)	

...Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
397.	PP	M_PL_Orford_2016_Field-49	Orford et al. (2016)	
398.	PP	M_PL_Orford_2016_Field-51	Orford et al. (2016)	
399.	PP	M_PL_Orford_2016_Field-54	Orford et al. (2016)	
400.	PP	M_PL_Orford_2016_Field-55	Orford et al. (2016)	
401.	PP	M_PL_Orford_2016_Field-58	Orford et al. (2016)	
402.	PP	M_PL_Orford_2016_Field-63	Orford et al. (2016)	
403.	PP	M_PL_Orford_2016_Field-64	Orford et al. (2016)	
404.	PP	M_PL_Orford_2016_Field-67	Orford et al. (2016)	
405.	PP	M_PL_Orford_2016_Field-7	Orford et al. (2016)	
406.	PP	M_PL_Orford_2016_Field-72	Orford et al. (2016)	
407.	PP	M_PL_Orford_2016_Field-9	Orford et al. (2016)	
408.	PP	M_PL_Percival1974	Percival (1974)	
409.	PP	M_PL_Philipp2006	Philipp et al. (2006)	
410.	PP	M_PL_Primack1983-1	Primack (1983)	
411.	PP	M_PL_Primack1983-2	Primack (1983)	
412.	PP	M_PL_Primack1983-3	Primack (1983)	
413.	PP	M_PL_Ramirez1989	Ramirez (1989)	
414.	PP	M_PL_Ramirez1992	Ramirez and Brito (1992)	
415.	PP	M_PL_Sabatino_1	Sabatino et al. (2010)	
416.	PP	M_PL_Sabatino_2	Sabatino et al. (2010)	
417.	PP	M_PL_Sabatino_3	Sabatino et al. (2010)	
418.	PP	M_PL_Sabatino_4	Sabatino et al. (2010)	
419.	PP	M_PL_Sabatino_5	Sabatino et al. (2010)	
420.	PP	M_PL_Santos2010	de Mendonça Santos et al. (2010)	
421.	PP	M_PL_Schemske1978	Schemske et al. (1978)	

Table continued ...

... Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
422.	PP	M_PL_Small1976	Small (1976)	Yes
423.	PP	M_PL_Smith-Ramirez2005	Smith-Ramírez et al. (2005)	
424.	PP	M_PL_Sritongchuay_bat	Sritongchuay et al. (2019)	
425.	PP	M_PL_Llaviuco_Tinoco	Tinoco et al. (2017)	Yes
426.	PP	M_PL_Nero_Tinoco	Tinoco et al. (2017)	Yes
427.	PP	M_PL_Trojelsgaard_2015_Site1_WesternSahara1	Trøjelsgaard et al. (2015)	Yes
428.	PP	M_PL_Trojelsgaard_2015_Site10_TenerifeTeno2	Trøjelsgaard et al. (2015)	Yes
429.	PP	M_PL_Trojelsgaard_2015_Site11_Gomera1	Trøjelsgaard et al. (2015)	Yes
430.	PP	M_PL_Trojelsgaard_2015_Site12_Gomera2	Trøjelsgaard et al. (2015)	Yes
431.	PP	M_PL_Trojelsgaard_2015_Site13_Hierro1	Trøjelsgaard et al. (2015)	Yes
432.	PP	M_PL_Trojelsgaard_2015_Site14_Hierro2	Trøjelsgaard et al. (2015)	Yes
433.	PP	M_PL_Trojelsgaard_2015_Site2_WesternSahara2	Trøjelsgaard et al. (2015)	Yes
434.	PP	M_PL_Trojelsgaard_2015_Site3_Fuerteventura1	Trøjelsgaard et al. (2015)	Yes
435.	PP	M_PL_Trojelsgaard_2015_Site4_Fuerteventura2	Trøjelsgaard et al. (2015)	Yes
436.	PP	M_PL_Trojelsgaard_2015_Site5_GranCanaria1	Trøjelsgaard et al. (2015)	Yes
437.	PP	M_PL_Trojelsgaard_2015_Site6_GranCanaria2	Trøjelsgaard et al. (2015)	Yes
438.	PP	M_PL_Trojelsgaard_2015_Site7_TenerifeSouth1	Trøjelsgaard et al. (2015)	Yes
439.	PP	M_PL_Trojelsgaard_2015_Site8_TenerifeSouth2	Trøjelsgaard et al. (2015)	Yes
440.	PP	M_PL_Trojelsgaard_2015_Site9_TenerifeTeno1	Trøjelsgaard et al. (2015)	Yes
441.	PP	M_PL_Tur2013-CN	Tur et al. (2013)	
442.	PP	M_PL_Tur2013-PC	Tur et al. (2013)	
443.	PP	M_PL_Vazquez	Vázquez (2002); Vázquez and Simberloff (2002, 2003)	Yes
444.	PP	M_PL_Vizentin	Vizentin-Bugoni et al. (2016)	Yes
445.	PP	M_PL_Weiner2011	Weiner et al. (2011)	Yes
446.	PP	M_PL_Yamazaki2003	Yamazaki and Kato (2003)	

Table continued ...

... Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
447.	SD	M_SD_Aguiar_2007	Aguiar and Marinho-Filho (2007)	Yes
448.	SD	M_SD_Aguilar-Garavito_2014_mature	Aguilar-Garavito et al. (2014)	Yes
449.	SD	M_SD_Albrecht_102_2012	Albrecht et al. (2015)	Yes
450.	SD	M_SD_Albrecht_11_2012	Albrecht et al. (2015)	Yes
451.	SD	M_SD_Albrecht_111_2011	Albrecht et al. (2015)	Yes
452.	SD	M_SD_Albrecht_111_2012	Albrecht et al. (2015)	Yes
453.	SD	M_SD_Albrecht_112_2011	Albrecht et al. (2015)	Yes
454.	SD	M_SD_Albrecht_112_2012	Albrecht et al. (2015)	Yes
455.	SD	M_SD_Albrecht_13_2012	Albrecht et al. (2015)	Yes
456.	SD	M_SD_Albrecht_15_2012	Albrecht et al. (2015)	Yes
457.	SD	M_SD_Albrecht_203_2012	Albrecht et al. (2015)	Yes
458.	SD	M_SD_Albrecht_30_2012	Albrecht et al. (2015)	Yes
459.	SD	M_SD_Albrecht_301_2012	Albrecht et al. (2015)	Yes
460.	SD	M_SD_Albrecht_314_2012	Albrecht et al. (2015)	Yes
461.	SD	M_SD_Albrecht_315_2011	Albrecht et al. (2015)	Yes
462.	SD	M_SD_Albrecht_315_2012	Albrecht et al. (2015)	Yes
463.	SD	M_SD_Albrecht_35_2012	Albrecht et al. (2015)	Yes
464.	SD	M_SD_Albrecht_36_2012	Albrecht et al. (2015)	Yes
465.	SD	M_SD_Andrade_2011	Andrade et al. (2011)	Yes
466.	SD	M_SD_Arias-Arone_2016	Arias Arone (2016)	Yes
467.	SD	M_SD_Athie_2009	Athié (2009)	Yes
468.	SD	M_SD_Baird1980	Baird (1980)	Yes
469.	SD	M_SD_Balasubramanian_1996	Balasubramanian (1996)	
470.	SD	M_SD_Bastazini_2018	Bastazini et al. (2019)	
471.	SD	M_SD_Beehler1983	Beehler (1983)	Yes

Table continued ...

#	Type	Network name	Reference	Weighted
472.	SD	M_SD_Blake_1992	Blake and Loiselle (1992)	Yes
473.	SD	M_SD_Bleher_2003	Bleher et al. (2003)	
474.	SD	M_SD_Blendinger_2015	Blendinger et al. (2015)	Yes
475.	SD	M_SD_Bollen_2000	Bollen (2003)	
476.	SD	M_SD_Brito_2010	Brito et al. (2010)	Yes
477.	SD	M_SD_Burns_2013	Burns (2013)	Yes
478.	SD	M_SD_Camargo_2009	Calonge Camargo (2009)	
479.	SD	M_SD_Carlo2003-1	Carlo et al. (2003)	Yes
480.	SD	M_SD_Carlo2003-2	Carlo et al. (2003)	Yes
481.	SD	M_SD_Carlo2003-3	Carlo et al. (2003)	Yes
482.	SD	M_SD_Carlo2003-4	Carlo et al. (2003)	Yes
483.	SD	M_SD_Carvalho_2008	Carvalho (2008)	Yes
484.	SD	M_SD_Casallas-Pabon_2017	Casallas-Pabón et al. (2017)	
485.	SD	M_SD_Castano_2009	Castaño (2009)	
486.	SD	M_SD_Castano_2018	Castaño et al. (2018)	Yes
487.	SD	M_SD_Castley_2001	Castley et al. (2001)	Yes
488.	SD	M_SD_Castro-Luna_2012	Castro-Luna and Galindo-González (2012)	Yes
489.	SD	M_SD_Castro_2015	Castro (2007)	Yes
490.	SD	M_SD_Chama_2013_net1	Chama et al. (2013)	
491.	SD	M_SD_Chama_2013_net2	Chama et al. (2013)	
492.	SD	M_SD_Chama_2013_net3	Chama et al. (2013)	
493.	SD	M_SD_Chama_2013_net4	Chama et al. (2013)	
494.	SD	M_SD_Chama_2013_net5	Chama et al. (2013)	
495.	SD	M_SD_Chama_2013_net6	Chama et al. (2013)	
496.	SD	M_SD_Chama_2013_net7	Chama et al. (2013)	

... Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
497.	SD	M_SD_Chama_2013_net8	Chama et al. (2013)	
498.	SD	M_SD_Chama_2013_net9	Chama et al. (2013)	
499.	SD	M_SD_Chapman_1996	Chapman and Chapman (1996)	
500.	SD	M_SD_Chatterjee_2014	Chatterjee and Basu (2015)	
501.	SD	M_SD_Chaves_2018_forest_edge	Chaves (2018)	
502.	SD	M_SD_Chaves_2018_mature_forest	Chaves (2018)	
503.	SD	M_SD_Chen_1999	Chen and Chou (1999)	Yes
504.	SD	M_SD_Chimera_2010	Chimera and Drake (2010)	Yes
505.	SD	M_SD_Combined_Schleuning	Schleuning et al. (2011)	Yes
506.	SD	M_SD_continuous_Farwig	Farwig et al. (2017)	Yes
507.	SD	M_SD_Correa_2016_Apaporis	Correa et al. (2016)	Yes
508.	SD	M_SD_Correa_2016_Caqueta	Correa et al. (2016)	Yes
509.	SD	M_SD_Correia_2016_non-sanctuary	Correia et al. (2017)	
510.	SD	M_SD_Correia_2016_sanctuary	Correia et al. (2017)	
511.	SD	M_SD_Costa_2013_endozoochory	Costa et al. (2014)	Yes
512.	SD	M_SD_Costa_2016	Costa et al. (2016)	
513.	SD	M_SD_Costa_2018_before_only	Costa et al. (2018)	
514.	SD	M_SD_Crome1975	Crome (1975)	
515.	SD	M_SD_Cruz_2013_Autumn	Cruz et al. (2013)	Yes
516.	SD	M_SD_Cruz_2013_Summer	Cruz et al. (2013)	Yes
517.	SD	M_SD_Cruz_2013_Winter	Cruz et al. (2013)	Yes
518.	SD	M_SD_da_Silva_2015_site_A	Ribeiro da Silva et al. (2015)	
519.	SD	M_SD_da_Silva_2015_site_B	Ribeiro da Silva et al. (2015)	
520.	SD	M_SD_da_Silva_2015_site_C	Ribeiro da Silva et al. (2015)	
521.	SD	M_SD_Daru_2015	Daru et al. (2015)	Yes

Table continued ...

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... Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
522.	SD	M_SD_David_2011_tree_focal_watches	David et al. (2011)	Yes
523.	SD	M_SD_de_la_Pena_2003	de la Peña and Pensiero (2003)	
524.	SD	M_SD_de_Oliveira_1999	de Oliveira (1999)	Yes
525.	SD	M_SD_Debussche_1989	Debussche and Isenmann (1989)	
526.	SD	M_SD_Dehling_2017_San_Pedro_1	Dehling et al. (2014)	Yes
527.	SD	M_SD_Dehling_2017_San_Pedro_2	Dehling et al. (2014)	Yes
528.	SD	M_SD_Dehling_2017_San_Pedro_3	Dehling et al. (2014)	Yes
529.	SD	M_SD_Dehling_2017_San_Pedro_4	Dehling et al. (2014)	Yes
530.	SD	M_SD_Dehling_2017_Wayqecha_1	Dehling et al. (2014)	Yes
531.	SD	M_SD_Dehling_2017_Wayqecha_2	Dehling et al. (2014)	Yes
532.	SD	M_SD_Dehling_2017_Wayqecha_3	Dehling et al. (2014)	Yes
533.	SD	M_SD_Dehling_2017_Wayqecha_4	Dehling et al. (2014)	Yes
534.	SD	M_SD_Donatti_2011	Donatti et al. (2011)	
535.	SD	M_SD_Dos_Reis_1983_Cult_et_form_sec	Dos Reis and Guillaumet (1983)	Yes
536.	SD	M_SD_Dowsett-Lemaire_1988	Dowsett-Lemaire (1988)	
537.	SD	M_SD_Dubost_1984	Dubost (1984)	
538.	SD	M_SD_Dupont_1997	Dupont et al. (1997)	
539.	SD	M_SD_Engel_2000	Engel (2000)	Yes
540.	SD	M_SD_Estrada-Villegas_2010	Estrada-Villega et al. (2010)	
541.	SD	M_SD_Fadini_2004	Fadini and De Marco Jr. (2004)	Yes
542.	SD	M_SD_Falcon_2018	Falcón (2018)	
543.	SD	M_SD_Faria_1996	Faria (1996)	Yes
544.	SD	M_SD_Faustino_2006	Faustino and Machado (2006)	Yes
545.	SD	M_SD_Fleming_1977	Fleming et al. (1977)	Yes
546.	SD	M_SD_Fonseca_2007	Fonseca and Antunes (2007)	

Table continued ...

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#	Type	Network name	Reference	Weighted
547.	SD	M_SD_Fontanari_2018	Fontanari (2018)	
548.	SD	M_SD_fragmented_Farwig	Farwig et al. (2017)	Yes
549.	SD	M_SD_Fricke_2018_Saipan	Fricke et al. (2018)	Yes
550.	SD	M_SD_Frost1980	Frost (1980)	Yes
551.	SD	M_SD_Fuentes_1994	Fuentes (1994)	Yes
552.	SD	M_SD_Galetti1996-1	Galetti and Pizo (1996)	Yes
553.	SD	M_SD_Galetti1996-2	Galetti and Pizo (1996)	Yes
554.	SD	M_SD_Garcia-Estrada_2012	García-Estrada et al. (2012)	Yes
555.	SD	M_SD_Garcia-Morales_2012	Morales et al. (2012)	Yes
556.	SD	M_SD_Garcia_2014_Blue_Duck	García et al. (2014)	Yes
557.	SD	M_SD_Garcia_2014_Charles_Plimmer	García et al. (2014)	Yes
558.	SD	M_SD_Garcia_2014_George_Denton	García et al. (2014)	Yes
559.	SD	M_SD_Garcia_2014_Mount_Fyfee_Reserve	García et al. (2014)	Yes
560.	SD	M_SD_Garcia_2014_Puhi-Puhi_River	García et al. (2014)	Yes
561.	SD	M_SD_Garcia_2014_Zealandia	García et al. (2014)	Yes
562.	SD	M_SD_Garcia_2016	García (2016)	Yes
563.	SD	M_SD_Garcia_et_al	Garcia et al. (2000)	Yes
564.	SD	M_SD_Genrich_2017	Genrich et al. (2017)	Yes
565.	SD	M_SD_Githiru_2002	Githiru et al. (2002)	
566.	SD	M_SD_Gomes_2013	Gomes (2013)	Yes
567.	SD	M_SD_Gorchov_1995	Gorchov et al. (1995)	Yes
568.	SD	M_SD_Hamann1999	Hamann and Curio (1999)	
569.	SD	M_SD_Hasui_1998	Hasui and Höfling (1998)	
570.	SD	M_SD_Hayashi_1996	Hayashi (1996)	Yes
571.	SD	M_SD_Heleno	Heleno et al. (2013)	Yes

... Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
572.	SD	M_SD_Hernandez-Montero_2015_B4_Dry	Hernández-Montero et al. (2015)	Yes
573.	SD	M_SD_Hernandez-Montero_2015_B4_Norte	Hernández-Montero et al. (2015)	Yes
574.	SD	M_SD_Hladik_1969	Hladik and Hladik (1969)	
575.	SD	M_SD_Hodgkison_2001	Hodgkison (2001)	
576.	SD	M_SD_Hovestadt_1997	Hovestadt (1997)	Yes
577.	SD	M_SD_Innis_1989_ANVF	Innis (1989)	
578.	SD	M_SD_Innis_1989_NVF_CNVF	Innis (1989)	
579.	SD	M_SD_Jaroszewicz_2013	Jaroszewicz et al. (2013)	Yes
580.	SD	M_SD_Jayasekara_2003	Jayasekara et al. (2003)	Yes
581.	SD	M_SD_Jayasekara_2007	Jayasekara et al. (2007)	Yes
582.	SD	M_SD_Jordano-1	Rezende et al. (2007)	Yes
583.	SD	M_SD_Junior_2010	Alves Junior (2010)	
584.	SD	M_SD_Kalko_BCI_zero_intx_removed	Giannini and Kalko (2004)	
585.	SD	M_SD_Kamruzzaman_2008	Kamruzzaman (2008)	Yes
586.	SD	M_SD_Kantak1979	Kantak (1979)	
587.	SD	M_SD_Kessler-Rios_2012	Kessler-Rios and Kattan (2012)	Yes
588.	SD	M_SD_KITA_mammals_added	Kitamura et al. (2005)	
589.	SD	M_SD_Kitamura_2002	Kitamura et al. (2002)	
590.	SD	M_SD_Koike_2008	Koike et al. (2008)	Yes
591.	SD	M_SD_Kone_2008	Koné et al. (2008)	
592.	SD	M_SD_Labbe_2011	Labbe (2011)	Yes
593.	SD	M_SD_Lambert1989	Lambert (1989)	
594.	SD	M_SD_Lefevre_2008	Lefevre (2008)	
595.	SD	M_SD_Lessa_2010	Lessa and da Costa (2010)	Yes
596.	SD	M_SD_Lessa_2013	Lessa et al. (2013)	Yes

Table continued ...

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... Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
597.	SD	M_SD_Lima_2016	Lima et al. (2016)	Yes
598.	SD	M_SD_Llewellyn_1952	Llewellyn and Uhler (1952)	
599.	SD	M_SD_Loayza_2006	Loayza et al. (2006)	
600.	SD	M_SD_Lopez_&_Vaughn_2004	Lopez and Vaughan (2004)	Yes
601.	SD	M_SD_Lou_2005	Lou and Yurrita (2005)	Yes
602.	SD	M_SD_Lou_2007	Lou (2007)	Yes
603.	SD	M_SD_MacFarlane_2016	Macfarlane et al. (2016)	Yes
604.	SD	M_SD_Machado-de-Souza_2019	Machado-de Souza et al. (2019)	Yes
605.	SD	M_SD_Mack1996	Mack and Wright (1996)	
606.	SD	M_SD_Malacco_da_Silva_2014	da Silva and Fernando (2014)	Yes
607.	SD	M_SD_Malmborg_1988_1980	Malmborg and Willson (1988)	Yes
608.	SD	M_SD_Malmborg_1988_1981	Malmborg and Willson (1988)	Yes
609.	SD	M_SD_Malmborg_1988_1982	Malmborg and Willson (1988)	Yes
610.	SD	M_SD_Mancina_2007_dry	Mancina et al. (2007)	Yes
611.	SD	M_SD_Marcos_da_Silva_2013	Silva (2008)	Yes
612.	SD	M_SD_Mello_2014_Mata_de_Grota	Mello et al. (2014)	Yes
613.	SD	M_SD_Menke_2012_edge_highly_dist	Menke et al. (2012)	Yes
614.	SD	M_SD_Menke_2012_edge_little_dist	Menke et al. (2012)	Yes
615.	SD	M_SD_Menke_2012_interior_highly_dist	Menke et al. (2012)	Yes
616.	SD	M_SD_Menke_2012_interior_little_dist	Menke et al. (2012)	Yes
617.	SD	M_SD_Milton_2001	Milton and Dean (2001)	
618.	SD	M_SD_Montalvan_2015	Montalván and Giannina (2015)	
619.	SD	M_SD_Moreno-Mosquera_2011	Moreno (2011)	
620.	SD	M_SD_Munin_2012	Munin et al. (2012)	Yes
621.	SD	M_SD_Munster_2008	Munster (2008)	Yes

Table continued ...

... Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
622.	SD	M_SD_Nogales_2017	Passos et al. (2003)	Yes
623.	SD	M_SD_Noma_1997	Noma and Yumoto (1997)	Yes
624.	SD	M_SD_Novoa_2011	Novoa et al. (2011)	Yes
625.	SD	M_SD_Odonnell_1994	O'Donnell and Dilks (1994)	Yes
626.	SD	M_SD_Olesen_2018	Olesen et al. (2018)	
627.	SD	M_SD_Ortiz-Pulido_2000	Ortiz-Pulido et al. (2000)	
628.	SD	M_SD_Palacios_2016	Palacio et al. (2016)	
629.	SD	M_SD_Palita_2011	Palita et al. (2011)	Yes
630.	SD	M_SD_Passos_2003	Passos et al. (2003)	Yes
631.	SD	M_SD_Pedro_1992	Pedro (1992)	Yes
632.	SD	M_SD_Peredo_2013_Pto_de_San_Lorenzo	Peredo et al. (2013)	Yes
633.	SD	M_SD_Peredo_2013_Puertos_de_Marabio	Peredo et al. (2013)	Yes
634.	SD	M_SD_Perez-Torres_2004	Préz-Torres (2004)	
635.	SD	M_SD_Plein_2013_Farmland_autumn	Plein et al. (2013)	
636.	SD	M_SD_Plein_2013_Farmland_summer	Plein et al. (2013)	
637.	SD	M_SD_Plein_2013_Forest_autumn	Plein et al. (2013)	
638.	SD	M_SD_Plein_2013_Orchard_autumn	Plein et al. (2013)	
639.	SD	M_SD_Plein_2013_Orchard_summer	Plein et al. (2013)	
640.	SD	M_SD_Poulin1999_psychotria	Poulin et al. (1999)	Yes
641.	SD	M_SD_Poulsen_2001_2002_primates	Poulsen et al. (2001)	
642.	SD	M_SD_Prather_2000	Prather et al. (2000)	
643.	SD	M_SD_Pratt_1985	Pratt and Stiles (1985)	Yes
644.	SD	M_SD_Preciado-Benítez_2015	Preciado-Benítez et al. (2015)	Yes
645.	SD	M_SD_Purificacao_2014_forest_dry	Purificação et al. (2014)	
646.	SD	M_SD_Purificacao_2014_savannah_dry	Purificação et al. (2014)	

Table continued ...

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... Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
647.	SD	M_SD_Purificacao_2014_savannah_rainy	Purificação et al. (2014)	
648.	SD	M_SD_Quijano-Vasquez_2017	Quijano-Vasquez (2017)	
649.	SD	M_SD_Quitián_2018_1000Fragmented	Quitián et al. (2019)	Yes
650.	SD	M_SD_Quitián_2018_1000Natural	Quitián et al. (2019)	Yes
651.	SD	M_SD_Quitián_2018_2000Fragmented	Quitián et al. (2019)	Yes
652.	SD	M_SD_Quitián_2018_2000Natural	Quitián et al. (2019)	Yes
653.	SD	M_SD_Ramaswami_2017	Ramaswami et al. (2017)	
654.	SD	M_SD_Ramos-Robles_2016_net10	Ramos-Robles et al. (2016)	Yes
655.	SD	M_SD_Ramos-Robles_2016_net2	Ramos-Robles et al. (2016)	Yes
656.	SD	M_SD_Ramos-Robles_2016_net3	Ramos-Robles et al. (2016)	Yes
657.	SD	M_SD_Ramos-Robles_2016_net4	Ramos-Robles et al. (2016)	Yes
658.	SD	M_SD_Ramos-Robles_2016_net6	Ramos-Robles et al. (2016)	Yes
659.	SD	M_SD_Ramos-Robles_2016_net7	Ramos-Robles et al. (2016)	Yes
660.	SD	M_SD_Ramos-Robles_2016_net8	Ramos-Robles et al. (2016)	Yes
661.	SD	M_SD_Ramos-Robles_2018	Ramos-Robles et al. (2018)	
662.	SD	M_SD_Reid_2011	Reid and Armesto (2011)	
663.	SD	M_SD_Robinson_2015	Robinson (2015)	Yes
664.	SD	M_SD_Rosalino_2010	Rosalino et al. (2010)	
665.	SD	M_SD_Rozzi_1996	Rozzi et al. (1996)	
666.	SD	M_SD_Ruggera_2016_A	Ruggera et al. (2016)	
667.	SD	M_SD_Ruggera_2016_Chorro_de_Loros	Ruggera et al. (2016)	
668.	SD	M_SD_Ruggera_2016_EcoPortal	Ruggera et al. (2016)	
669.	SD	M_SD_Ruggera_2016_El_Noglar	Ruggera et al. (2016)	
670.	SD	M_SD_Ruggera_2016_La_Florida	Ruggera et al. (2016)	
671.	SD	M_SD_Ruggera_2016_Los_Chorizos	Ruggera et al. (2016)	

Table continued ...

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#	Type	Network name	Reference	Weighted
672.	SD	M_SD_Ruggera_2016_Pozo_Verde	Ruggera et al. (2016)	
673.	SD	M_SD_Ruggera_2016_Quebrada_del_Port	Ruggera et al. (2016)	
674.	SD	M_SD_Ruggera_2016_San_Javier	Ruggera et al. (2016)	
675.	SD	M_SD_Ruggera_2016_Sevenguillar	Ruggera et al. (2016)	
676.	SD	M_SD_SAAV1	Saavedra et al. (2014)	Yes
677.	SD	M_SD_SAAV2	Saavedra et al. (2014)	Yes
678.	SD	M_SD_Sanchez_2012_Iguazu	Sánchez et al. (2012)	Yes
679.	SD	M_SD_Sanitjan_2009_ML_primary_forest	Sanitjan and Chen (2009)	
680.	SD	M_SD_Sanitjan_2009_XTBG_arboretum	Sanitjan and Chen (2009)	
681.	SD	M_SD_Sankamethawee_2011	Sankamethawee et al. (2011)	
682.	SD	M_SD_Santiago_2014_close_to_remnant	Del Valle (2014)	Yes
683.	SD	M_SD_Santiago_2014_far_from_remnant	Del Valle (2014)	Yes
684.	SD	M_SD_SARM_whole_network_from_paper	Sarmento et al. (2014)	Yes
685.	SD	M_SD_Scherer_2007	Scherer et al. (2007)	
686.	SD	M_SD_Sethi_2012	Sethi and Howe (2012)	Yes
687.	SD	M_SD_Silva_Oliveira_2018	Oliveira (2018)	Yes
688.	SD	M_SD_Silveira_2006	Silveira (2006)	Yes
689.	SD	M_SD_Skeate_1985	Skeate (1985)	
690.	SD	M_SD_Skutch_1980	Skutch (1980)	
691.	SD	M_SD_Snow_1988_DJF	Snow and Snow (1988)	Yes
692.	SD	M_SD_Snow_1988_JJA	Snow and Snow (1988)	Yes
693.	SD	M_SD_Snow_1988_MAM	Snow and Snow (1988)	Yes
694.	SD	M_SD_Snow_1988_SON	Snow and Snow (1988)	Yes
695.	SD	M_SD_Sorensen_1981	Sorensen (1981)	Yes
696.	SD	M_SD_Souza_Gomes_2008_primary_forest	Gomes (2008)	

... Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
697.	SD	M_SD_Souza_ Gomes_2008_secondary_fore	Gomes (2008)	
698.	SD	M_SD_Souza_Laurindo_2017	de Souza Laurindo et al. (2017)	Yes
699.	SD	M_SD_Suarez-Castro_2015	Suárez-Castro and Montenegro (2015)	
700.	SD	M_SD_Suzuki_2007	Suzuki et al. (2007)	Yes
701.	SD	M_SD_Tavares_2007	Tavares et al. (2007)	Yes
702.	SD	M_SD_Toledo_2018	Toledo (2018)	
703.	SD	M_SD_Traveset_1992	Traveset (1992)	Yes
704.	SD	M_SD_Tutin1997	Tutin et al. (1997)	
705.	SD	M_SD_Velazquez_2010	Moreno Velázquez (2010)	
706.	SD	M_SD_VELHO	Velho et al. (2012)	Yes
707.	SD	M_SD_VELHO2	Velho et al. (2012)	Yes
708.	SD	M_SD_Vizentin-Bugoni_2019_EKA	Vizentin-Bugoni et al. (2019)	
709.	SD	M_SD_Vizentin-Bugoni_2019_KAH	Vizentin-Bugoni et al. (2019)	
710.	SD	M_SD_Vizentin-Bugoni_2019_MOA	Vizentin-Bugoni et al. (2019)	
711.	SD	M_SD_Vizentin-Bugoni_2019_MTK	Vizentin-Bugoni et al. (2019)	
712.	SD	M_SD_Vizentin-Bugoni_2019_PAH	Vizentin-Bugoni et al. (2019)	
713.	SD	M_SD_Vizentin-Bugoni_2019_TAN	Vizentin-Bugoni et al. (2019)	
714.	SD	M_SD_Vizentin-Bugoni_2019_WAI	Vizentin-Bugoni et al. (2019)	
715.	SD	M_SD_Walther_2018	Walther et al. (2018)	
716.	SD	M_SD_Williams_1996_Eves	Williams and Karl (1996)	Yes
717.	SD	M_SD_Williams_1996_Marsden	Williams and Karl (1996)	Yes
718.	SD	M_SD_Wilms_2006	Wilms and Kappelle (2006)	
719.	SD	M_SD_Wolfe_2014	Wolfe et al. (2014)	Yes
720.	SD	M_SD_Wyman_2017	Wyman and Kelly (2017)	Yes
721.	SD	M_SD_Young_2012	Young (2012)	

Table continued ...

...Continuation of Table S3.7.

#	Type	Network name	Reference	Weighted
722.	SD	M_SD_Zamora-Delgado_2008	Zamora Delgado (2008)	Yes
723.	SD	M_SD_Zapata-Mesa_2017_MR_September	Zapata-Mesa et al. (2017)	Yes

Chapter 4

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

4.1 Abstract

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

4.2 Introduction

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

Luna et al. (2022) added to this discussion by assessing how current and historical environmental factors structure specialization 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 specialization—niche overlap, linkage density and mean normalized degree. They found significant relationships with these specialization metrics and thus concluded that the environment—in particular climate and resource availability—explained global variation in trophic specialization.

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 (Hemprich-Bennett et al., 2021; Bodner et al., 2022). 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 and Allesina, 2019). Indeed, controlling for this potential bias in open networks can influence results as Morris et al. (2014) found no relationships 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 specialization metrics and network size are independent.

4.3   Analyses

We tested how network size (i.e., the product of the number of rows and columns) influenced the specialization 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 specialization 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 specialization with network size and found for each a strong and statistically significant correlation, i.e., all had an absolute correlation between 0.71 and 0.79 (Figure 4.1). The relationships between sampling intensity and specialization metrics were also quite strong (S4.8 Appendix: Figure S4.1).

Next, we tested linear mixed models for each specialization 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 4.1). 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 specialization metrics—niche overlap and linkage density. For mean normalized 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 (S4.8 Appendix: Table S4.1). Hence, we found that both network size and sampling intensity were the strongest individual contributors for explaining the variation across the specialization metrics.

4.4 Conclusion

Environmental factors are correlated with the specialization metrics of niche overlap, linkage density and mean normalized 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 specialization metrics. Our results provide a more parsimonious alternative to explain the variation in specialization metrics and question the conclusion of Luna et al. (2022) that the environment determines specialization in plant-pollinator communities.

4.5 Data and code availability

All data and code to reproduce our results are available at: `www.osf.io/q23vz/`.

4.6 Figure
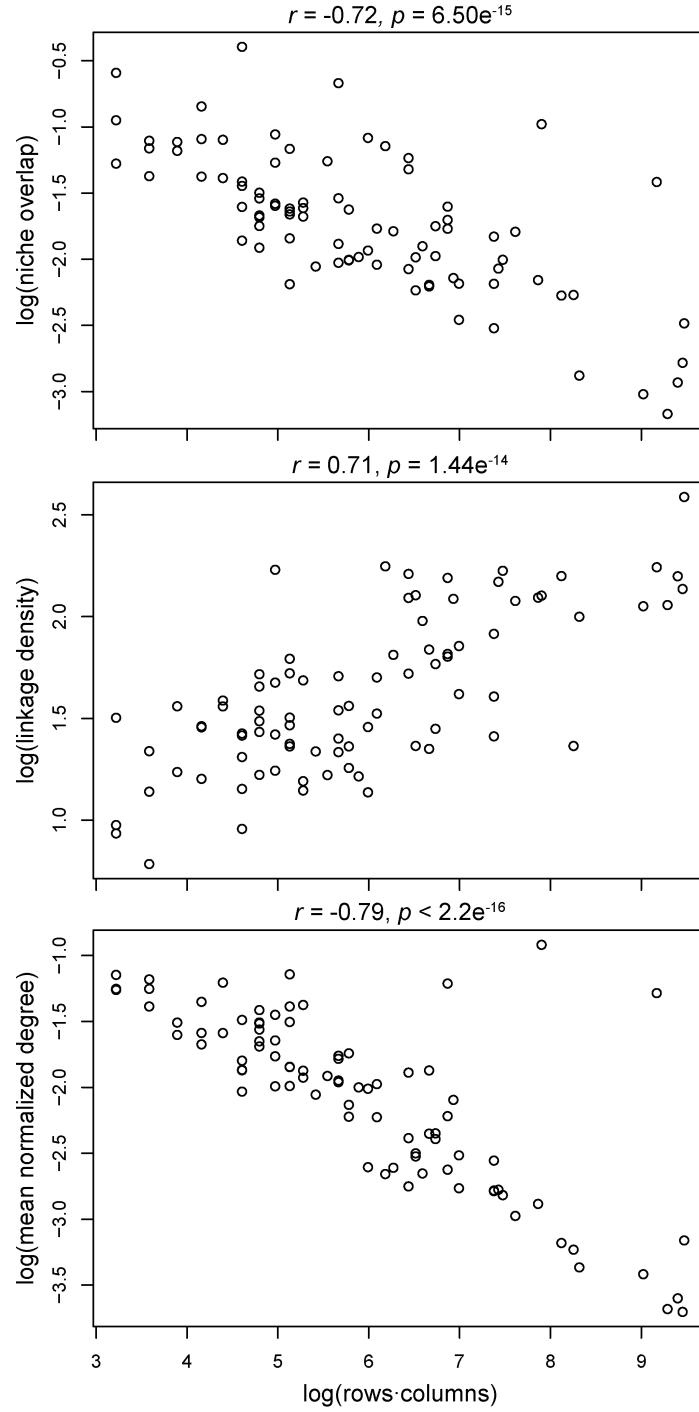
Figure 4.1. Pearson correlation (r) between network size (defined by the product of the number of plant and pollinator species; i.e., rows·columns) and the three specialization metrics of niche overlap, linkage density, and mean normalized degree for 87 plant-pollinator networks.

4.7 Table

Table 4.1. Linear mixed models (LMMs) for the three specialization metrics of niche overlap, mean normalized 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 specialization metric. The amount of variation explained by the fixed effects is represented by R^2_{marg}, and the amount explained by both the fixed and random effects is represented by R^2_{cond}. The random effect used in all models is network location.

Metric	Description	Fixed effects variables	R^2_{marg}	R^2_{cond}
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 normalized 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

S4.8 Appendix

S4.8.1 Supplementary figure
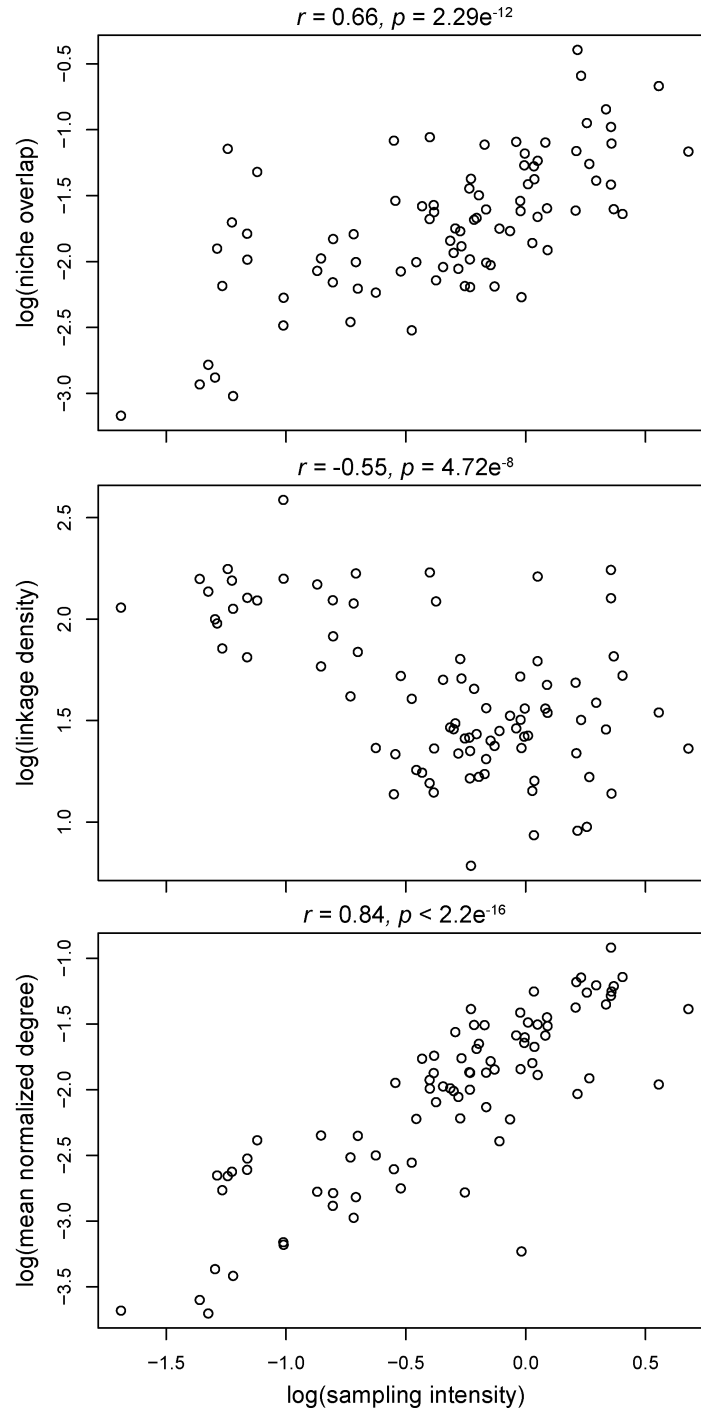
Figure S4.1. Pearson correlation (r) between sampling intensity and the three specialization metrics of niche overlap, linkage density, and mean normalized degree for 87 plant-pollinator networks.

S4.8.2   Supplementary table

Table S4.1. Linear mixed models (LMMs) for the three specialization metrics of niche overlap, mean normalized degree, and linkage density with log transformed sampling intensity, 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 specialization metric. The amount of variation explained by the fixed effects is represented by R^2_{marg}, and the amount explained by both the fixed and random effects is represented by R^2_{cond}. The random effect used in all models is network location.

Metric	Description	Fixed effects variables	R^2_{marg}	R^2_{cond}
Niche overlap	Only sampling intensity	Sampling intensity	0.321	0.487
	Luna et al. (2022) best model	*NPP, mean annual temp., mean annual precip., historical temp. stability, elevation*	0.133	0.465
	Sampling intensity +*Luna et al. (2022) best model*	Sampling intensity, *NPP, mean annual temp., mean annual precip., historical temp. stability, elevation*	0.322	0.509
Mean normalized degree	Only sampling intensity	Sampling intensity	0.581	0.871
	Luna et al. (2022) best model	*NPP, mean annual precip., historical temp. stability, historical precip. stability, elevation*	0.467	0.749
	Sampling intensity +*Luna et al. (2022) best model*	Sampling intensity, *NPP, mean annual precip., historical temp. stability, historical precip. stability, elevation*	0.686	0.874
Linkage density	Only sampling intensity	Sampling intensity	0.255	0.519
	Luna et al. (2022) best model	*NPP, mean annual temp., mean annual precip., historical precip. stability, elevation*	0.285	0.801
	Sampling intensity +*Luna et al. (2022) best model*	Sampling intensity, *NPP, mean annual temp., mean annual precip., historical precip. stability, elevation*	0.355	0.735

Chapter 5

Shortcomings of reusing species interaction networks created by different sets of researchers

5.1 Abstract

Given the requisite cost associated with observing species interactions, ecologists often reuse species interaction networks created by different sets of researchers to test their hypotheses regarding how ecological processes drive network topology. Yet, topological properties identified across these networks may not be sufficiently attributable to ecological processes alone as often assumed. Instead, much of the totality of topological differences between networks—topological heterogeneity—could be due to variations in research designs and approaches that different researchers use to create each species interaction network. To evaluate the degree to which this topological heterogeneity is present in available ecological networks, we first compared the amount of topological heterogeneity across 723 species interaction networks created by different sets of researchers with the amount quantified from non-ecological networks known to be constructed following more consistent approaches. Then, to further test whether the topological heterogeneity was due to differences in study designs, and not only to inherent variation within ecological networks, we compared the amount of topological heterogeneity between species interaction networks created by the same sets of researchers (i.e., networks from the same publication) with the amount quantified between networks that were each from a unique publication source. We found that species interaction networks are highly topologically heterogeneous: while species interaction networks from the same publication are much more topologically similar to each other than interaction networks that are from a unique publication, they still show at least twice as much heterogeneity as any category of non-ecological networks that we tested. Altogether, our findings suggest that extra care is necessary to effectively analyze species interaction networks created by different researchers, perhaps by controlling for the publication source of each network.

5.2 Introduction

Network approaches are routinely used as a tool to analyze ecological systems (Blüthgen, 2010; Poisot et al., 2016b; Delmas et al., 2019; Fortin et al., 2021). This popularity extends to species interaction networks which model ecological communities, where nodes represent species and edges represent their corresponding species interactions (Dormann et al., 2017). Due to the effort needed to observe species and their interactions *in situ*, creating species interaction networks requires a tremendous amount of resources for their adequate construction (Jordano, 2016; Pellissier et al., 2018; McLeod et al., 2021). Given this requisite effort, instead of creating their own networks, ecologists often reuse available species interaction networks which happen to be created by different sets of researchers, to test their own ecological hypotheses (Poisot et al., 2021; Brimacombe et al., 2022b). These available species interaction networks have therefore been used in many ecological studies including when determining the complexity of networks (Strydom et al., 2021b), identifying common topological properties across networks (Mora et al., 2018; Michalska-Smith and Allesina, 2019), and evaluating how network topology is shaped by species traits (Dalsgaard et al., 2021), environmental factors/space (Olesen and Jordano, 2002; Dalsgaard et al., 2017; Pellissier et al., 2018; Doré et al., 2021), and time (CaraDonna and Waser, 2020; Schwarz et al., 2020; CaraDonna et al., 2021).

A current crux of reusing available species interaction networks created by different sets of researchers, however, is the unwanted topological differences that can exist due to the lack of consistency in the way ecological systems are translated into networks by different sets of researchers (Dormann et al., 2009; Ings et al., 2009; Gibson et al., 2011; Doré et al., 2021; Mestre et al., 2022a; Quintero et al., 2022; Salim et al., 2022; Vázquez et al., 2022) [Figure 5.1]. While some criticisms related to this issue had been raised in the 1980s/90s, e.g., Paine (1988); Polis (1991), with the increasing availability to the internet and growth in computational power, a renewed interest in networks was sparked, and many of these concerns were overlooked (Pringle and Hutchinson, 2020).

In order to effectively reflect on these criticisms and overall problems that occur when reusing species interaction networks created by different sets of researchers, we thought it necessary to first have a vocabulary to do so. As such, we introduce a framework that partitions how the totality of these topological differences—topological heterogeneity—between species interaction networks created by different sets of researchers can originate, by broadly organizing its sources into three classes (Table 5.1): *biological and environmental drivers*, *sampling strategies*, and *network construction methods*. The *biological and environmental drivers* class consists of sources of topological heterogeneity that arise from the different (a)biotic conditions that shape species and their interactions across different communities. For example, abiotic conditions including temperature can influence whether a species persists as well as modify their interactions (Welti and Joern, 2015). Likewise, biotic drivers such as population sizes can influence both the existence and strength of interactions (Vázquez et al., 2007, 2009). The *sampling strategies* class consists of sources of topological heterogeneity that arise from the different study design decisions made by researchers when observing species and their interactions, and determines which effects from (a)biotic factors are included in the network, e.g., how larger sampling area and larger sampling time can capture greater environmental factors. The *network construction methods* class consists of sources of topological heterogeneity that are introduced via the different decisions made by researchers when constructing each network, e.g., only using plant species from a single genus (Fig 5.2A) or including unidentified

species in the network (Fig 5.2B). In combination, these classes of topological heterogeneity make it incredibly difficult to decipher which topological properties in species interaction networks might be due to the ecological process of interest rather than due to unwanted sources of heterogeneity.

Structural differences between species interaction networks are not problematic *per se* since topological heterogeneity is necessary for determining drivers of that topology. However, large amounts of topological heterogeneity between networks created by different sets of researchers may be indicative of networks that lack commensurability (Brimacombe et al., 2022a). While some studies attempt to control for inconsistencies in the way species interaction networks are created by different researchers, e.g., controlling for sampling effort (Schleuning et al., 2012) or network size (Morris et al., 2014), these controls do not account for all associated unwanted topological heterogeneity when using the many different topological metrics adopted by ecologists. Hence, evaluating the amount of topological heterogeneity present in species interaction networks created by different researchers is a necessity. One approach to do this is by comparing the dispersion of network topology within species interaction networks to other real world networks that are not significantly hampered by the classes of heterogeneity listed in Table 5.1. If a system is accurately portrayed by its own networks, we would expect these networks to have a small amount of dispersion expressed within the metrics used to capture their topology.

As an attempt to quantify ecological topological heterogeneity, we used the largest set of bipartite networks and measured the amount of topological dispersion in (i) species interaction networks compared to non-ecological networks, and (ii) species interaction networks created by the same set of researchers (i.e., networks from the same publication) compared to the species interaction networks each a product of their own publication. We quantified differences in network topology using directed graphlet correlation distance (Yaveroğlu et al., 2014); a heuristic method that measures the Euclidean distance between networks, where networks closer together are those that are more topologically similar.

To measure topological heterogeneity, we evaluated the total dispersion in directed graphlet correlation distances between networks of the same domain (defined below). As most ecological networks do not have metadata regarding the conditions under which each network was created (i.e., their associated *biological and environmental drivers*, *sampling strategies*, and *network construction methods*) we could not partition topological heterogeneity across the heterogeneity classes. However, as we quantified the total dispersion in non-ecological networks from different domains which are, to a large extent, not hampered by the three classes of heterogeneity, we could use these dispersion values to estimate the total amount of topological heterogeneity as a result of all three heterogeneity classes in species interaction networks. Furthermore, we compared the total dispersion of species interaction networks from the same publication to those that are not from the same publication to determine if there are topological biases due to the ways in which different sets of researchers construct networks.

5.3 Methods

5.3.1 Data

A total of 3476 bipartite networks were used in this study (see Table 5.2 for a description of all networks and their domains). Of the non-ecological bipartite networks included in our analysis, 1830 were of the crime domain, 109 were of the journal domain, 245 were of the legislature domain, 172 were of the actor domain, 194 were of the sports domain, and 203 were of the microbiome domain. We classified microbiome networks as non-ecological since, among other properties, they were not built using observational data (instead, for example, by swabs and subsequent RNA sequencing), and had concrete definitions for their edges/nodes (i.e., locations on the human body where a bacterial operational taxonomic unit was found)—two stark features that differ from species interaction networks (our ecological networks). See Aagaard et al. (2013) for a thorough description of how patients were selected, and operational taxonomic units were sampled, which were the data we used to build the microbiome networks. Although microbiome networks could be considered ecological, we believed that their topological heterogeneity would more resemble non-ecological networks and thus grouped them accordingly. Except for sports networks which we constructed for this paper, and whose data were obtained from Lahman (2021), `www.basketball-reference.com`, and `www.hockey-reference.com`, all non-ecological networks were obtained from Michalska-Smith and Allesina (2019). Of the 723 species interaction networks used in this analysis [obtained from Brimacombe et al. (2022b)], 10 were ant-plant networks, 97 were host-parasite networks, 41 were plant-herbivore networks, 298 were plant-pollinator networks, and 277 were seed-dispersal networks. All networks that were included in our analysis were unweighted (i.e., interactions between nodes were binary).

We included non-ecological systems for comparison in our study given the strict definitions used to define their systems, thereby eliminating much of the *biological and environmental drivers*, *sampling strategies*, and *network construction methods* classes of heterogeneity that can strongly influence the topology of species interaction networks created by different sets of researchers. Here, "strict" refers to the high likelihood that the data for these non-ecological systems were recorded consistently using such definitions that their respective nodes/edges would more accurately and precisely reflect their intended purpose when implemented as a network, as compared to species interaction networks. Furthermore, we either built each non-ecological network ourselves (i.e., sports networks), or used those previously built by us [i.e., all non-ecological networks other than sports were obtained from Michalska-Smith and Allesina (2019)], thus ensuring appropriate data were used to build each non-ecological network. Indeed, the data used to build these networks came from specific databases for each domain (or subgroup within each domain, where subgroup refers to the different categories of a domain that networks represented, see Table 5.2). Moreover, as the data for each domain/subgroup of non-ecological networks came from the same database, if any class of heterogeneity were to influence their topology, the resulting heterogeneity would at least be *consistent*, and thereby reduce potential dispersion in measured topological heterogeneity. While undoubtedly the three classes of heterogeneity still influence non-ecological networks, for instance, due to the misidentification of nodes, we expected that these classes would be significantly less influential than those within species interaction networks. In particular, we expected large amounts of topological heterogeneity in available species interaction networks created by different sets of researchers resulted from the

inconsistent ways ecological communities were translated into networks by the different sets of researchers. We expected this would have introduced *inconsistent* topology across species interaction networks thereby increasing the dispersion in measured topological heterogeneity.

To avoid extremely small bipartite networks that may bias our results (Michalska-Smith and Allesina, 2019), we only included networks that had at least five nodes in either disjoint sets of nodes, e.g., we required at least five pollinator and five plant species in a plant-pollinator network. Additionally, only the giant component of each network was used (i.e., the largest connected component of a graph), given that it is unclear how to appropriately analyze disconnected networks.

5.3.2 Directed graphlet correlation distance (DGCD)

In ecology, the most adopted subgraph technique is based on motifs. Generally, for a graph G composed of a set of nodes V and a set of links L, denoted as $G(V,L)$; a motif of G is a subgraph $G'(V',L')$ with a subset of nodes V' from V where *any* edges linking the nodes of V' found in V are contained in L' (Milo et al., 2002; Stouffer et al., 2007). As differences in network structure are measured by which motifs are under-/over-represented in the real network compared to a chosen network null model (Pržulj et al., 2010; Yaveroğlu et al., 2014), like many statistical analyses, the results from the motif analysis depend on the choice of null model. As a consequence, motifs have been cited for possibly relying on ill-posed null models as a basis for significance testing (Artzy-Randrup et al., 2004).

To overcome the null model limitation, we instead adopted the subgraph technique of directed *graphlet* correlation distance (DGCD) (Sarajlić et al., 2016) to characterize the topological differences between networks. Generally, DGCD evaluates network pairwise dissimilarity without relying on a network null model, and does so by quantifying differences in the associations between the appearance of directed graphlets (Figure 5.3A) within a given network to those of another empirical network.

Formally, graphlets are the induced subgraphs $G'(V',L')$, consisting of a subset of nodes V' from V where *all* the edges linking the nodes of V' found in V are in the set L'. Within graphlets, nodes are often indistinguishable from one another. Take for example the graphlet G_2 in Figure 5.3A: in this case, both black nodes in this graphlet are indistinguishable, and thus form an automorphism orbit—simply "orbit"—of a graphlet. For this reason, there is only two orbits within G_2, labelled 5 and 6.

Generally, the DGCD relies on the directed graphlet correlation matrix (DGCM) of each network which contains Spearman's correlations between the number of times nodes appear as particular orbits with the number of times nodes appear as all other orbits within the given network (see Figure 5.3B for an example count of orbit 6 for a particular node of a bipartite network). For example, the Spearman's correlation between orbits 1 and 6 represented in a DGCM is calculated by taking the Spearman's correlation between: (i) a vector where each index corresponds to a specific node and the entry of that index would be the number of times that node appeared as orbit 1, and (ii) same as (i) except for orbit 6. Thus, when using all 13 orbits, DGCMs were symmetric 13×13 matrices containing the respective Spearman's correlations between the appearances of all 13 orbits within a network. Using the DGCMs, the pairwise DGCD was evaluated by measuring the pairwise Euclidean distances between all networks. See eq. (5.1) for a single pairwise DGCD measure between networks K_i and K_j using the 13 orbits from Figure 5.3A (termed DGCD-13 since it uses 13 orbits), and S5.10 Appendix: Subsection S5.10.1 for an example derivation of the DGCD technique. We used

DGCD in our study since recently Tantardini et al. (2019) found that this method performs best at characterizing and distinguishing between networks of different domains.

$$\text{DGCD-13}\left(K_i, K_j\right) = \sqrt{\sum_{n=0}^{12} \sum_{m=n+1}^{12} \left(\text{DGCM-13}_{K_i}(n, m) - \text{DGCM-13}_{K_j}(n, m)\right)^2} \qquad (5.1)$$

where $\text{DGCM-13}_{K_i}(n, m)$ is the directed graphlet correlation matrix-13's value of network K_i for orbits n and m.

Since it is expected that networks from the same domain have similar topology, it is also expected that their DGCMs are similar, and consequently have small pairwise DGCD. Thus, when projected in visual space, networks from the same domain should be clustered together.

We calculated the pairwise DGCD-13 for all bipartite networks, where we assigned directions to the edges in the networks. Since bipartite networks are characterized by two sets of nodes where nodes belonging to the same set cannot have an edge, we assigned nodes belonging to one set to always represent a "to" direction and the other set of nodes to always represent a "from" direction in the directed edges. Simply put, this means that the DGCD-13 technique could recognize which nodes belonged to which set of nodes (e.g., which nodes belonged to the pollinator set of nodes and which nodes belonged to the plant set of nodes in a plant-pollinator network). According to these direction definitions imposed on the networks, only graphlets G_0, G_2, and G_3 could appear although all six graphlets and 13 orbits were used for better visualization—specifically Figure 5.4—but see S5.10 Appendix: Subsection S5.10.1 for subsequent analyses using only the six orbits from graphlets G_0, G_2, and G_3, termed DGCD-6. Nevertheless, we note that the results presented in this article for DGCD-13 agree with those those presented in S5.10 Appendix: Subsection S5.10.1 using DGCD-6.

From all pairwise DGCD-13s, we measured the dispersion of network topology by calculating the mean pairwise distances between all networks of the same domain. In cases where subgroups (e.g., hockey networks) formed coherent topology that was different from their domain (e.g., the mean pairwise DGCD-13 was much smaller for hockey networks compared to all other sports networks) we instead evaluated the mean pairwise DGCD-13 for that subgroup. If the set of networks from the same domain or subgroup had small mean pairwise DGCD-13 then this would indicate that these networks have small dispersion in their topology, i.e., they are similarly structured.

Additionally, we tested whether species interaction networks created by the same set of researchers (i.e., networks sourced from the same publication) were more topologically similar than networks not sourced from the same publication, see S5.10 Appendix: Table S5.3 for a list of publications that provided more than a single network. Specifically, we compared the mean pairwise DGCD-13 of networks from the same publication to the mean pairwise DGCD-13 of networks that were each a product of their own publication. Given that networks constructed by the same researchers are likely more parsimonious in terms of their topology, we expected that the mean pairwise DGCD-13 between networks from the same publication were going to be smaller than networks each produced by different publications.

5.4 Results

The pairwise DGCD-13 between all networks was projected via multidimensional scaling [MDS] (Borg and Groenen, 2005), also commonly known as principal coordinate analysis, using the `MDS` function in the Scikit-learn library (Pedregosa et al., 2011) of Python. Except for species interaction networks, only networks that formed clear clusters were uniquely coloured and identified in the MDS plot (Figure 5.4). Most networks from the same domain occurred in the same location in the plot and were isolated from other networks' domains in the MDS space except for species interaction, sports, and crime networks. With regards to species interaction networks, no coherent topology was observed as these networks covered all other types of non-ecological networks besides microbiome and sports networks. With regards to sports and crime networks, specific cities (i.e., the subgroups of Chicago, Denver, Minneapolis, San Francisco, and Washington) and specific sports (i.e., the subgroups of hockey, baseball, and basketball) had unique topology and formed their own respective subgroupings within the plot, and thus despite not having the same topology, there was clear topological coherence within a city's own set of crime networks and a sports' own set of networks. Here, subgrouping refers to networks from a specific subgroup that formed clear and unique clusters in the MDS plot. Since every network's domain was composed of multiple different subgroups (e.g., actor networks were made from action, adventure, ..., western movie genres/subgroups, Table 5.2) each domain could have potentially formed their own distinct subgroupings within Figure 5.4 if they exhibited unique substructure like crime and sports networks.

Of networks from the same domain or networks that had their own subgroupings within the MDS plot (Figure 5.4), species interaction networks had the largest mean pairwise DGCD-13 of 1.101—about twice as much as the set of legislation networks which was the next domain or subgrouping with the most topological dispersion (Table 5.3). This pattern also held when using median pairwise DGCD-13 (S5.10 Appendix: Table S5.2) and so mean DGCD-13 was not significantly influenced by outliers. As well, the large variability in the size of species interaction networks did not contribute to this larger mean pairwise DGCD-13 value (S5.10 Appendix: Table S5.4). Interestingly, both legislation and Minneapolis crime networks also had relatively high mean pairwise DGCD-13 (0.578 and 0.509, respectively), although legislation networks were composed of four subgroups that did not form subgroupings in the MDS plot (i.e., U.S. House, U.S. Senate, U.N. General Assembly, and European Parliament) which likely contributed to this larger value.

Exclusively within the species interaction domain, networks from the same publication were more topologically similar, by about a factor of two, than networks that were each a product of their own publication (0.544 and 1.134 mean pairwise DGCD-13, respectively, Table 5.4). This smaller dispersion within networks from the same publication was also about 32% less than the topological dispersion within the ecological subgroup that had the least topological dispersion, i.e., ant-plant (0.794 pairwise DGCD-13, Table 5.3). It should be noted, however, that while ant-plant networks were the least topologically heterogeneous subgroup of species interaction networks tested, this should not be generalized given that we only had a few networks available to us ($n = 10$) which were sourced from only three publications. Nevertheless, although networks from the same publication were generally of the same species interaction subgroup (i.e., most networks from a specific publication belonged to only one of either ant-plant, host-parasite, plant-herbivore, plant-pollinator, or seed-dispersal subgroup), networks from the same publication were more topologically similar than any single species interaction subgroup.

5.5 Discussion

Ecologists commonly reuse species interaction networks created by different sets of researchers to test how ecological and environmental processes shape network topology across space and time (Poisot et al., 2021; McLeod et al., 2021; Mestre et al., 2022*a*). However, unwanted topological differences as a result of the different ways in which researchers translate ecological communities into networks could inhibit their commensurability (Gibson et al., 2011; Brimacombe et al., 2022*b*; Quintero et al., 2022). When assessing the degree of topological heterogeneity, i.e., the total amount of topological differences between a group of networks, we find that species interaction networks created by different sets of researchers are extremely topologically heterogeneous—about twice the amount than the next most heterogeneous network domain tested—and that this large heterogeneity is linked to the publication source of each network. Altogether, these findings suggest that species interaction networks created by different sets of researchers can be problematic for deducing ecological topological rules since much of the topological heterogeneity is likely not due to ecological processes as is often assumed.

A general principle in statistics is that an increased sample size reduces uncertainties of estimators (Dietze, 2017). Armed with this principle, and the ease with which species interaction networks can be obtained from online resources (Salim et al., 2022), it may then be tempting to assume that increasing one's data set by collecting all possible networks available alleviates any data issues. However, using the largest set of bipartite species interaction networks available ($n = 723$), we illustrate how large amounts of topological heterogeneity (via the mean pairwise DGCD-13, Table 5.3) and consequently uncertainty exists in the topology of species interaction networks created by different sets of researchers, confirming that more data is not always better when biases are present (Dietze, 2017). While some metrics, including sampling intensity and effort, have previously been used to control for biases and sources of topological heterogeneity in species interaction networks (Brimacombe et al., 2022*a*), these controls do not effectively account for all sources of heterogeneity (e.g., differences in node taxonomy across networks) or when using different topological metrics (e.g., modularity, nestedness). Hence, careful consideration, beyond a single metric of control, is required when deciding which networks to include in one's analyses, so that the majority of topological differences measured between species interaction networks are a result of the ecological process-of-interest and not from confounding factors.

The large amount of topological heterogeneity in species interaction networks created by different sets of researchers likely reflects their topological uniqueness due to the distinct (a)biotic conditions each represented community experiences, the distinct sampling strategies adopted to characterize each ecological system as a network, and the distinct construction methods used to create each network (Table 5.1). Indeed, the large difference in the amount of topological heterogeneity between species interaction networks and non-ecological networks may be attributed to these three classes of topological heterogeneity given that the non-ecological networks were created in a consistent way to try to eliminate much of their influence. For example, we built non-ecological networks using data attained from consistent *sampling strategies* (e.g., each sampled crime network represented a specific city and day of the year in 2016) and we used consistent *network construction* definitions when building the networks from the data (e.g., all interactions in crime networks always represented a type of crime occurring in a city's specific neighborhood). This is not to say that non-ecological networks are devoid of their own sources of topological heterogeneity. For instance, differences in both voter

sentiment across time and differences in the political landscape across space within the legislative networks (e.g., between U.S. House and U.N. General Assembly networks) likely contribute some topological heterogeneity. However, the *biological and environmental drivers*, *sampling strategies*, and *network construction methods* classes of heterogeneity seem to be accentuated in species interaction networks created by different sets of researchers as compared to the tested non-ecological networks.

Importantly, even though *biological and environmental drivers*, *sampling strategies*, and *network construction methods* classes of heterogeneity are known to influence the topology of species interaction networks, they are nevertheless rarely acknowledged or appropriately controlled in ecological studies. This is especially problematic when reusing networks created by different sets of researchers since the influence of these classes are likely to vary considerably depending on the methods and approaches that different researchers use to create each network. In fact, rarely are differences in *sampling strategies* controlled for when reusing networks, even though sampling strategies influence network topology. For example, species interaction networks are already topologically different when constructed from observational data collected over different amounts of time (CaraDonna and Waser, 2020; Schwarz et al., 2020; CaraDonna et al., 2021), or over different amounts of area (Galiana et al., 2018, 2022). Furthermore, related to variations in *sampling strategies*, networks may also vary in their sampling sufficiency (Casas et al., 2018). Insufficiency can occur when the sampling design does not match the biology of the community and can make networks incommensurable even when networks are built using the same *sampling strategies*. Moreover, differences in *biological and environmental drivers* that ecological communities experience are sometimes not controlled for when reusing networks, even though these drivers can influence network topology. For instance, species interaction networks are already topologically different depending on the temperature each community experiences (Welti and Joern, 2015). As well, despite the widespread reuse of species interaction networks created by different sets of researchers for testing ecological hypotheses, it is still relatively unknown how different *network construction methods* influence topology, which may also make network comparison difficult. For example, interactions in one plant-pollinator network can represent a pollinator touching a plant and in another network represent pollen of a plant being found on a pollinator (Hagen et al., 2012), or networks may or may not contain pollinators which are commensals or parasitic to plants (Guimarães Jr., 2020). Thus, without care and appropriate control of the topological differences from the three heterogeneity classes, one is liable to find erroneous relationships when reusing species interaction networks created by different sets of researchers (Ollerton and Cranmer, 2002; Morris et al., 2014).

All is not lost when reusing species interaction networks created by different sets of researchers, as one approach to avoid a large amount of the topological heterogeneity may be to attempt to control for the publication source of each network. While we found a large amount of topological heterogeneity between all species interaction networks, we also found that networks created by the same set of researchers (i.e., networks from the same publication) were more topologically similar to each other (Table 5.4). Interestingly, we also found that networks from the same publication were more topologically similar than networks from any species interaction subgroup (i.e., networks belonging only to either ant-plant, host-parasite, plant-herbivore, plant-pollinator or seed-dispersal). Consequently, it appears that publication has an even greater impact on the topology of species interaction networks than biological processes alone. This may occur since researchers of a given publication generally construct networks under parsimonious conditions (Brimacombe et al., 2022*b*),

for example by observing and characterizing ecological communities across the same time duration [e.g., Trøjelsgaard et al. (2015)], or by classifying nodes across networks using the same protocol [e.g., Pereira Martins et al. (2020)], and thus inadvertently control for many sources of topological heterogeneity. Of course, biological effects are likely influencing the topology of all networks but they can be more easily obscured when analyzing networks across publications. It is then likely that controlling for the effect of publication can reduce unwanted topological heterogeneity between networks. We do, however, strongly caution those that only attempt to account for the publication source of each reused network. Similar to how different network metrics are sensitive to different amounts of sampling sufficiency (Casas et al., 2018), the strong similarity between networks from the same publication may be more or less relevant when investigating network structure using other metrics.

Although most researchers do not originally intend for their networks to be reused and compared to other networks, often they are included in meta-analysis type studies if they are made freely-available. Original authors of networks can improve the scientific utility of their networks by providing other researchers with information about how they were constructed (Mestre et al., 2022a). In particular, by providing detailed network metadata, including information on relevant *biological and environmental drivers*, *sampling strategies*, and *network construction methods*, authors of the networks can help others understand the specific conditions under which each network was created. Additionally, given the recent developments of composite methods designed to estimate sampling sufficiency for ecological networks [e.g., Casas et al. (2018)], authors of species interaction networks could also calculate this metric or provide the information to do so to check if communities have been sufficiently sampled. Then, beyond controlling for sources of topological heterogeneity (e.g., node taxonomy), researchers reusing these networks could also control for sampling sufficiency which is another means to improve network commensurability. Given appropriate metadata, researchers could also study how each class of heterogeneity influences the topology of species interaction networks, rather than the totality of topological heterogeneity as we have done here.

Nevertheless, as users of species interaction networks that happen to be constructed by different sets of researchers, the onus is on us to know the limitations of our data and to ensure that they effectively represent the systems in the corresponding models we use (Bodner et al., 2022). Given that all species interaction networks are models and are thus subject to imperfections [e.g., Pringle and Hutchinson (2020); Thomson (2021)], we should be aware of their overall shortcomings and attempt to correct for them, especially since our findings are often used to inform policy aimed at conserving ecological systems.

5.5.1 Caveats

A limitation in our analyses was the use of small species interaction networks (e.g., <100 nodes). Since networks with a small number of nodes and edges are generally more difficult to classify than larger networks (Yaveroğlu et al., 2014), we perhaps inadvertently increased the perceived topological heterogeneity of species interaction networks as compared to some of the non-ecological networks. Regardless, the crime networks we used were of similar size to species interaction networks (S5.10 Appendix: Table S5.1), but were less topologically heterogeneous (Table 5.3 and Figure 5.4). Clearly then, it was still possible to find topological consistency even in small networks, but less so when networks were both small and ecological. This suggests that the topological heterogeneity in species

interaction networks created by different sets of researchers was due to more than just the difficulty of classifying small networks, but likely also from *biological and environmental drivers*, *sampling strategies*, and *network construction methods* classes of heterogeneity, which reused networks created by different sets of researchers are especially prone to. Importantly, this same problem of using small networks is also relevant when applying any other types of metrics to ecological networks, e.g., nestedness, modularity.

Although we generally failed to find pervasive and coherent topology within species interaction networks created by different sets of researchers, we highlight that our results do not necessarily invalidate patterns others have found [e.g., high nestedness in plant-animal networks (Bascompte and Jordano, 2007)]. Instead, these patterns are perhaps *true* under strict conditions, such as controlling for the unwanted differences in topology between studies when reusing their networks.

5.6   Conclusion

Species interaction networks created by different sets of researchers likely suffer from comparison problems due to many sources of topological heterogeneity, i.e., via *biological and environmental drivers*, *sampling strategies*, or *network construction methods* classes of heterogeneity. Quantitatively, our findings show that these species interaction networks are remarkably topologically diverse and that we should be especially careful when reusing this source of data for deducing rules of community assembly, perhaps by controlling for the publication source of each network.

5.7   Data and code availability

All data and code to reproduce our results are available at: `www.osf.io/my9tv`.

5.8   Figures

Biological and environmental drivers that alter a community's network topology
- Type of environment
- Population size
- Interaction frequency

Sampling strategy decisions that affect which biological/environmental factors are observed during *in situ* sampling

Spatial elements
- Sampling location
- Extent and area resolution of observation

Temporal elements
- Sampling starting date/time
- Duration and time interval of observation

Network construction decisions that influence network topology
- Node resolution
- Selection of the type of interactions to include

Figure 5.1. Potential sources of topological heterogeneity that influence researchers' interpretation of a plant-pollinator community as a bipartite network. Here, the observed plant-pollinator community (green oval) is translated into a researcher's network representation (thought bubble). Sources of topological heterogeneity between different researchers' network interpretations of a community could be introduced from: (*i*) observing different *biological and environmental drivers* (purple text) that influence the community's interactions, (*ii*) the different selected *sampling strategies* (orange text) that influence which biological and environmental factors are included during a researcher's observation, and (*iii*) the different selected *network construction methods* (blue text) researchers use to design a species interaction network.
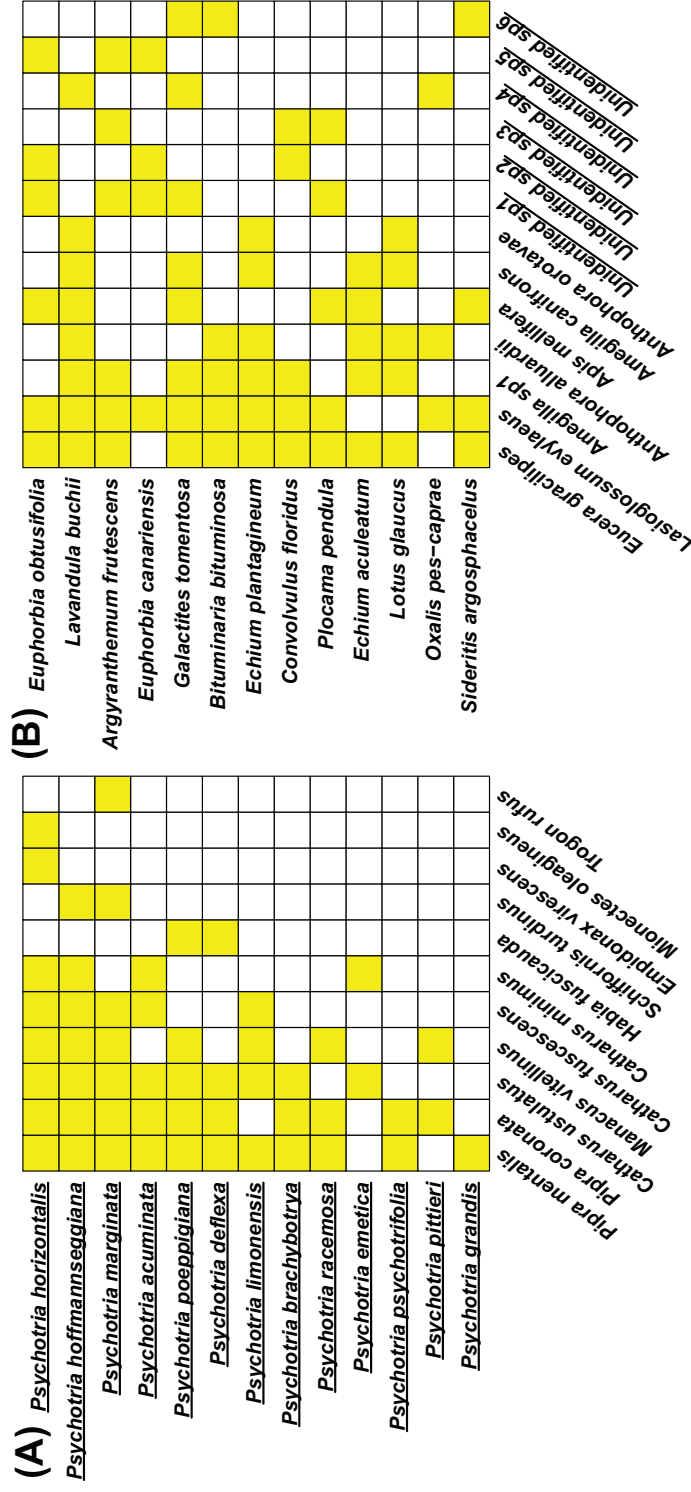
Figure 5.2. Matrix representations of two bipartite species interaction networks from www.web-of-life.es; an *open* species interaction network database. Yellow boxes in each matrix indicate the presence of an interaction between species at the corresponding row (plants) and column (animals). (**A**) Seed-dispersal network from Poulin et al. (1999), where all plant species (underlined) are from the genus *Psychotria*. (**B**) Subset of the plant-pollinator network from Stald (2003), which includes a large number of unidentified pollinator species (underlined; 34 of the 54 total pollinator species [not all shown here] in the whole network).
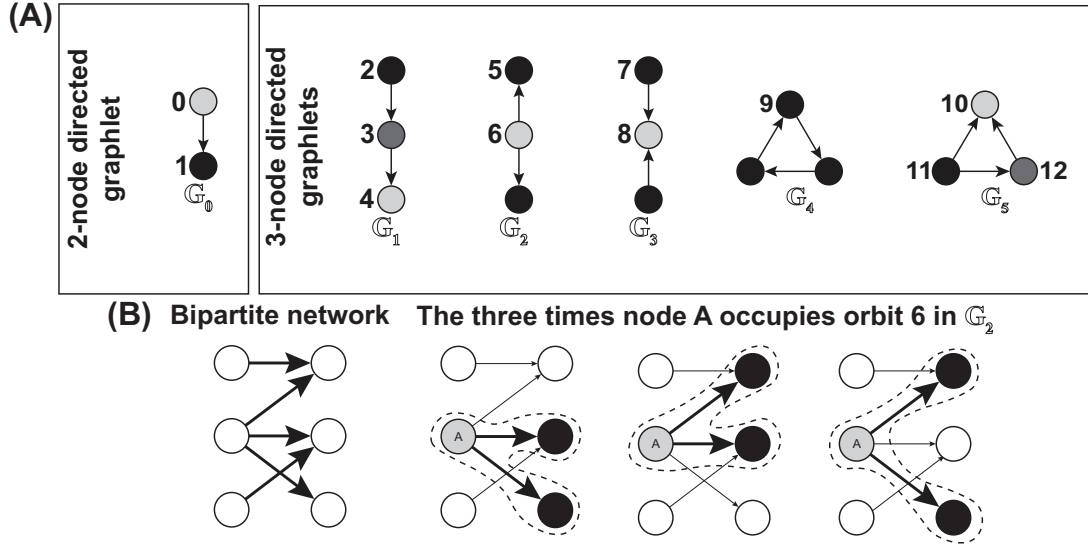
Figure 5.3. **(A)** The six directed graphlets (G_i) consisting of two to three nodes, and their respective orbits (i.e., the corresponding 13 numerically labelled node positions). Each unique shade in a single graphlet corresponds to a unique orbit in that graphlet. Note that for the directed bipartite networks used in this study, only graphlets G_0, G_2, and G_3 appear. **(B)** An example calculation of the number of times node A of a directed bipartite network occupies orbit 6, where dashed lines indicate the location of G_2.
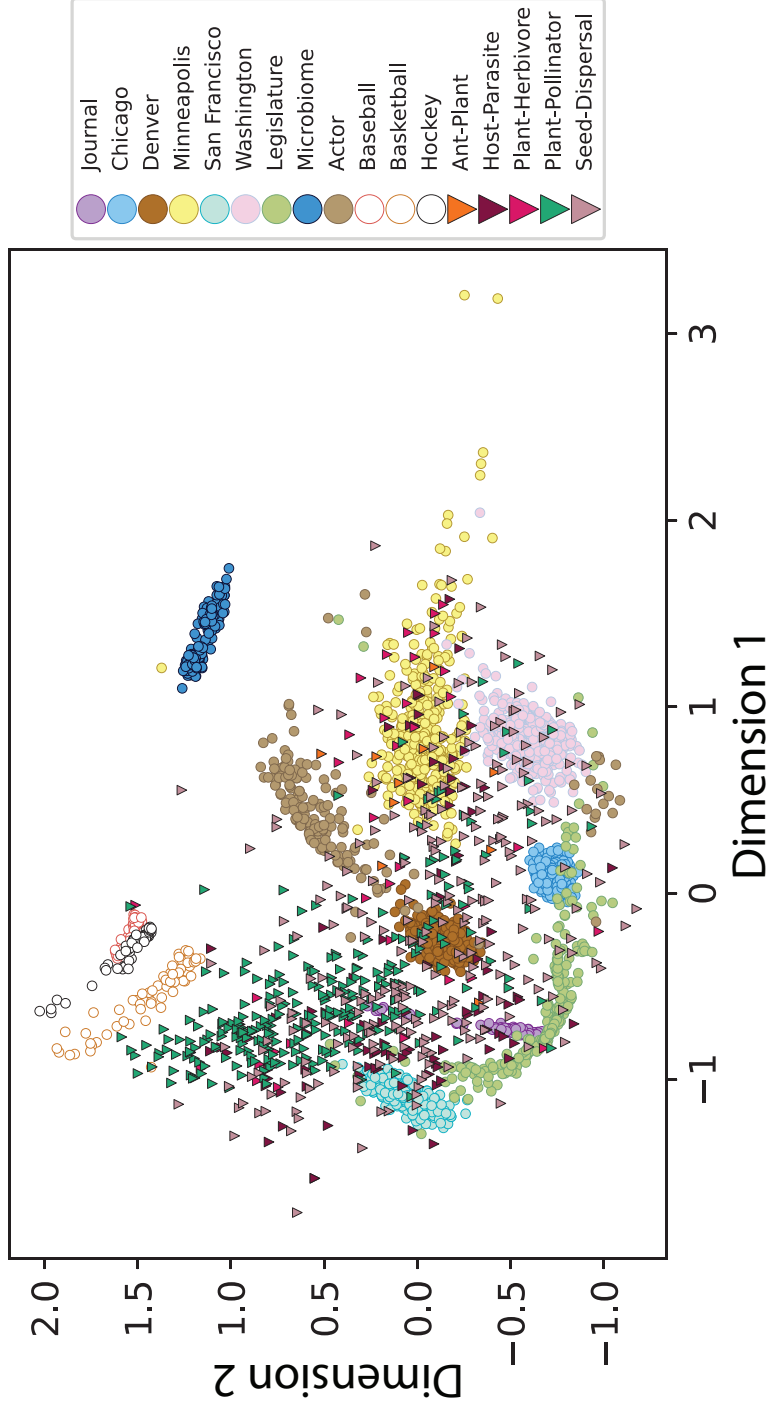
Figure 5.4. Multidimensional scaling of the pairwise directed graphlet correlation distance-13 (DGCD-13) between all bipartite networks ($n = 3476$). Except for species interaction networks (triangles), only networks that formed clear groups in the plot are uniquely identified by color. Each symbol is a single network.

5.9 Tables

Table 5.1. Classes of topological heterogeneity that influence species interaction networks, some sources of this topological heterogeneity, a description of the source, and some example references.

Classes of heterogeneity	Source	Description of source	Example references
	Type of environment	Abiotic conditions influence topology (e.g., plant–pollinator networks are structured differently across a temperature gradient)	Pellissier et al. (2018) Welti and Joern (2015)
Biological and environmental drivers	Population sizes	Species abundances influence probability of interaction (e.g., topological differences in communities with high abundances vs low abundances of all species)	Vázquez et al. (2007) Vázquez et al. (2009)
	Interaction frequencies	Number of interaction events an organism has influences the probability interactions are recorded in a network (e.g., topological differences in networks when cryptic interactions are included)	Pringle and Hutchinson (2020) Pringle (2020)
Sampling strategies	Temporal elements of study	The duration and time interval of observation used to characterize a community influence its representation as a network (e.g., topological differences when networks are constructed from data collected over a day vs week)	CaraDonna et al. (2021) CaraDonna and Waser (2020) Schwarz et al. (2020)

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Classes of heterogeneity	Source	Description of source	Example references
Sampling strategies	Spatial elements of study	The extent and area resolution of observation used to characterize a community influence its representation as a network (e.g., topological differences when networks are constructed from data collected in a patch vs a forest)	Galiana et al. (2018) Galiana et al. (2022)
	Selection of interaction types	Interaction types differently influence communities (e.g., topological differences between mutualistic and antagonistic systems)	Thébault and Fontaine (2010) Allesina and Tang (2012)
Network construction methods	Node resolution	Organismal classification and targeted species influences topology (e.g., topological differences when nodes represent species vs genus or when nodes additionally represent ontogentic stages)	Hemprich-Bennett et al. (2021) Bodner et al. (2022)

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Table 5.2. Description of bipartite networks used in this study. All bipartite networks were connected and had at least 5 nodes in either disjoint sets of nodes.

Network domain	Node set 1	Node set 2	A connection forms when	Subgroup each network represents
Species interaction	Species	Species	A species feeds on another	Ant-plant, host-parasite, plant-herbivore, plant-pollinator, or seed-dispersal community
Actor	Actors	Film	An actor appears in a film	Action, adventure, animation, comedy, crime, documentary, drama, family, fantasy, foreign, history, horror, music, mystery, romance, science fiction, thriller, tv movie, war, or western movie genre across a number of years
Crime	Type of crimes	A city's neighborhoods	A crime occurs in a city's neighborhood	Chicago, Denver, Minneapolis, San Francisco, or Washington of a given day in 2016
Journal	Authors	Academic journals	An author publishes in an academic journal	All authors that published in one of The American Naturalist, Ecography, Ecological Application, Ecological Monographs, Ecology, Ecology Letters, Journal of Animal Ecology, Journal of Applied Ecology, Journal of Ecology, or Oikos and all other academic journals within a given year (2006-2016)
Legislature	Legislators	Bills	A legislator votes positively for a bill	The U.S. House, the U.S. Senate, the U.N. General Assembly, or the European Parliament of a given year (1941-2016)
Microbiome	Bacteria operational taxonomic unit (OTU)	Locations on a human patient	A bacteria OTU is found on patient's site	A single patient
Sports	Athletes	Teams	An athlete plays for a team	The NBA, NHL, or MLB, of a given season (1950-2020)

Table 5.3. Mean pairwise directed graphlet correlation distance-13 (DGCD-13) between bipartite networks from the same domain or subgrouping. Subgrouping refers to a subgroup [i.e., networks classified as the same type of network from the same domain during network construction (e.g., the Chicago networks in the crime network domain)] that formed an obvious cluster within the MDS plot (Figure 5.4). See Table 5.2 for a list of network domains and their corresponding subgroups. All species interaction networks were classified into their appropriate subgroup even though they did not form subgroupings.

Network domain	Subgrouping or subgroup	Mean pairwise DGCD-13	Number of networks
	Ant-plant	0.794	10
	Host-parasite	1.064	97
Species	Plant-herbivore	1.264	41
interaction	Plant-pollinator	0.890	298
	Seed-dispersal	1.092	277
	None[1]	1.101	723
Actor		0.414	172
	Chicago	0.129	366
	Denver	0.180	366
Crime	Minneapolis	0.509	366
	San Francisco	0.169	366
	Washington	0.305	366
Journal		0.234	109
Legislation		0.578	245
Microbiome		0.241	203
	Baseball	0.200	71
Sports	Basketball	0.459	68
	Hockey	0.330	55

[1]DGCD-13 between all species interaction networks.

Table 5.4. Mean pairwise directed graphlet correlation distance-13 (DGCD-13) of bipartite species interaction networks from the same publication grouping. Multiple bipartite networks sourced from the same publication (i.e., networks created by the same set of researchers) are termed "multiple networks per publication" and bipartite networks sourced from publications that each produced only a single network are termed "one network per publication". See S5.10 Appendix: Table S5.3 for a list of publications that provided more than one network and each publication's mean pairwise DGCD-13.

Publication grouping	Mean pairwise DGCD-13	Number of networks	Number of publications
One network per publication	1.134	236	236
Multiple networks per publication	0.544[1]	487	58

[1]Calculated by taking the mean of the average pairwise DGCD-13s between networks from the same publication, weighted by the number of networks produced by each publication.

S5.10 Appendix

S5.10.1 Directed graphlet correlation distance general information

Here, we provide a brief introduction to the directed graphlet correlation distance 6 (DGCD-6). While the same calculations are performed for DGCD-13, note that *all* graphlets with three or fewer nodes (i.e., all 6 graphlets and 13 orbits in Figure S5.1) are used when employing DGCD-13, instead of the 3 graphlets (G_0, G_2, G_3) and 6 orbits (0, 1, 5, 6, 7, 8) when employing DGCD-6. We chose to present DGCD-6 as an example derivation as opposed to DGCD-13 to simplify derivation in Figures S5.2, S5.3, and S5.4. Specifically, the only difference between the two methods is that using DGCD-13 with bipartite networks results in (*i*) additional zero entries in orbits 2, 3, 4, 9, 10, 11, and 12 for the directed graphlet degree vector in Figure S5.2, (*ii*) additional corresponding zero vectors for orbits 2, 3, 4, 9, 11, and 12 in Figure S5.3, and (*iii*) similar to (*ii*) additional corresponding zero vectors for orbits 2, 3, 4, 9, 11, and 12 for the two directed graphlet correlation matrices, as well as additional squared terms when evaluating the DGCD equation in Figure S5.4.

Given a network, such as the one depicted in the first row of Figure S5.2, we must first determine the number of times nodes occupy specific orbit positions. For DGCD-6, this amounts to counting the number of times nodes occupy the orbits of graphlets G_0 (orbits 0 and 1), G_2 (orbits 5 and 6), and G_3 (orbits 7 and 8). In tallying the number of times a node occupies orbital positions, the *directed graphlet degree vector* for a node is constructed. In Figure S5.2, we provide the directed graphlet degree vector for node A.

Once directed graphlet degree vectors for each node in a network are determined (where a single directed graphlet degree vector is highlighted in red in Figure S5.3), the *directed graphlet correlation matrix* can be assembled. In doing so, all possible Spearman's correlations between the number of times all nodes in a network occupy specific orbits are evaluated (see the highlighted green boxes in Figure S5.3 as an example of a single Spearman's correlation).

By computing the pairwise Euclidean distances between directed graphlet correlation matrices, we can obtain an estimate of the topological differences between networks in a given set. An example of a single pairwise Euclidean distance between two directed graphlet correlation matrices (i.e., two networks) is shown in Figure S5.4.

Using all pairwise Euclidean distances between networks (i.e., all pairwise DGCD-6 between networks/graphlet correlation matrices), we can visualize their dissimilarity by projecting their distances using multidimensional scaling (MDS; see Figure S5.5 for an example). We performed MDS using the `MDS` function in the Scikit-learn library of Python (Pedregosa et al., 2011).
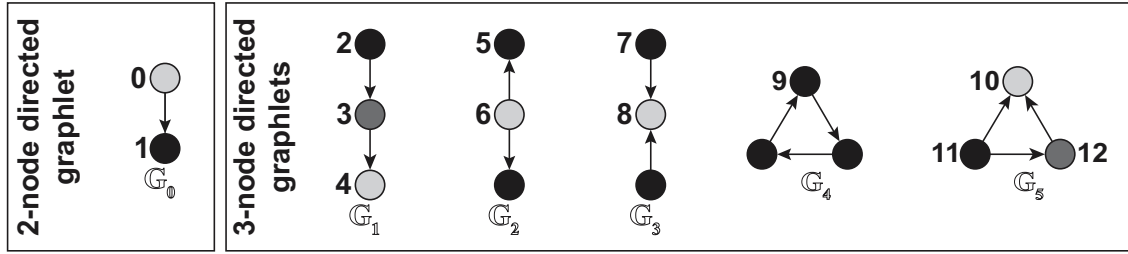
Figure S5.1. The six directed graphlets (G_i) consisting of two to three nodes, and their orbits (i.e., the corresponding 13 numerically labelled node positions). Each unique shade in a single graphlet corresponds to a unique orbit in that graphlet.
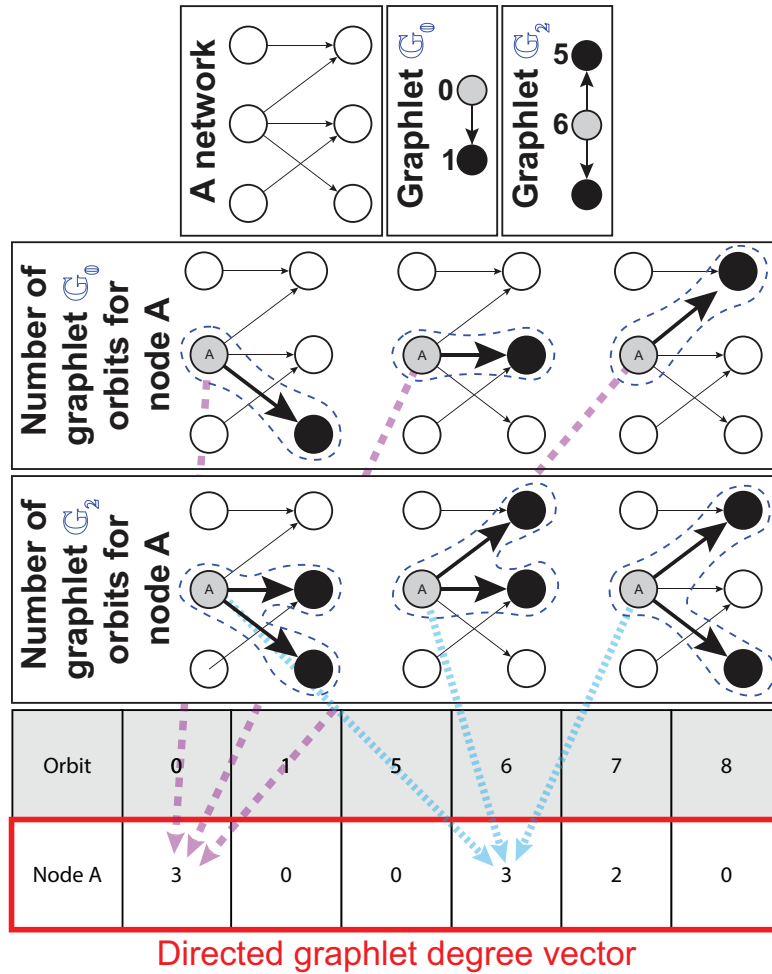
Figure S5.2. Example calculation of a directed graphlet degree vector for a single node (node A) using the 6 orbits (i.e., 0, 1, 5, 6, 7, 8 of Figure S5.1) that comprise the directed graphlet correlation distance 6 method.
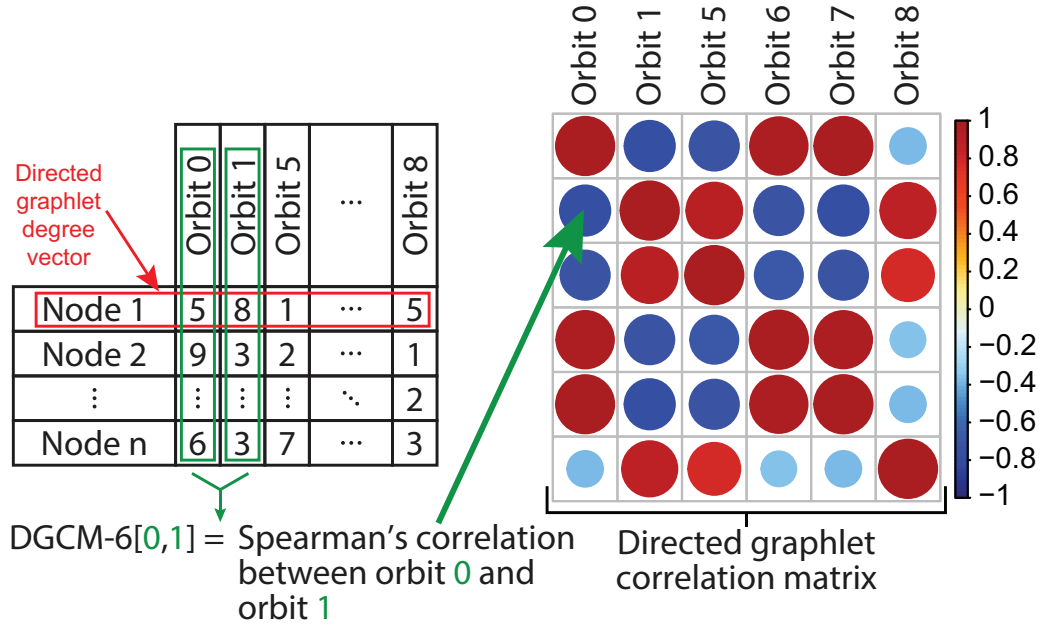
Figure S5.3. Example calculation of a directed graphlet correlation matrix (DGCM-6) using 6 orbits that comprise the directed graphlet correlation distance 6 method. First, directed graphlet degree vectors for each node in a network are calculated (a single vector is highlighted in red). Next, Spearman's correlations are calculated between all pairs of orbits using the number of times each node occupies each orbit (an example of the vectors used in a single correlation is highlighted in green). The resulting correlations form entries within the directed DGCM-6.

Directed graphlet correlation matrix of bipartite network 1

Directed graphlet correlation matrix of bipartite network 2

Pairwise Euclidean distance

$$\text{DGCD-6}\,(K_i, K_j) = \sqrt{\sum_{n=0}^{5}\sum_{m=n+1}^{5}\big(\text{DGCM-6}_{K_i}(n,m) - \text{DGCM-6}_{K_j}(n,m)\big)^2}$$

$$= \sqrt{\left(-0.741 - [-0.650]\right)^2 + \cdots + \left(-0.373 - [-0.571]\right)^2}$$

$$= 1.293$$
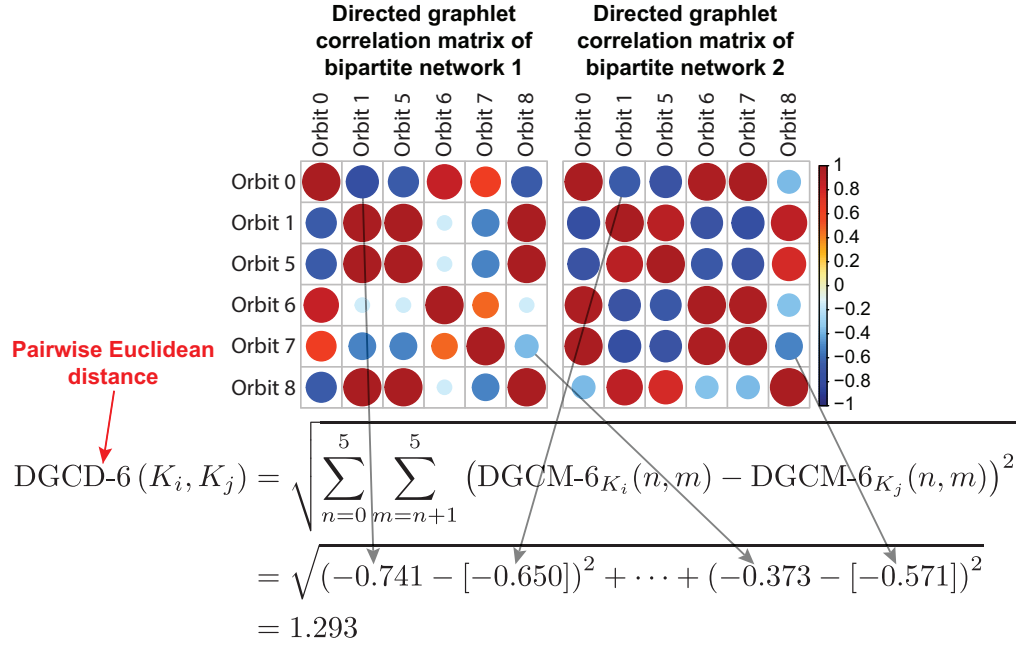
Figure S5.4. The formula and an example calculation of the pairwise directed graphlet correlation distance 6 (DGCD-6) using the directed graphlet correlation matrices of two bipartite networks.

	Network 1	Network 2	...	Network n
Network 1	0.000	1.293	...	0.671
Network 2	1.293	0.000	...	1.039
...	...	...	⋱	...
Network n	0.671	1.039	...	0.000

Matrix of all pairwise DGCD-6 values between networks
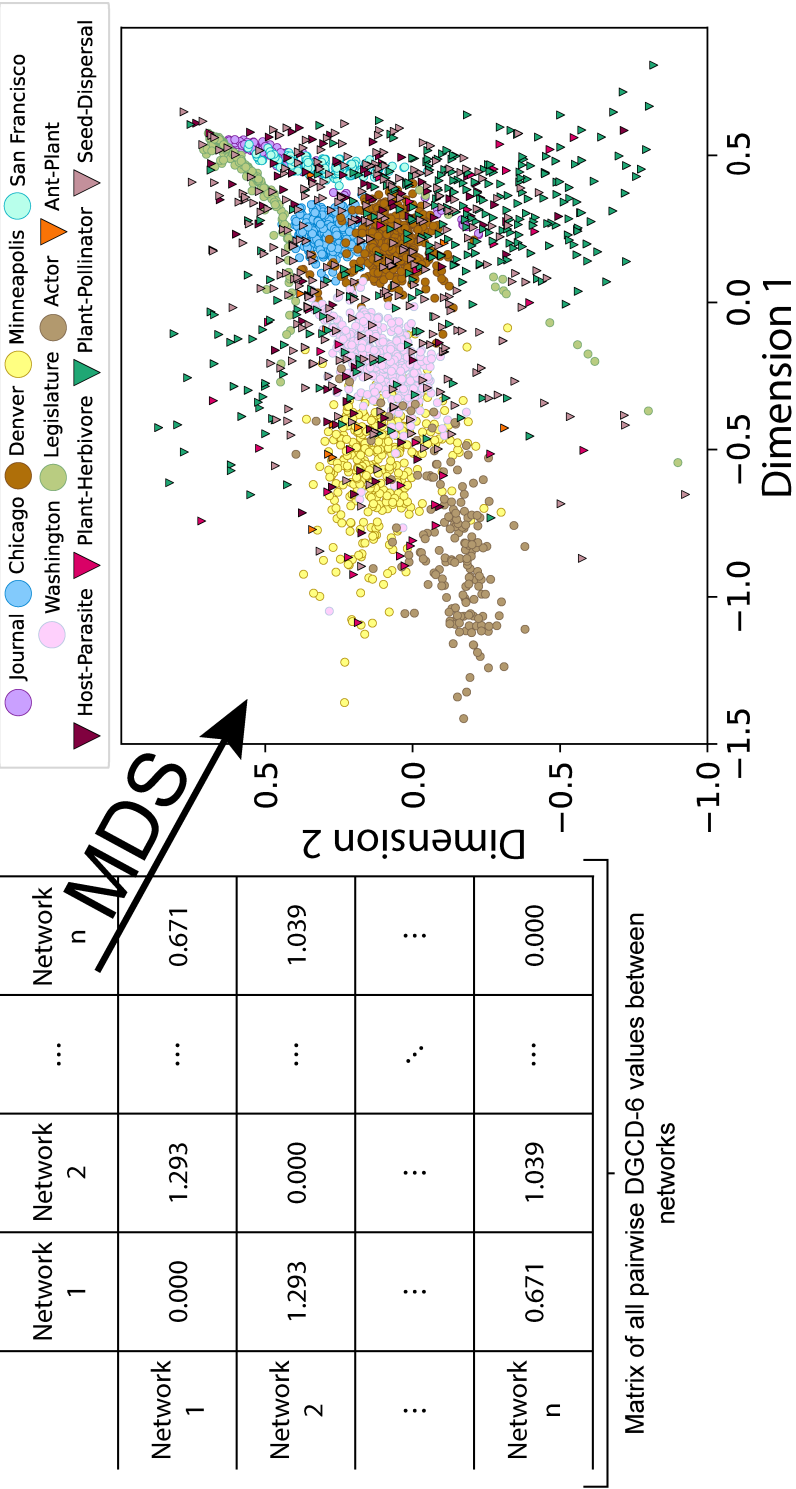
Figure S5.5. An example of a 2-dimensional multidimensional scaling (MDS) projection of all pairwise DGCD-6s between a set of bipartite networks. This MDS projection is a subset of Figure S5.7.

S5.10.2 Network general information

Table S5.1. Additional bipartite network information. Subgrouping refers to a subgroup [i.e., networks classified as the same type of network from the same domain during network construction (e.g., the Chicago networks in the crime network domain)] that formed an obvious cluster within the MDS plot (Figure 5.4). See Table 5.2 for a list of network domains and their corresponding subgroups. All species interaction networks were classified into their appropriate subgroup even though they did not form subgroupings (e.g., Ant-plant).

Network domain	Subgrouping or subgroup	Mean connectance (Standard deviation)	Mean rows (Sd)	Mean columns (Sd)	Number of networks
	Ant-plant	0.262 (0.082)	15.9 (9.632)	11.3 (13.039)	10
	Host-parasite	0.279 (0.13)	20.227 (30.054)	23.32 (20.057)	97
Species	Plant-herbivore	0.185 (0.107)	73.488 (171.286)	47.415 (122.832)	41
interaction	Plant-pollinator	0.196 (0.096)	26.124 (52.037)	42.738 (74.494)	298
	Seed-diserspal	0.303 (0.134)	23.599 (39.563)	17.032 (13.345)	277
	None[1]	0.249 (0.128)	26.91 (59.952)	30.115 (58.326)	723
Actor		0.005 (0.009)	7354.5 (8371.04)	1037.75 (1391.519)	172
	Chicago	0.24 (0.018)	73.943 (1.694)	21.251 (1.595)	366
	Denver	0.06 (0.006)	55.85 (5.321)	47.858 (6.304)	366
Crime	Minneapolis	0.162 (0.059)	27.735 (7.695)	10.12 (2.842)	366
	San Francisco	0.491 (0.038)	10.003 (0.052)	24.631 (1.95)	366
	Washington	0.303 (0.04)	29.929 (2.834)	6.779 (0.746)	366
Journal		0.04 (0.006)	389.349 (138.151)	623.138 (55.206)	109
Legislation		0.593 (0.139)	167.898 (161.857)	151.698 (198.062)	245
Microbiome		0.103 (0.025)	8625.236 (2607.786)	22.616 (7.693)	203
	Baseball	0.002 (0.001)	23.972 (5.144)	930.563 (278.695)	71
Sports	Basketball	0.012 (0.008)	16.618 (7.87)	246.794 (135.802)	68
	Hockey	0.004 (0.003)	21.818 (7.855)	697.364 (272.129)	55

[1]All species interaction networks without subgroups.

S5.10.3 DGCD-13 information

Table S5.2. Median pairwise directed graphlet correlation distance 13 (DGCD-13) between bipartite networks from the same domain or subgrouping. Subgrouping refers to a subgroup [i.e., networks classified as the same type of network from the same domain during network construction (e.g., the Chicago networks in the crime network domain)] that formed an obvious cluster within the MDS plot (Figure 5.4). See Table 5.2 for a list of network domains and their corresponding subgroups. All species interaction networks were classified into their appropriate subgroup even though they did not form subgroupings (e.g., Ant-plant).

Network domain	Subgrouping or subgroup	Median pairwise DGCD-13	Number of networks
Species interaction	Ant-plant	0.744	10
	Host-parasite	1.011	97
	Plant-herbivore	1.260	41
	Plant-pollinator	0.802	298
	Seed-dispersal	1.032	277
	None[1]	1.042	723
Actor		0.359	172
Crime	Chicago	0.122	366
	Denver	0.167	366
	Minneapolis	0.431	366
	San Francisco	0.146	366
	Washington	0.277	366
Journal		0.123	109
Legislation		0.482	245
Microbiome		0.233	203
Sports	Baseball	0.197	71
	Basketball	0.399	68
	Hockey	0.254	55

[1]DGCD-13 between all species interaction networks.

Table S5.3. Mean pairwise directed graphlet correlation distance 13 (DGCD-13) between bipartite species interaction networks from the same publication grouping. Bipartite networks sourced from publications that produced only a single network are termed "one network per publication".

Bipartite type(s)/ subgroup	Publication grouping	Mean pairwise DGCD-13	Number of networks
Ant-plant, host-parasite, plant-herbivore, plant-pollinator, seed-dispersal	One network per publication	1.134	236
Ant-plant	Passmore et al. (2012)	0.622	8
Host-parasite	Arai and Mudry (1983)	0.387	2
	Kirjušina and Vismanis (2007)	0.717	2
	Violante-González et al. (2007)	0.160	2
	Hadfield et al. (2014)	0.765	47
	Pilosof et al. (2013)	0.214	6
Host-parasite, plant-herbivore	Macfadyen et al. (2009)	0.608	33
Plant-herbivore	Henneman and Memmott (2001)	0.411	2
	Pereira Martins et al. (2020)	0.350	9
Plant-pollinator	Arroyo et al. (1982)	0.481	3
	Brosi et al. (2017)	0.562	30
	Carstensen et al. (2018)	0.478	14
	Dicks et al. (2002)	0.260	2
	Dupont and Olesen (2009)	0.254	2
	Gilarranz et al. (2015)	0.283	12
	Kaiser-Bunbury et al. (2010)	0.585	24
	Kaiser-Bunbury et al. (2014)	0.605	44
	Lara-Romero et al. (2016)	0.514	38
	Norfolk et al. (2018)	0.516	2
	Maglianesi et al. (2014)	0.475	3
	Magrach et al. (2018)	0.298	12
	Medan et al. (2002)	0.295	2
	Olesen et al. (2002)	0.429	2
	Orford et al. (2016)	0.564	37
	Primack (1983)	0.361	3
	Sabatino et al. (2010)	0.336	5
	Tinoco et al. (2017)	0.737	3
	Trøjelsgaard et al. (2015)	0.454	14
	Tur et al. (2013)	0.191	2

Table continued . . .

Bipartite type(s)/ subgroup	Publication grouping	Mean DGCD-13 per group	Number of networks
	Albrecht et al. (2015)	0.525	16
	Carlo et al. (2003)	0.284	4
	Chama et al. (2013)	0.321	9
	Chaves (2018)	0.960	2
	Correa et al. (2016)	0.554	2
	Correia et al. (2017)	0.674	2
	Cruz et al. (2013)	0.633	3
	Ribeiro da Silva et al. (2015)	0.747	3
	Dehling et al. (2014)	0.527	8
	Farwig et al. (2017)	0.190	2
	Galetti and Pizo (1996)	1.230	2
	García et al. (2014)	0.561	6
	Innis (1989)	0.575	2
	Malmborg and Willson (1988)	0.623	3
Seed-dispersal	Menke et al. (2012)	0.220	4
	Passos et al. (2003)	0.673	2
	Peredo et al. (2013)	1.084	2
	Plein et al. (2013)	0.358	5
	Purificação et al. (2014)	0.627	3
	Quitián et al. (2019)	0.473	4
	Ramos-Robles et al. (2016)	0.634	7
	Ruggera et al. (2016)	0.536	10
	Saavedra et al. (2014)	0.556	2
	Del Valle (2014)	0.238	2
	Snow and Snow (1988)	0.781	4
	Gomes (2008)	0.357	2
	Velho et al. (2012)	0.272	2
	Vizentin-Bugoni et al. (2019)	0.687	7
	Williams and Karl (1996)	0.767	2

S5.10.3.1 DGCD-13 as a function of the number of species interaction networks sourced from each publication (for publications that provide more than a single network)

It was possible that the mean pairwise DGCD-13 for publications which provided more than a single species interaction network were influenced by the number of networks sourced from each publication. For example, it could have been the case that publications that each only provided two species interaction networks had lower mean pairwise DGCD-13 between their own networks than publications that each provided ten species interaction networks. However, we found no strong relationships between the number of networks a publication provided and the mean pairwise DGCD-13. Specifically, when dividing publications (which provided more than a single network) into quartiles based on the number of networks each provided, there were no large differences in mean pairwise DGCD-13 between quartiles (Figure S5.6). Thus, the mean pairwise DGCD-13 for species interaction networks sharing a publication source was not strongly influenced by the number of networks each publication provided.
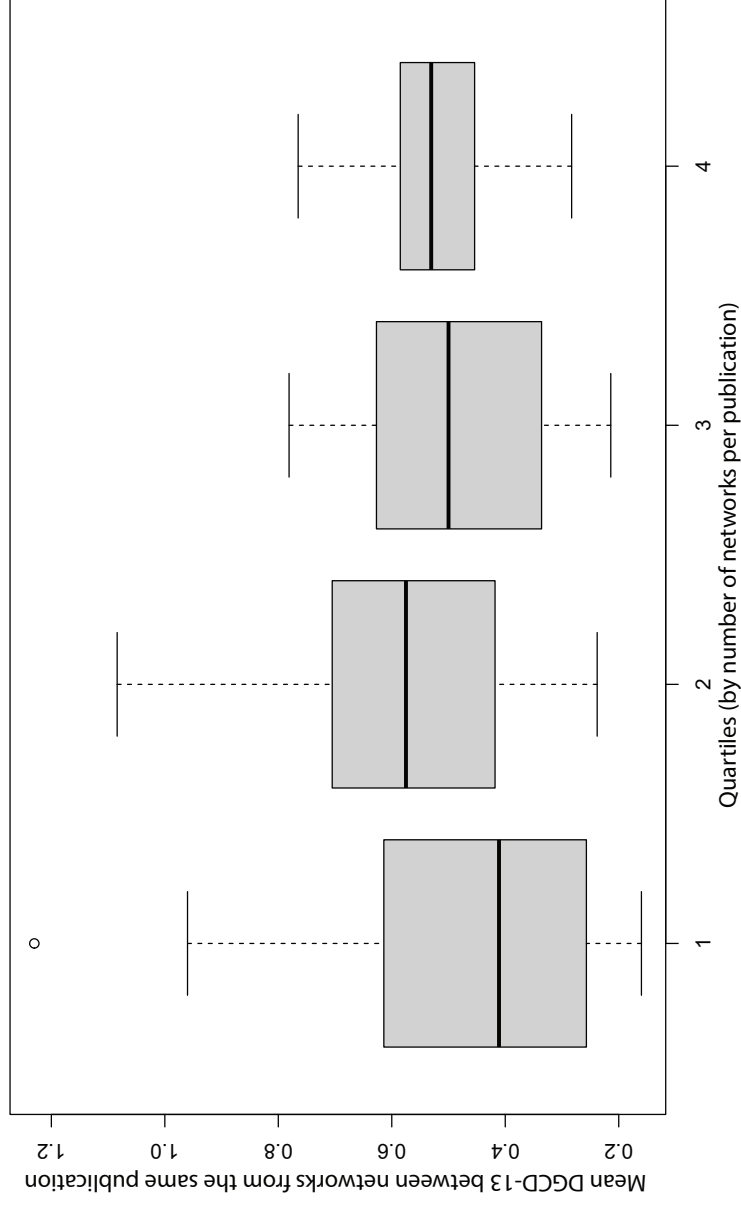
Figure S5.6. The relationship between the mean pairwise DGCD-13 of species interaction networks sourced from the same publication ($n = 487$) and the number of networks a publication provided (represented by quartiles). Note that each publication included in the analyses provided at least two networks. See Table S5.3 for a list of publications and the number of networks each provided.

S5.10.3.2   DGCD-13 as a function of the variability in species interaction network size

It could have been the case that the larger variability in species interaction network size (i.e., number of nodes) caused its larger mean pairwise DGCD-13, as compared to other non-ecological networks which generally had less variability in network size. To test whether this was true, we divided species interaction networks into quartile groups (by network size) to reduce variability in size across a group. We then evaluated the mean pairwise DGCD-13 between the smallest networks (i.e., those within the first quartile) and the largest networks (i.e., those within the fourth quartile) [Table S5.4]. We removed any networks sourced from the same publication to eliminate the effect of publication in this analysis. If multiple networks were sourced from the same publication within a quartile, we only kept a single network from that publication. A single network was chosen using a simple criterion: first, we kept the network with the largest size. If more than one network from the same publication had the same size, we then chose the network with the highest connectance value. If again, more than one network had the same connectance, we chose the network with the greatest number of rows in its adjacency matrix.

Altogether, we found that the standard deviation in network size for the first quartile (representing the smallest networks in our analyses) was considerably smaller in relation to its mean network size as compared to the fourth quartile (representing the largest networks in our analyses). Specifically, the first quartile had a standard deviation in network size of 4.259 and mean network size of 18.544 while the fourth quartile had a standard deviation in network size of 217.844 and mean network size of 170.652 (Table S5.4). However, the first quartile had a larger mean pairwise DGCD-13 than the fourth quartile (1.088 vs. 0.982, respectively) which would not have been expected if the variability in network size influenced mean pairwise DGCD-13. Hence, it does not appear that the variability of network size strongly affected the mean pairwise DGCD-13 in species interaction networks.

Table S5.4. Pairwise directed graphlet correlation distance 13 (DGCD-13) between species interaction networks using the smallest and largest networks classified into quartiles (whereby size was determined by number of nodes).

Network domain	Size quartile	Mean network size (Std. dev.)	Mean pairwise DGCD-13 (Std. dev.)	Number of networks[1]
Species interaction	1	18.544 (4.259)	1.088 (0.464)	90
	4	170.652 (217.844)	0.982 (0.507)	112

[1]All networks included in each quartile were from different publications.

S5.10.4 DGCD-6 information

Here, we reanalyzed the same bipartite networks as those in the main manuscript but instead with the directed graphlet correlation distance that used only the six orbits (termed DGCD-6) from graphlets G_0, G_2, and G_3—specifically, orbits 0, 1, 5, 6, 7, and 8 (Figure S5.1). Generally, the same results were obtained as in the main manuscript: species interaction networks were still the most topologically heterogeneous networks (mean pairwise DGCD-6 of 0.620)—about 76% more heterogeneous than the domain with the second most heterogeneity (i.e., Actor networks with mean pairwise DGCD-6 of 0.352) [Table S5.5 and Figure S5.7]. When instead using median pairwise DGCD-6 (Table S5.6), these results still held, and so the large mean pairwise DGCD-6 found between species interaction networks was not primarily driven by outliers. Moreover, exclusively within the species interaction domain, networks from the same publication were much more topologically similar (by a factor of about 2) than networks that were each a product of their own publication (0.331 and 0.634 mean pairwise DGCD-6, respectively, Table S5.7).
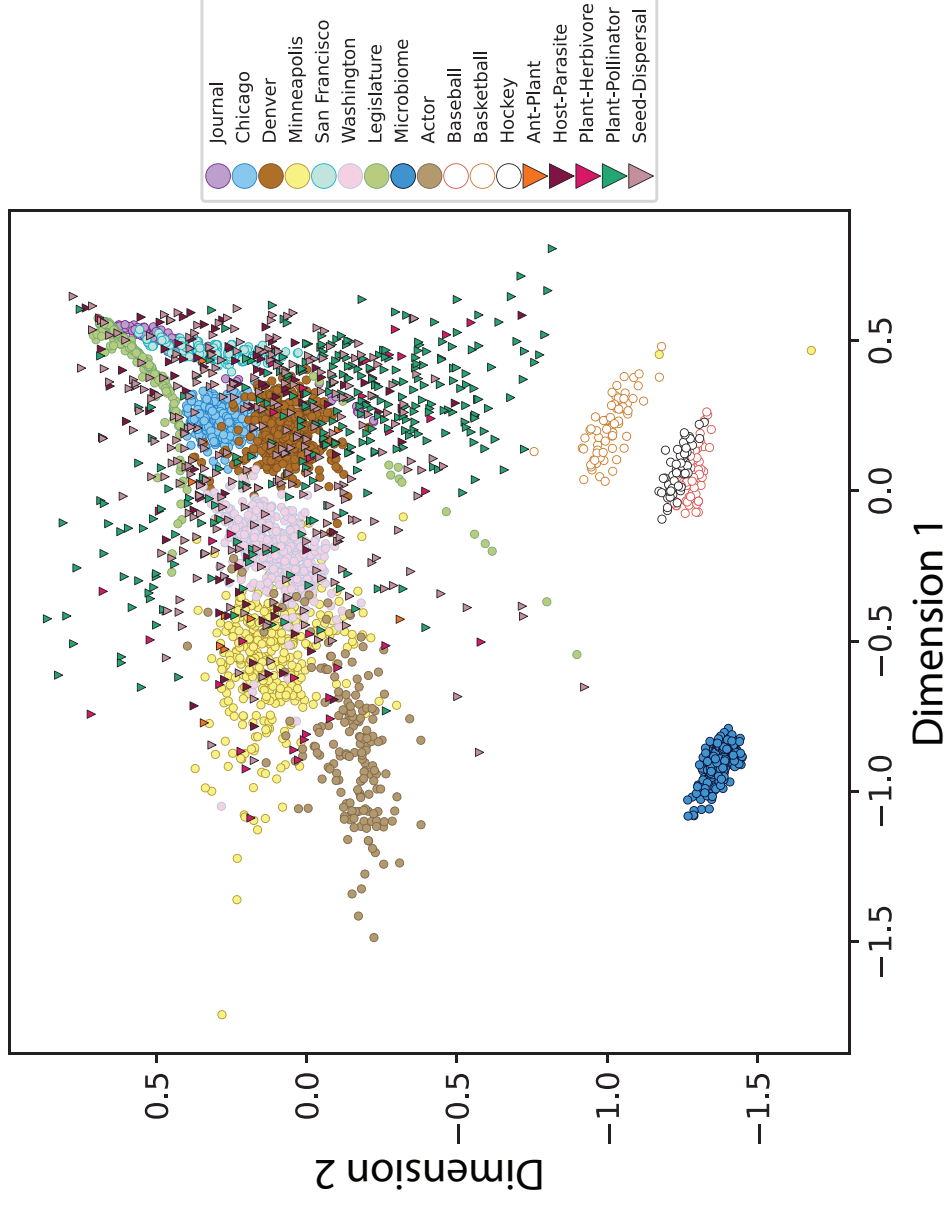
Figure S5.7. Multidimensional scaling of the pairwise directed graphlet correlation distance 6 (DGCD-6) between all bipartite networks ($n = 3476$). Each symbol in plot is a single network.

Table S5.5. Mean pairwise directed graphlet correlation distance 6 (DGCD-6) between bipartite networks from the same domain or subgrouping. Subgrouping refers to a subgroup [i.e., networks classified as the same type of network from the same domain during network construction (e.g., the Chicago networks in the crime network domain)] that formed an obvious cluster within the MDS plot (Figure S5.7). See Table 5.2 for a list of network domains and their corresponding subgroups. All species interaction networks were classified into their appropriate subgroup even though they did not form subgroupings (e.g., Ant-plant).

Network domain	Subgrouping or subgroup	Mean pairwise DGCD-6	Number of networks
Species interaction	Ant-plant	0.543	10
	Host-parasite	0.586	97
	Plant-herbivore	0.774	41
	Plant-pollinator	0.526	298
	Seed-dispersal	0.567	277
	None[1]	0.620	723
Actor		0.352	172
Crime	Chicago	0.105	366
	Denver	0.150	366
	Minneapolis	0.334	366
	San Francisco	0.127	366
	Washington	0.217	366
Journal		0.214	109
Legislation		0.300	245
Microbiome		0.115	203
Sports	Baseball	0.130	71
	Basketball	0.189	68
	Hockey	0.134	55

[1]DGCD-6 between all species interaction networks.

Table S5.6. Median pairwise directed graphlet correlation distance 6 (DGCD-6) between bipartite networks from the same domain or subgrouping. Subgrouping refers to a subgroup [i.e., networks classified as the same type of network from the same domain during network construction (e.g., the Chicago networks in the crime network domain)] that formed an obvious cluster within the MDS plot (Figure S5.7). See Table 5.2 for a list of network domains and their corresponding subgroups. All species interaction networks were classified into their appropriate subgroup even though they did not form subgroupings (e.g., Ant-plant).

Network domain	Subgrouping or subgroup	Median pairwise DGCD-6	Number of networks
Species interaction	Ant-plant	0.507	10
	Host-parasite	0.555	97
	Plant-herbivore	0.784	41
	Plant-pollinator	0.487	298
	Seed-dispersal	0.531	277
	None[1]	0.589	723
Actor		0.306	172
Crime	Chicago	0.096	366
	Denver	0.138	366
	Minneapolis	0.295	366
	San Francisco	0.108	366
	Washington	0.198	366
Journal		0.113	109
Legislation		0.194	245
Microbiome		0.097	203
Sports	Baseball	0.111	71
	Basketball	0.173	68
	Hockey	0.125	55

[1]DGCD-6 between all species interaction networks.

Table S5.7. Mean pairwise directed graphlet correlation distance 6 (DGCD-6) of bipartite species interaction networks from the same publication grouping. Bipartite networks sourced from the same publication are termed "multiple networks per publication" and bipartite networks sourced from publications that each produced only a single network are termed "one network per publication". See Table S5.8 for a list of publication that provided more than one network and each publication's mean pairwise DGCD-6.

Publication grouping	Mean pairwise DGCD-6	Number of networks	Number of publications
One network per publication	0.634	236	236
Multiple networks per publication	0.331^1	487	58

[1]Calculated by taking the mean of the average pairwise DGCD-6s between networks from the same publication, weighted by the number of networks produced by each publication.

Table S5.8. Mean pairwise directed graphlet correlation distance 6 (DGCD-6) between bipartite species interaction networks from the same publication grouping. Bipartite networks sourced from publications that produced only a single network are termed "one network per publication".

Bipartite type(s)/ subgroup	Publication grouping	Mean pairwise DGCD-6	Number of networks
Ant-plant, host-parasite, plant-herbivore, plant-pollinator, seed-dispersal	One network per publication	0.634	236
Ant-plant	Passmore et al. (2012)	0.457	8
Host-parasite	Arai and Mudry (1983)	0.322	2
	Kirjušina and Vismanis (2007)	0.330	2
	Violante-González et al. (2007)	0.047	2
	Hadfield et al. (2014)	0.369	47
	Pilosof et al. (2013)	0.144	6
Host-parasite, plant-herbivore	Macfadyen et al. (2009)	0.420	33
Plant-herbivore	Henneman and Memmott (2001)	0.291	2
	Pereira Martins et al. (2020)	0.233	9
Plant-pollinator	Arroyo et al. (1982)	0.312	3
	Brosi et al. (2017)	0.335	30
	Carstensen et al. (2018)	0.328	14
	Dicks et al. (2002)	0.199	2
	Dupont and Olesen (2009)	0.152	2
	Gilarranz et al. (2015)	0.209	12
	Kaiser-Bunbury et al. (2010)	0.337	24
	Kaiser-Bunbury et al. (2014)	0.354	44
	Lara-Romero et al. (2016)	0.350	38
	Norfolk et al. (2018)	0.227	2
	Maglianesi et al. (2014)	0.297	3
	Magrach et al. (2018)	0.174	12
	Medan et al. (2002)	0.252	2
	Olesen et al. (2002)	0.288	2
	Orford et al. (2016)	0.360	37
	Primack (1983)	0.224	3
	Sabatino et al. (2010)	0.216	5
	Tinoco et al. (2017)	0.470	3
	Trøjelsgaard et al. (2015)	0.286	14
	Tur et al. (2013)	0.185	2

Table continued . . .

Bipartite type(s)/ subgroup	Publication grouping	Mean DGCD-13 per group	Number of networks
	Albrecht et al. (2015)	0.315	16
	Carlo et al. (2003)	0.195	4
	Chama et al. (2013)	0.219	9
	Chaves (2018)	0.667	2
	Correa et al. (2016)	0.377	2
	Correia et al. (2017)	0.238	2
	Cruz et al. (2013)	0.434	3
	Ribeiro da Silva et al. (2015)	0.498	3
	Dehling et al. (2014)	0.231	8
	Farwig et al. (2017)	0.144	2
	Galetti and Pizo (1996)	0.777	2
	García et al. (2014)	0.370	6
	Innis (1989)	0.476	2
	Malmborg and Willson (1988)	0.255	3
Seed-dispersal	Menke et al. (2012)	0.143	4
	Passos et al. (2003)	0.279	2
	Peredo et al. (2013)	0.757	2
	Plein et al. (2013)	0.237	5
	Purificação et al. (2014)	0.346	3
	Quitián et al. (2019)	0.241	4
	Ramos-Robles et al. (2016)	0.372	7
	Ruggera et al. (2016)	0.329	10
	Saavedra et al. (2014)	0.391	2
	Del Valle (2014)	0.152	2
	Snow and Snow (1988)	0.386	4
	Gomes (2008)	0.233	2
	Velho et al. (2012)	0.210	2
	Vizentin-Bugoni et al. (2019)	0.421	7
	Williams and Karl (1996)	0.631	2

Chapter 6

Publication-driven consistency in food web structures: Implications for comparative ecology

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6.1 Abstract

Large collections of freely available food webs are commonly reused by researchers to infer how biological or environmental factors influence the structure of ecological communities. Although reusing food webs expands sample sizes for community analysis, this practice also has significant drawbacks. Since food webs are meticulously crafted by researchers for their own specific research endeavours and resulting publications (i.e., books and scientific articles), the structure of these webs inherently reflects the unique methodologies and protocols of their source publications. Consequently, combining food webs sourced from different publications without accounting for discrepancies that influence network structure may be problematic. Here, we investigate determinants of structure in freely available food webs sourced from different publications, examining potential disparities that could hinder their effective comparison. Specifically, we quantify structural similarity across 274 commonly reused webs sourced from 105 publications using a subgraph technique. Surprisingly, we found no increased structural similarity between webs from the same ecosystem nor webs built using similar network construction methodologies. Yet, webs sourced from the same publication were very structurally similar and this degree of similarity increased over time. As webs sourced from the same publication are typically sampled, constructed, and/or exposed to similar biological and environmental factors, publications likely holistically drive their own webs' structure to be similar. Our findings demonstrate the large effect that publications have on the structure of their own webs which stymies inference when comparing the structure of webs sourced from different publications. We conclude by proposing different approaches that may be useful for reducing these publication-related structural issues.

6.2 Introduction

Food webs have a rich history in ecology (May, 1983; Paine, 1988; Winemiller, 1990; Dunne, 2006; Guimarães Jr., 2020; Pringle and Hutchinson, 2020; Vázquez et al., 2022) as gaining insights into aspects of who eats whom has major implications for individual fitness, population dynamics, community structure, and evolutionary trajectories [e.g., Cohen et al. (1993); Pringle (2020)]. Beyond depicting single interspecific interactions, whole food webs distill the complexity of intertwining feeding interactions into mathematically tractable networks (Guimarães Jr., 2020), most often defining an ecological community's species as nodes and corresponding feeding interactions as links (Cartozo et al., 2005). In this regard, many community-level properties have been inferred from network topology (Delmas et al., 2019; Fortin et al., 2021), including stability, resilience, and sustainability (McCann, 2011; Landi et al., 2018; Carpentier et al., 2021).

Much of our knowledge about food webs has relied on and continues to rely on reusing and comparing the structure of freely available empirical webs (Winemiller, 1990; Goldwasser and Roughgarden, 1993; Dunne, 2006; Poisot et al., 2021; Xing and Fayle, 2021). These freely available webs are networks previously constructed by researchers for their own publications (i.e., books and scientific articles) that have been uploaded onto online open access repositories. For example, the commonly used repository for obtaining species interaction networks, Web of Life (`www.web-of-life.es`), contains 316 networks originally sourced from a purported 127 scientific articles, and other published and unpublished works. Because constructing webs *de novo* from original field data is extremely difficult, time consuming, and expensive (Polis, 1991; McLeod et al., 2021; Borrelli et al., 2023)—not to mention ancillary to the expertise of many researchers who work on food webs—freely available webs represent a cornucopia of community-level data that can be used to investigate and test novel hypotheses (Xing and Fayle, 2021; Kita et al., 2022). Thus, webs from online repositories are routinely reused in meta-analysis-like studies under the implicit assumption that they are reliable and comparable, with little to no scrutiny of the properties of individual webs (Pringle and Hutchinson, 2020; Brimacombe et al., 2023).

Similar to other types of species interaction networks, the drivers influencing food web structure can be generally categorized into three broad classes: *biological and environmental factors*, *sampling strategies*, and *network construction methodologies* (Brimacombe et al., 2023). Of the three classes, ecologists are often most interested in *biological and environmental factors*, which include the biotic and abiotic drivers that shape interspecific interactions in communities [e.g., how the presence of transient seasonal predators alter food web structure (Brimacombe et al., 2021); how warmer temperatures reduce community stability (Zhao et al., 2023)]. The remaining two classes, *sampling strategies* and *network construction methodologies*, include drivers that researchers themselves create when attempting to measure and model the structure of food webs. First, the *sampling strategies* class consists of the study design decisions that shape web structure [e.g., amount of time (Kitching, 1987; Tavares-Cromar and Williams, 1996), and area (Galiana et al., 2022) sampled]. These design decisions determine the particular suite of abiotic and biotic drivers acting on a community during a study period and influence the likelihood of detecting a given species or interaction. Second, the *network construction methodologies* class consists of the methodological approaches that influence food web structure via the decisions researchers make when assembling a web [e.g., node taxon resolution (Gauzens et al., 2013; Hemprich-Bennett et al., 2021; Bodner et al., 2022), the focal organisms under study (Goldwasser and Roughgarden, 1993), and trophic interaction evidence (e.g.,

faecal, stomach, and direct observation (Hutchinson et al., 2022))].

When the *sampling strategies* and *network construction methodologies* do not effectively capture the species and trophic interactions of interest, the structure of an ecological community will be misrepresented (Paine, 1988; Goldwasser and Roughgarden, 1993; Hodkinson and Coulson, 2004; Pringle and Hutchinson, 2020; Carpentier et al., 2021). Even when the sampling and construction methodology accurately and precisely capture the species and trophic interactions in a web, inconsistencies in *biological and environmental factors*, *sampling strategies*, and *network construction methods* across webs can cause issues when comparing their structure (Brimacombe et al., 2023) [Figure 6.1]. While it is possible to mitigate some of these structural discrepancies via network null models (Dormann et al., 2009; Farine, 2017), effective control relies on null models that are carefully posed for each analyzed network (Artzy-Randrup et al., 2004). However, the creation of appropriate null models is especially challenging when networks sourced from different books and scientific articles [hereafter, *publication(s)*] are built using many different *sampling strategies*, and *network construction methodologies*. For example, trophic interactions were measured by Valiela (1974) using direct observations of feeding habits and through feeding trials in petri dish arenas for their dung food webs, whereas Parker and Huryn (2006) used the gut contents of invertebrates and vertebrates manually caught in a river for evidence of interactions in their aquatic webs (Figure 6.1). Additionally, the careful tailoring of a null model, or other controls may depend on additional information about each web which are very rarely reported (Poisot et al., 2016*a*; Kita et al., 2022); for example, the amount of area and time used to delineate the respective community. In some contexts, this information is perhaps even empirically unknowable given that many animals travel (with their gut contents) across large areas, effectively "importing" interactions into what might otherwise be small focal areas.

One way to assess the combined contributions of *biological and environmental factors*, *sampling strategies*, and *network construction methodologies* on freely available food webs is by comparing the structure of webs originally sourced from the same publication to webs originally sourced from different publications. Often, multiple food webs are built by a single publication to evaluate the structure of (*i*) the same community across time [e.g., Valiela (1974); Tavares-Cromar and Williams (1996)], or (*ii*) different communities across space [e.g., Thompson and Townsend (2003, 2004)]. Since multiple webs from the same publication likely experience similar *biological and environmental factors*, *sampling strategies*, and/or *network construction methodologies*, the structure of food webs from the same publication are likely constrained to be similar (Closs and Lake, 1994), which could cause issues when comparing webs from different publications. Potentially then, the frequency of subgraphs (i.e., smaller webs defined by their configuration of nodes and links, see Figure 6.2) could be over expressed in food webs sourced from the same publication as previously shown for bipartite networks (Brimacombe et al., 2023). But unlike bipartite networks, links in food webs can connect any nodes in a given network, producing a greater number of possible subgraphs. This characteristic of food web structure could lead to different structural relationships when assessing the potential effect of publication.

In a more focused perspective to the possible role of publication, if the *network construction methodologies* class is a dominant driver of structure, as has been suggested for instance by Lin et al. (2022), then webs built using similar methodology should be much more structurally similar than a set of webs constructed using an assortment of construction methodologies. If so, then it

may be best to only compare the structure of freely available food webs that were constructed using similar methodologies, e.g., similar rules for assigning trophic links between nodes in webs. One approach to test this is to compare the structural similarity of aquatic food webs constructed via the commonly employed software tool Ecopath (Christensen and Walters, 2004) with those constructed not with Ecopath, but with various different methods (e.g., via gut contents, reports from the literature). Webs from Ecopath are developed using a mass-balance model to describe the energy flow between compartments (e.g., species, functional groups), and require additional empirical information including biomass of prey and predators from the desired community (Baeta et al., 2011).

In this paper, we assess a collection of freely available food webs to identify and offer controls for potential structural issues that might otherwise limit their comparability in studies seeking to deduce ecological properties related to their structure. To this end, we compared the structural similarity in defined groups of freely available food webs to determine if these sets of networks exhibit measurable structural disparities. We compared the similarity within and between groups of webs defined by their (*i*) ecosystem, (*ii*) publication source, and (*iii*) *network construction methodology*. With regards to (*i*), if food webs sampled from the same ecosystem (i.e., aquatic, aquatic and terrestrial, and terrestrial) are more structurally similar within their own ecosystem than across ecosystems, then structural differences exist that are driven by their experienced *biological and environmental factors*. For (*ii*), if webs originally sourced from the same publication have much higher structural similarity than webs originally sourced from different publications, then there likely exists structural disparities driven by the networks' source publications that uniquely represents their network(s)' experienced *biological and environmental factors*, *sampling strategies*, and *network construction methodologies*. For (*iii*), if aquatic food webs constructed via Ecopath are more structurally similar than aquatic webs constructed via an assortment of other methodologies, then structural disparities are likely due to differences in *network construction methodologies*.

6.3 Methods

6.3.1 Food webs

All freely available food webs—originally sourced from different publications—that we reused for our own study came from four commonly cited network repositories [e.g., Carpentier et al. (2021); Barbosa and Siqueira (2023)]: Global Web Database (`www.canberra.edu.au/globalwebdb`), Web of Life (`www.web-of-life.es`), Interaction Web Database (`www.ecologia.ib.usp.br/iwdb`), and GlobAL daTabasE of traits and food Web Architecture (`https://idata.idiv.de/ddm/Data/ShowData/283`). While each web had a putatively associated publication from which it was originally sourced that was provided by each repository, we discarded webs from our analyses when (*i*) further investigation indicated that a given web may not actually have been from the associated publication, or (*ii*) we could not gain access to the original publication to confirm it as the source. We then manually inspected each food web's nodes to correct typographical errors. We list all changes we made to the food webs in S6.10 Appendix: Subsection S6.10.1.

In addition, we imposed structural requirements for food webs to be included in our analyses. First, we included only multitrophic networks excluding bipartite networks. We excluded bipartite

networks as they are likely to be structurally different due to the requirement that links can only exist between nodes in the two different sets. Second, we chose to analyze food webs as undirected networks to eliminate the potential for incorrectly labeled directed interactions from influencing our results. Third, to reduce potential bias arising from using small networks (Michalska-Smith and Allesina, 2019), we included only webs with at least 10 total nodes, comprising at least five unique consumer and resource nodes, respectively. Fourth, when a network was not fully connected, we only analyzed the giant component [i.e., the largest connected component (Fortin et al., 2021)] of each food web given the uncertainty with regards to how to analyze disconnected networks (Brimacombe et al., 2022b, 2023). Under our criteria, of the 531 unfiltered food webs originally downloaded from the four repositories, we were left with 274 webs. From these, 191 were originally sourced from 22 publications that each provided multiple networks and 83 were sourced from one of the 83 publications that each provided only a single network. See S6.10 Appendix: Table S6.7 for a list of all 274 food webs, and their publication sources.

For each of the remaining 274 food webs obtained from the four aforementioned repositories, we identified the type of ecosystem from which it was sampled. Specifically, we classified webs into one of three ecosystem types (i) "aquatic", which included marine, lakes, rivers, streams, and springs, (ii) "aquatic and terrestrial" which included salt marshes, ponds, bogs, mudflats, pitcher plants, and tree holes filled with water, or (iii) "terrestrial" which included sand dunes, forests, meadows, prairie, and farmlands. In total, 167 webs were classified as "aquatic", 28 webs were classified as "aquatic and terrestrial", and 79 webs were classified as "terrestrial". Webs classified as "aquatic" were further investigated to determine whether Ecopath was the method used in their construction.

6.3.2 Pairwise graphlet correlation distance-11 (GCD-11)

We evaluated food web structural similarity using pairwise graphlet correlation distance-11 [GCD-11] (Yaveroğlu et al., 2014). We evaluated structural similarity of networks using GCD-11 because of its previous success in both correctly identifying groups of networks based on structure alone (Tantardini et al., 2019) and quantifying their structural differences (Brimacombe et al., 2023). Briefly, this heuristic method characterizes a web's structure by the correlations between the number of times each node in the web occupies each of the 11 orbit positions in 6 graphlets (Figure 6.2) and leverages this information to determine graphlet structural similarity between webs via orbit correlation patterns. See S6.10 Appendix: Subsection S6.10.2 for a thorough and graphical example of this method.

While motifs [e.g., Milo et al. (2002); Stouffer et al. (2007)] are another common subgraph technique used to analyze a single web's structure in ecology, GCD-11 is able to additionally use graphlets to measure structural similarity across a set of webs without a network null model, and does so with the highest success compared to other approaches (Tantardini et al., 2019). Current network null models are challenging to use as benchmarks for empirical networks since the relationship between statistical significance and biological importance is unclear, and minor modifications to network null models can lead to large changes in significance (Artzy-Randrup et al., 2004).

Generally, there are two steps involved when evaluating structural similarity between a set of webs using GCD-11. In step one, the structure of each web is characterized using graphlets, which involves tallying the number of times each node in the web occupies each of the 11 orbit positions. For a node, this is represented by a vector with 11 entries (called a graphlet degree vector-11) where

each entry is the number of times the node occupies the respective orbit position. For a whole web consisting of n nodes, this is represented by a $n \times 11$ matrix containing orbit counts on each n node. Next, Spearman's correlation between all possible combinations of orbit counts in the web is evaluated, i.e., correlations between each 11 column vectors in the $n \times 11$ matrix. The resulting output is a symmetric 11×11 matrix, referred to as a graphlet correlation matrix-11 (GCM-11), where entry (i, j) is the respective correlation between orbit vector counts of i and j. Simply put, these correlations are indicative of how nodes in the web act as interaction partners across graphlets. In step two, the pairwise Euclidean distance between each web's GCM-11 is evaluated:

$$\text{pairwise GCD-11}(K_i, K_j) = \sqrt{\sum_{n=1}^{11} \sum_{m=n+1}^{11} \left(\text{GCM-11}_{K_i}(n, m) - \text{GCM-11}_{K_j}(n, m)\right)^2}, \qquad (6.1)$$

where $\text{GCM-11}_{K_i}(n, m)$ is the graphlet correlation matrix-11's value of network K_i for orbits n and m.

6.3.3 Assessing structural similarity using mean pairwise GCD-11

To quantify web structural similarity, we measured and compared the mean pairwise GCD-11 between defined sets of food webs (see S6.10 Appendix: Subsection S6.10.3 for more information). Here, mean pairwise GCD-11 can be thought of as a measure of structural dispersion, where the average of the pairwise GCD-11s between all webs in a given set of webs is computed (i.e., mean of the pairwise GCD-11s given by eq. 6.1). We partitioned and evaluated similarity between: (i) webs from the same ecosystem and webs from different ecosystems, (ii) webs from the same publication source and webs each sourced from a different publication, and (iii) aquatic webs constructed using Ecopath and aquatic webs constructed using any other method. With regards to (i), to ensure that the ecosystem groupings of "aquatic", "aquatic and terrestrial", and "terrestrial" were not too coarse, we also evaluated mean pairwise GCD-11 across aquatic food webs further identified as "lake", "marine", "river", "stream", and "spring". With regards to (ii), when publications provided multiple networks, we evaluated only the mean pairwise GCD-11 between webs from the given publication, and when publications provided only a single network each, we evaluated the mean pairwise GCD-11 between all webs from this group. This subset of "one food web per publication" was chosen as an imperfect null model to compare to, where the effect of publication was at least consistent between each and every web since each web was sourced from a different publication. For visualization purposes only, the pairwise GCD-11 between all food webs were mapped in two-dimensional visual space using multidimensional scaling (Borg and Groenen, 2005).

We remark that no tests were performed to determine the statistical significance of differences between mean pairwise GCD-11 values of the partitioned web groups, as our goal was to perform an exploratory data analysis rather than hypothesis testing. Moreover, since our data were unbalanced and partitioned groups had differences in the dispersion of their pairwise GCD-11 values as well as likely differences in their centroid's location (i.e., the location of the center of the dispersion of networks for each group when projected in space), techniques like PERMANOVA would not be useful. Furthermore, the data were pairwise dissimilarity values, and so statistical tests that use measures of variances (or standard deviations), would not have been useful without first projecting pairwise distances into an n-dimensional space. We do, however, provide measures of absolute

differences (i.e., differences between mean pairwise GCD-11) to emphasize an average effect size of our measurements, which is more informative than statistical significance. We also repeated all measurements presented in the main text using median pairwise GCD-11, to help ensure that our results were not affected by outliers [see S6.10 Appendix: Subsection S6.10.6].

6.3.4   Network size

Since food web size (i.e., number of nodes) is regarded as a metric of sampling effort or intensity (Martinez et al., 1999), accounting for it may be necessary in web analyses (Brimacombe et al., 2022a). We tested to ensure neither web size nor the variability in web size influenced pairwise GCD-11 measurements. In other words, we wanted to make sure our results were not simply an artefact of sampling effort or intensity. To do so, we compared the relationship between mean pairwise GCD-11 and (i) food web size; and (ii) variability in food web size. See S6.10 Appendix: Subsection S6.10.7 for more information.

6.4   Results

There were no apparent differences between pairwise GCD-11s (Figure 6.3) across ecosystems' food webs to suggest that specific *biological and environmental factors* associated with ecosystem type coherently influenced web structure. Food webs representing "aquatic" or "aquatic and terrestrial" were found to be comparatively structurally similar having a mean pairwise GCD-11 of 3.07, and 3.04, respectively (Table 6.1). Food webs representing "terrestrial" ecosystems were found to be more structurally similar than webs from "aquatic" and "aquatic and terrestrial", having a mean pairwise GCD-11 of 2.41. However, this lower mean pairwise GCD-11 between "terrestrial" food webs was likely driven by similarities between webs sourced exclusively from Digel et al. (2014) ($n = 48$) as removing these webs increased the mean pairwise GCD-11 of "terrestrial" food webs to 3.53. Given that the mean pairwise GCD-11 between webs of *different* ecosystems were similar to webs within the *same* ecosystems (3.11 for "aquatic" and "aquatic and terrestrial", 3.08 for "aquatic" and "terrestrial", 2.96 for "aquatic and terrestrial" and "terrestrial"), ecosystem type—and hence a suite of shared biotic or abiotic drivers—appeared to have no measurable effect on food web structure. Similar patterns were also found when comparing webs from specific types of aquatic systems: "lake", "marine", "river", and "stream" (S6.10 Appendix: Subsection S6.10.5). Note that "spring" aquatic food webs were omitted from this analysis since only a single spring food web was identified and measures of structural similarity requires ≥ 2 webs.

In contrast, publication source had a much stronger effect on web structure. The multiple food webs that were sourced from the same publication were on average much more structurally similar—by a factor of about two—than webs sourced from publications that each provided only a single network (i.e., mean pairwise GCD-11: 1.51 vs. 3.13 respectively, Table 6.2). Recall that webs sourced from publications that each produced only a single network were used as an imperfect control to capture a possible publication effect on food web structure. Interestingly, over 85% of the structural similarities measured between food webs that shared a publication source in this study had a pairwise GCD-11 ≤ 2.5. In comparison, only about 30% of the structural similarities of food webs from publications that produced only a single network and 30% of the structural similarities of all other possible pairwise distances between webs (e.g., between two food webs from

two different publications that produced multiple networks) had pairwise GCD-11 $\leq$ 2.5 (S6.10 Appendix: Subsection S6.10.4). Moreover, the majority (i.e., about 62%) of the smallest pairwise GCD-11s (i.e., those $\leq$ 1.5) measured across all food webs were only between those webs sourced from the same publication that produced multiple networks, despite only making up 7% of total pairwise distances. When mean pairwise GCD-11 measures were averaged by decade, food webs sourced from publications that produced only a single network all had comparatively large mean pairwise GCD-11 over time (i.e., > 2.45; teal solid lines/points in Figure 6.4). However, considering only webs sourced from publications that produced multiple networks, webs from the same publication published after the 1990s were on average about 1.6 times more structurally similar than webs published before or during the 1990s (mean pairwise GCD-11 of 1.28 vs. 2.07, respectively, Table 6.2, and blue dashed line/points in Figure 6.4).

Within "aquatic" food webs, there was no strong evidence to suggest that *network construction methodology* (i.e. Ecopath) coherently influenced web structure. Although the 28 "aquatic" webs that were constructed using Ecopath had a minimally lower mean pairwise GCD-11 than all 167 "aquatic" food webs (2.55 vs. 3.07, respectively), this moderate difference was likely due to a publication effect, i.e., four publications contributed 13 of the 28 Ecopath webs. Once we removed this publication effect, the mean pairwise GCD-11 between "aquatic" webs constructed via Ecopath increased to 2.78. This structural similarity was only marginally improved upon compared to the mean pairwise GCD-11 of 3.02 found between "aquatic" food webs not constructed via Ecopath (see S6.10 Appendix: Subsection S6.10.8).

6.5 Discussion

Using a collection of 274 commonly reused and freely available food webs from four repositories, we found food web structure to be strongly determined by the publication source of networks. This suggests a significant lack of comparability among food webs sourced from different publications, due to cryptic publication effects embedded within the structure of all webs. Consequently, caution should be exercised when adopting food webs sourced from different publications to infer structural properties about their respective ecological communities.

Although we expect *biological and environmental factors* to have a strong influence on species interactions [e.g., Abdala-Roberts et al. (2019); Brose et al. (2019)], we found no evidence that ecosystem type coherently influenced the structure across all freely available food webs. Specifically, the structural similarity between webs from the same ecosystem (i.e., "aquatic", "aquatic and terrestrial", and "terrestrial") were close to that found between webs from different ecosystems [e.g., between "aquatic" and "aquatic and terrestrial"] (Table 6.1). The absence of increased structural similarity among webs from the same ecosystem may be attributed to the fact that webs were built using distinctly diverse *sampling strategies* and *network construction methodologies*. In the "aquatic" ecosystem, for example, Peterson (1979) sampled the aquatic environment using transects and based feeding interactions on field observations, reports in the literature, and feeding responses in an aquarium, whereas Parker and Huryn (2006) sampled the aquatic environment using 100-meter study reaches, and based feeding interactions on only the gut contents of caught invertebrates and a single fish species. While we recognize that our reported ecosystem type is a coarse categorization, we also did not find improved structural similarity within the more precise subsets of "aquatic" food

webs identified as sampled from "lake", "marine", "river", or "stream" ecosystems (S6.10 Appendix: Subsection S6.10.5). When limiting webs to a single ecosystem type and using only those constructed with the same methodology (i.e., Ecopath), we still only observed a marginal increase in their degree of structural similarity (S6.10 Appendix: Subsection S6.10.8). Hence, neither collections of freely available webs from the same ecosystem nor freely available webs from the same ecosystem *and* built using the same *network construction methodology* appear to substantively influence structure coherently.

From the outset, it may have been obvious that publication source would have strong influence on structure [e.g., Closs and Lake (1994)], but it was less clear that this effect would mask other drivers that we could detect across all freely available webs (Figure 6.3). We are not suggesting that *biological or environmental factors* do not shape food web structure. Rather, *biological or environmental factors* paired with *sampling strategies*, and *network construction methodologies* are holistically, uniquely, and cryptically captured in a publication's food web(s) leaving something like a "structural fingerprint" within each web, which make comparing networks from different publications difficult. The reason for this is made plainly evident when comparing webs sourced from Valiela (1974) and Parker and Huryn (2006), wherein the former is only concerned with the daily arthropod interactions found in bovine dung, while the later is mainly concerned with the interactions between aquatic invertebrates and a single fish species across a month (Figure 6.1). In this light, it is almost trivial that webs sourced from the same publication appeared about (*i*) two-times more structurally similar than either webs from the same ecosystem or webs each sourced from different publications (Tables 6.1 and 6.2, respectively), and (*ii*) 1.84-times more structurally similar than aquatic webs constructed using Ecopath (S6.10 Appendix: Subsection S6.10.8). The same strong publication effect we found here also conforms with that previously found by Brimacombe et al. (2023), where bipartite networks from the same publication were also about 2-times more structurally similar to each other than bipartite networks each sourced from different publications. It is important to note that while we found multiple webs sourced from the same publication to be structurally unique (i.e., had a publication's "structural fingerprint"), webs sourced from publications that each produced only a single web also have their own publication's structural fingerprint, but it could not be revealed using our methods. Like drawing a line requires at least two points, we needed at least two food webs sourced from the same publication to deduce that publication's structural fingerprint.

We are not the first to recognize the issues with reusing collections of freely available food webs. In fact, guided by the many ways food webs can be structured differently, researchers in the 1980s/90s challenged the very utility of freely available webs as data for meaningfully testing ecological hypotheses (Dunne, 2006; Pringle and Hutchinson, 2020). Recently, studies have begun to reveal some of these previously outlined drawbacks. In particular, quantitative measurements have begun to test how differences in *sampling strategies* and *network construction methodologies* influence network structure, including the amount of area sampled (Galiana et al., 2022), amount of sampling effort (Bersier et al., 1999; Banašek-Richter et al., 2004), and node taxon resolution (Hemprich-Bennett et al., 2021). Altogether, these findings—along with our quantitative results—highlight the many complex drivers shaping food web structure that can make network comparison difficult. This is likely the reason why many studies that reuse collections of freely available bipartite networks built by many different researchers often do not find significant relationships in network structure across space (Brimacombe et al., 2022*b*).

As far as we know, we are the first to have found that structural similarity between freely available food webs sourced from the same publication has generally increased across time (blue dashed line of Figure 6.4). This somewhat agrees with the assertion that networks published before 1990 may not have been built with the intention of evaluating structure (Carpentier et al., 2021). Although, we find this true only of publications that produce multiple webs after the 1990s, and not for those webs each sourced from a unique publication (teal solid line of Figure 6.4). The increase in web structural similarity within a given publication may be due to the recommendations made in the late 1980s and early 1990s to improve the ways in which food webs are built [e.g., Lawton (1989); Winemiller (1990); Cohen et al. (1993)].

The cryptic and nonlinear ways the classes of structure act holistically within a publication's own food web(s) likely make it erroneous to simply control for publication via a random effect and then deem networks comparable. Since each freely available web is built by researchers for their own motives (Goldwasser and Roughgarden, 1993), the influence of each one of the three classes of structure varies substantially between publications. Hence, simply controlling for publication is unlikely to remedy the many nonlinear ways webs can be structurally different within and across publications. Importantly, it is also not possible to control for publication as a random effect in cases where food webs were each sourced from a single publication, which comprise a large portion of the freely available food webs (i.e., 83 of the 274 food webs in our study). In such scenarios, each publication grouping would contain only a single data point (i.e., food web) making it impossible to assess relationships between network structure and explanatory variables. Moreover, attempting to control for differences in the *three classes* that influence structure between webs is made difficult, if not impossible, by the lack of standardizations taken across publications (Cohen et al., 1993; Vázquez et al., 2022; Borrelli et al., 2023). The network metadata that would otherwise indicate how the different classes of structure influence each food web—e.g., the amount of time or area used to encapsulate an ecological community as a network (i.e., *sampling strategies*), the biological evidence used to define links between nodes (i.e., *network construction methods*), or the type of environment the ecological community is exposed to (i.e., *biological and environmental factors*)— are almost always absent (Poisot et al., 2016a; Kita et al., 2022).

We recognize that our findings regarding structural similarity are not infallible, but we believe our conclusions regarding publication's effect on freely available food web structure is robust to variations in selected networks. First, while networks with weighted links [e.g., biomass, frequency of interaction (Cohen et al., 1993; Guimarães Jr., 2020)] have been touted as reflecting a more realistic ecological community (Bersier et al., 2002; Banašek-Richter et al., 2004; Vázquez et al., 2022), we suspect that using weighted webs would result in similar patterns as our results with binary webs. As the litany of weighted interaction definitions may render a publication's web(s) even more unique by the chosen interaction definition, publication is likely to constrain its own webs' structure more when building weighted food webs. Second, while reducing the set of webs to only those well sampled or controlling for sampling effort has been recommended (Winemiller, 1990; Goldwasser and Roughgarden, 1993; Martinez et al., 1999), we believe that implementing this restriction is also unlikely to eliminate publication's effect on structure. Since webs from the same publication have been built with similar approaches, these webs would have also been built with similar sampling effort. It follows that if webs with high sampling effort were sourced from publications that produced multiple webs, all other webs from those publications would also have high sampling effort, and thus

the publication effect would still be present. Third, although we did not use directed subgraphs (i.e., graphlets) to analyze food webs as is often done, e.g., Borrelli (2015); Cirtwill and Wootton (2022), we do not believe doing so would fundamentally alter our results. We hypothesize that including direction in the edges of graphlets would reveal more structural discrepancies between publications' network(s), and thus make them more unique and difficult to compare. For example, a publication's web consisting of a single top predator would likely become apparent and identifiable from a different publication's web that has many top predators, both of which can be entirely dependent upon the goals of the researchers building the networks rather than the biology of the system itself, e.g., the difference between the food webs from (Parker and Huryn, 2006) with a single top fish predator and (Valiela, 1974) with many top arthropod predators.

Looking forward, there are opportunities to improve our access to a greater number of freely available empirical food webs built by different researchers that are also less problematic to compare. The most ambitious suggestion involves a collaborative effort, in which a global set of food webs is built in a consistent and standardized manner by different researchers across the globe (Winemiller, 1990; Cohen et al., 1993). Currently, much of the structure of freely available species interaction networks is a blackbox; a result of different combinations of the drivers from the three different classes of structure applied in unbeknownst ways. Having available many food webs built using consistent and standardized protocols would allow for more effective comparison of their structure. A more immediate and achievable remedy is for authors of food webs to include as much information about the drivers of structure that each web experiences in their metadata (Poisot et al., 2016b; Kita et al., 2022). As users of free data, we could then more easily decide which sets of webs are comparable or attempt to control for these differences in reported structural drivers. It is also perhaps possible to improve existing webs using inferential methods. While these sorts of approaches are novel, they may be able to overcome sampling bias and data deficiency issues that plague species interaction networks by predicting interactions in cases where no such interaction has been recorded using data from other networks (Poisot et al., 2023). Of course, these methods still require validation to determine if predicted interactions are plausible.

6.6   Conclusion

In our study, we demonstrate that the structure of food webs is primarily defined by each web's publication source. This strong publication effect likely arises since webs are exposed to their publication's distinct combinations of structural drivers that can be broadly categorized into three classes: *biological and environmental factors*, *sampling strategies*, and *network construction methods*. Unfortunately, simply controlling for the publication source of each web is insufficient when comparing webs sourced from different publications since the *real* structural drivers (i.e., of the three aforementioned classes) are likely holistically acting on the structure of webs in nonlinear ways. We suggest that one of the simplest approaches to improve web comparability is for builders of a publication's web(s) to report in metadata the different ways the three classes of structure influence each food web. In this way, researchers that adopt freely available webs can attempt to control for the nonlinear and interacting ways in which the different structural drivers may act.

6.7 Data and code availability

All data and code to reproduce our results are available at: `https://github.com/Chrisb590/On-the-nature-of-structure-in-open-empirical-food-webs`.

6.8 Figures
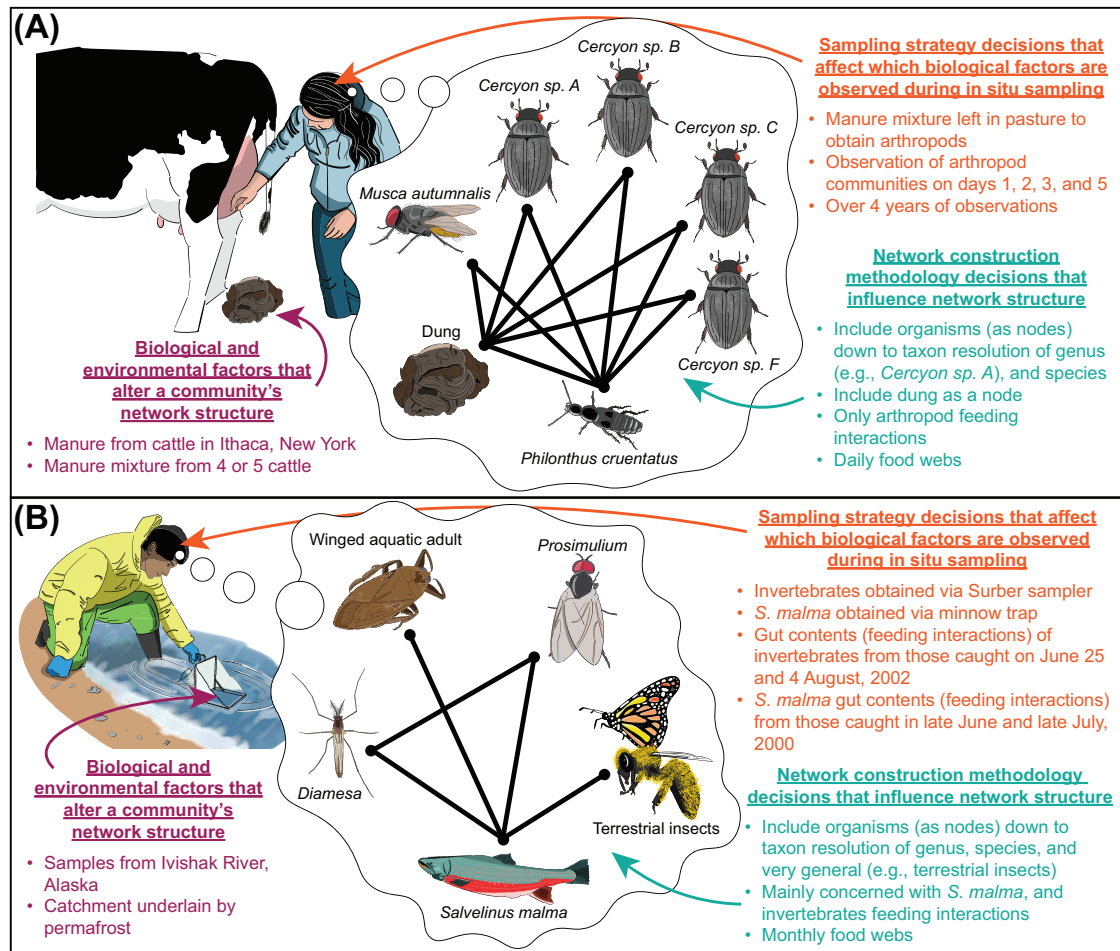
Figure 6.1. Example of how differences in the three classes of structure (i.e., *biological and environmental factors* [purple], *sampling strategies* [orange], and *network construction methodologies* [aqua]) cause food webs sourced from (A) Valiela (1974), and (B) Parker and Huryn (2006) to be very structurally different. Illustration reflects only a subset of nodes from each web (WEB200_ and WEB274_, respectively, from our food webs dataset, see S6.10 Appendix: Table S6.7).
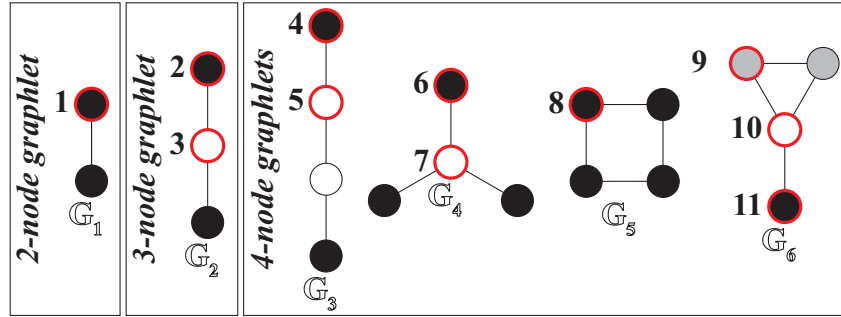
Figure 6.2. The six graphlets ($\mathbb{G}_i$) consisting of two-to-four nodes, and their respective automorphism orbits ("orbits", nodes that are numerically labelled and outlined in red). Each unique shade in a graphlet corresponds to an orbit, which are nodes in the subgraph that are topologically identical.
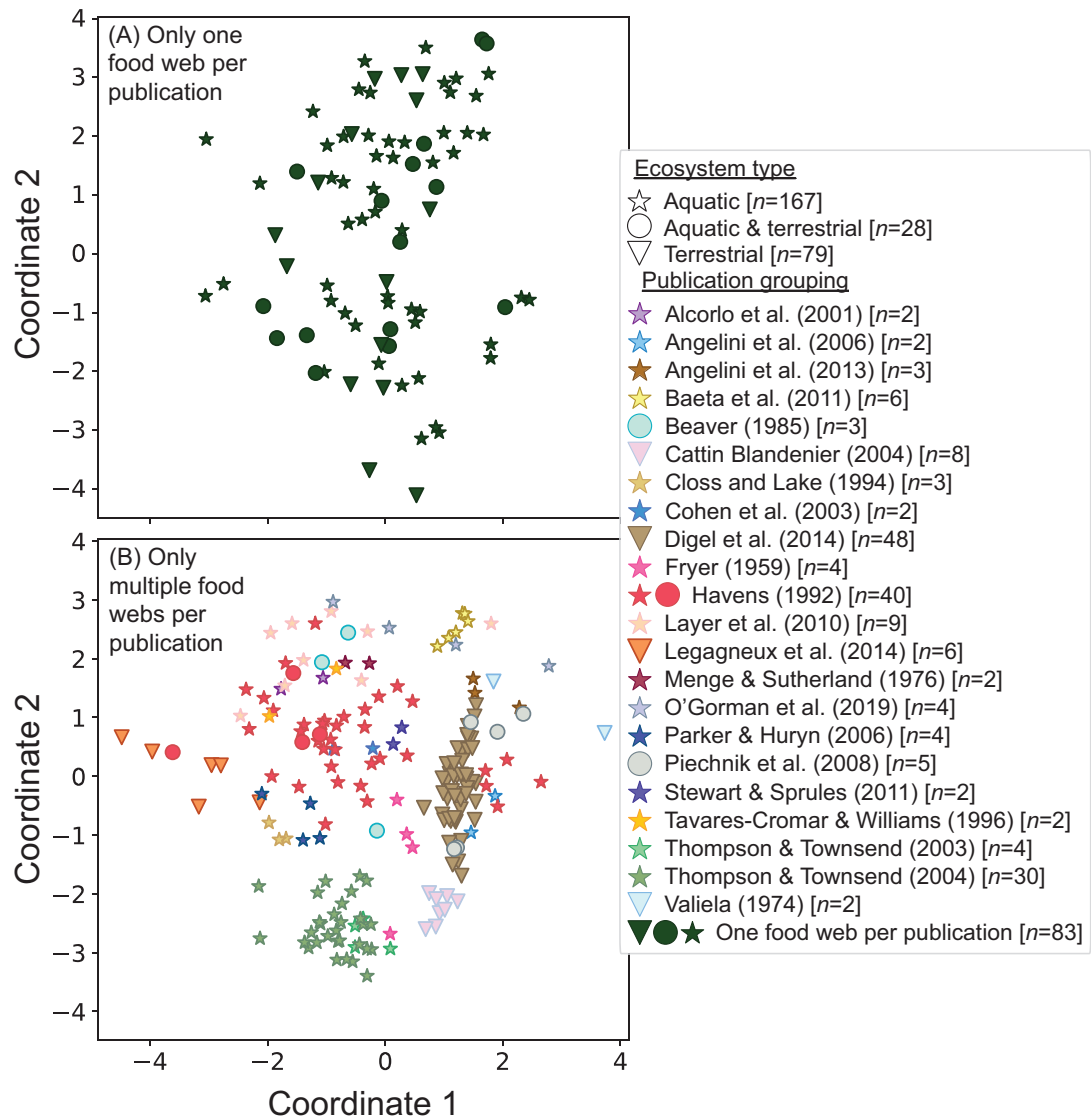
Figure 6.3. Multidimensional scaling of the pairwise graphlet correlation distance–11 (GCD-11) between (A) all food webs from publications that only produced a single network ($n = 83$) and (B) all food webs from publications that produced multiple networks ($n = 191$). Each symbol in the plot is a single food web, where colour reflects the respective food web's source publication grouping, and shape reflects the ecosystem type each food web represents. See S6.10 Appendix: Figure S6.7 for the distribution of all pairwise GCD-11s projected here. Note: this visual mapping is only an approximation of the high-dimensional true pairwise GCD-11s between all food webs.
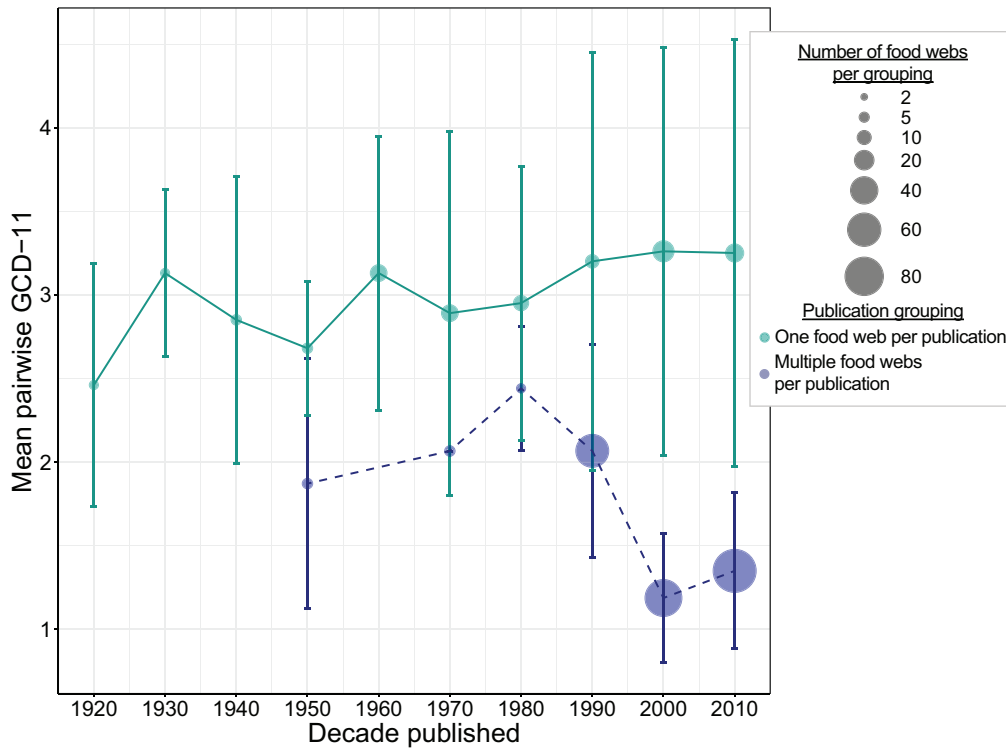
Figure 6.4. Mean pairwise graphlet correlation distance-11 (GCD-11) by decade of publication between food webs sourced from publications that each produced only a single network (teal solid line) and, multiple food webs sourced from the same publication, weighted by the number of networks produced by each publication (blue dashed line). Circle size corresponds to the number of food webs published in each decade. Bars represent mean standard deviation of the pairwise GCD-11 between specified subsets of food webs, which for decades representing publications that provided multiple networks, is weighted by each publication's number of networks.

6.9 Tables

Table 6.1. Mean pairwise graphlet correlation distance-11 (GCD-11) between food webs sampled from the same type of ecosystem or different type of ecosystem. Number of webs from each ecosystem are identified in parentheses. "Aquatic" food webs include those from marine, lakes, rivers, streams, and springs, "aquatic and terrestrial" food webs include those from salt marshes, ponds, bogs, mudflats, pitcher plants, and tree holes filled with water, and "terrestrial" food webs include those from sand dunes, forests, meadows, prairie, and farmlands.

	Aquatic	Aquatic and terrestrial	Terrestrial
Aquatic	3.07 ($n = 167$)		
Aquatic and terrestrial	3.11	3.04 ($n = 28$)	
Terrestrial	3.08	2.96	2.41 ($n = 79$) 3.53 ($n = 31$)[†]

[†]After removing all $n = 48$ "terrestrial" food webs sourced from Digel et al. (2014).

Table 6.2. Mean pairwise graphlet correlation distance-11 (GCD-11) between food webs sourced from the same publication grouping. Multiple food webs sourced from the same publication are termed "multiple food webs per publication" and food webs sourced from publications that each produced only a single network are termed "one food web per publication". See S6.10 Appendix: Table S6.6 for a list of publications that provided more than one web and each publication's mean pairwise GCD-11.

Publication grouping	Mean pairwise GCD-11	Number of food webs	Number of publications
One food web per publication	3.13	83	83
Multiple food webs per publication	1.51[‡]	191	22
Multiple food webs per publication (before or during 1990s)	2.07[‡]	56	7
Multiple food webs per publication (after 1990s)	1.28[‡]	135	15

[‡]Calculated by taking the average of the mean pairwise GCD-11s between food webs from the same publication, weighted by the number of networks produced by each publication.

S6.10 Appendix

S6.10.1 Errors in food webs

Here, we provide the changes we made to the collected binary webs' adjacency matrices (Table S6.1), where rows and columns correspond to biological entities.

Table S6.1. Changes to food web adjacency matrices. Although not listed here, it is important to ensure no extra white space characters are included either in front or behind column/row string names, otherwise R (R Core Team, 2023) will interpret these names as different nodes if there are also rows/columns with the same string name but without additional white space characters.

Network name	Changes made	Network result
WEB33_	Row labelled "Gyraulus costulatus\" was merged with the already present row labelled "Gyraulus costulatus".	Reduced network size by 1 node.
WEB41_	2 rows and 2 columns labelled "tuna" (different interaction configurations for each row and each column) were merged into a single row and a single column, respectively.	
WEB214_	Row labelled "Eukieffidriella 'naonella' type" was merged with the already present row labelled "Eukiefferiella 'naonella' type".	Reduced network size by 1 node.
	2 rows labelled "Melosira italica" (different interaction configurations for each row) were merged into a single row.	
WEB215_	Row labelled "Eukieferiella pseudomontana" was merged with the already present row labelled "Eukiefferiella pseudomontana".	Reduced network size by 1 node.
WEB217_	Row labelled "Eukieffidrella pseudomontana" was merged with the already present row labelled "Eukiefferiella pseudomontana".	Reduced network size by 1 node.
	Row labelled "Fatigia pele" was merged with the already present row labelled "Fattigia pele".	Reduced network size by 1 node.
WEB218_	Row labelled "Austrosimulium austranse" was merged with the already present row labelled "Austrosimulium australense".	Reduced network size by 1 node.
	Row labelled "Eukiefidrella brundini" was merged with the already present row labelled "Eukiefferiella brundini".	Reduced network size by 1 node.
	Row labelled "Eukieflidrella brundini" was merged with the already present row labelled "Eukiefferiella brundini".	Reduced network size by 1 node.

Network name	Changes made	Network result
WEB219_	Row labelled "Pycnocntria evecta" was merged with the already present row labelled "Pycnocentria evecta".	Reduced network size by 1 node.
	Row labelled "Zelanoperla sp." was merged with the already present row labelled "Zelandoperla sp.".	Reduced network size by 1 node.
WEB220_	Row labelled "Eukieflidriella brundini" was merged with the already present row labelled "Eukiefferiella brundini".	Reduced network size by 1 node.
	Row labelled "Eukieffidriella brundini" was merged with the already present row labelled "Eukiefferiella brundini".	Reduced network size by 1 node.
	Row labelled "Tiphobiosis montana" was merged with the already present row labelled "Tiphobiosis montana".	Reduced network size by 1 node.
	Row labelled "Aphrophila neozelandicus" was merged with the already present row labelled "Aphrophila neozelandica".	Reduced network size by 1 node.
WEB221_	Row labelled "Aotepsyche" was merged with the already present row labelled "Aoteapsyche".	Reduced network size by 1 node.
WEB223_	Row labelled "Cymbella kappi" was merged with the already present row labelled "Cymbella kappii".	Reduced network size by 1 node.
WEB224_	Row labelled "Stictoclcaius" was merged with the already present row labelled "Stictocladius".	Reduced network size by 1 node.
WEB236_	2 rows labelled "Zelandoperla agnetis (McLellan)" (different interaction configurations for each row) were merged into a single row.	
	Row labelled "Eukiefidrella" was merged with the already present row labelled "Eukiefferiella".	Reduced network size by 1 node.
	Row labelled "Eukiefiriella" was merged with the already present row labelled "Eukiefferiella".	Reduced network size by 1 node.

... Continuation of Table S6.1.

Network name	Changes made	Network result
WEB236_	Row labelled "Stictoclcaius" was merged with the already present row labelled "Stictocladius".	Reduced network size by 1 node.
	2 columns labelled "Zelandoperla agnetis (McLellan)" (different interaction configurations for each column) were merged into a single column.	
WEB238_	2 rows labelled "Achnanthes linearis" (different interaction configurations for each row) were merged into a single row.	
WEB240_	2 rows labelled "Achnanthes linearis" (different interaction configurations for each row) were merged into a single row.	
WEB244_	2 rows labelled "Achnanthes linearis" (different interaction configurations for each row) were merged into a single row.	
WEB246_	2 rows labelled "Achnanthes linearis" (different interaction configurations for each row) were merged into a single row.	
WEB257_	Row labelled "Amphithoe valida" was merged with the already present row labelled "Ampithoe valida".	Reduced network size by 1 node.
WEB258_	Row labelled "Amphithoe valida" was merged with the already present row labelled "Ampithoe valida".	Reduced network size by 1 node.
WEB259_	Row labelled "Amphithoe valida" was merged with the already present row labelled "Ampithoe valida".	Reduced network size by 1 node.
WEB260_	Row labelled "Amphithoe valida" was merged with the already present row labelled "Ampithoe valida".	Reduced network size by 1 node.
WEB262_	Row labelled "Glicera tridactyla" was merged with the already present row labelled "Glycera tridactyla".	Reduced network size by 1 node.

Network name	Changes made	Network result
WEB320_	Rows labelled "Import", "Sum", and "(1-Sum)" were removed.	Reduced network size by 3 nodes.
WEB321_	Rows labelled "Import", "Sum", and "(1-Sum)" were removed.	Reduced network size by 3 nodes.
WEB322_	Rows labelled "Import", "Sum", and "(1-Sum)" were removed.	Reduced network size by 3 nodes.
WEB323_	Row labelled "Import" was removed.	Reduced network size by 1 node.
WEB324_	Rows labelled "Import", "Sum", and "(1-Sum)" were removed.	Reduced network size by 3 nodes.
WEB338_	Rows labelled "Import" and "Discard" were removed.	Reduced network size by 2 nodes.
WEB345_	2 rows and 2 columns labelled "Medium-sized ciliates (herbivore)" (different interaction configurations for each row and each column) were merged into a single row and a single column, respectively.	
WEB348_	Row labelled "Polychates" was merged with the already present row labelled "Polychaete".	Reduced network size by 1 node.
WEB350_	Row labelled "Polychates" was merged with the already present row labelled "Polychaetes".	Reduced network size by 1 node.
	2 rows labelled "Ostracods" (different interaction configurations for each row) were merged into a single row.	
WEB352_	Row labelled "Import" was removed.	Reduced network size by 1 node.
WEB353_	Row labelled "Import" was removed.	Reduced network size by 1 node.
WEB359_	11 rows and 11 columns labelled "unknown bacterium" (different interaction configurations for each row and column) were merged into a single row and a single column, respectively.	

Network name	Changes made	Network result
WEB359_	12 rows and 12 columns labelled "unknown protozoan" (different interaction configurations for each row and column) were merged into a single row and a single column, respectively.	
	3 rows and 3 columns labelled "Sphingomonas" (different interaction configurations for each row and column) were merged into a single row and a single column, respectively.	
	3 rows and 3 columns labelled "Flectobacillus" (different interaction configurations for each row and column) were merged into a single row and a single column, respectively.	
	2 rows and 2 columns labelled "Chromobacterium" (different interaction configurations for each row and column) were merged into a single row and a single column, respectively.	
Carpinteria_	2 rows and 2 columns labelled "eugregarine" (different interaction configurations for each row and each column) were merged into a single row and a single column, respectively.	
Beaver_Lake_	Row and column labelled "Salmo rutta" was corrected to "Salmo trutta".	
Kongsfjorde_	Row labelled "Eumicotremus derjugini" was merged with the already present column labelled "Eumicrotremus derjugini".	Reduced network size by 1 node.
mown_Clmown1_	Changed row and column labelled "Edaphus_blÅ¸hweissi" to "Edaphus".	
mown_Scmown2_	Changed row and column labelled "Edaphus_blÅ¸hweissi" to "Edaphus".	
not_mown_ClControl1_	Changed row and column labelled "Edaphus_blÅ¸hweissi" to "Edaphus".	
not_mown_ScControl1_	Changed row and column labelled "Edaphus_blÅ¸hweissi" to "Edaphus".	

Network name	Changes made	Network result
not_mown_ScControl2	Changed row and column labelled "Edaphus_blÅ¸hweissi" to "Edaphus".	

S6.10.2 Graphlet correlation distance-11 example

Given a food web, such as "Network 1" depicted in Figure S6.2, we first count the number of times nodes occupy orbit positions (Figure S6.1). Specifically, the number of times nodes occupy the orbits of graphlets $\mathbb{G}_1$ (orbit 1), $\mathbb{G}_2$ (orbits 2 and 3), $\mathbb{G}_3$ (orbits 4 and 5), $\mathbb{G}_4$ (orbits 6 and 7), $\mathbb{G}_5$ (orbit 8), and $\mathbb{G}_6$ (orbits 9, 10, and 11). In tallying the number of times a node occupies different orbit positions, the *graphlet degree vector-11* for a node is constructed. In Figure S6.2, we provide the graphlet degree vector-11 for "node A" of Network 1.

Once graphlet degree vector-11s for each node in a food web are determined, the *graphlet correlation matrix-11* can be assembled. In doing so, all possible Spearman's correlations between the number of times all nodes in a food web occupy specific orbits are evaluated (see the highlighted green boxes in Figure S6.3 as an example of a single Spearman's correlation for Network 1).

By computing the pairwise Euclidean distances between graphlet correlation matrix-11s, we can obtain an estimate of the topological differences between food webs in a given set. An example of a single pairwise Euclidean distance between two graphlet correlation matrices (i.e., of two networks or food webs) is shown in Figure S6.4.

Using all pairwise Euclidean distances between food webs, we can visualize their dissimilarity by projecting their distances using multidimensional scaling (MDS; see Figure S6.5).
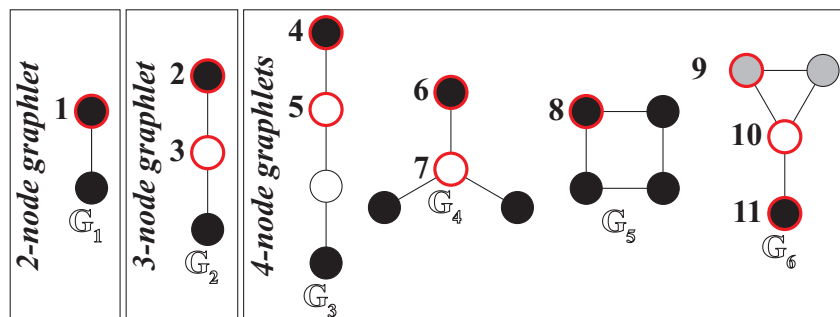
Figure S6.1. The six graphlets ($\mathbb{G}_i$) consisting of two-to-four nodes, and their respective orbits (i.e., the corresponding 11 numerically labelled node positions). Each unique shade in a single graphlet corresponds to a unique orbit in that graphlet.
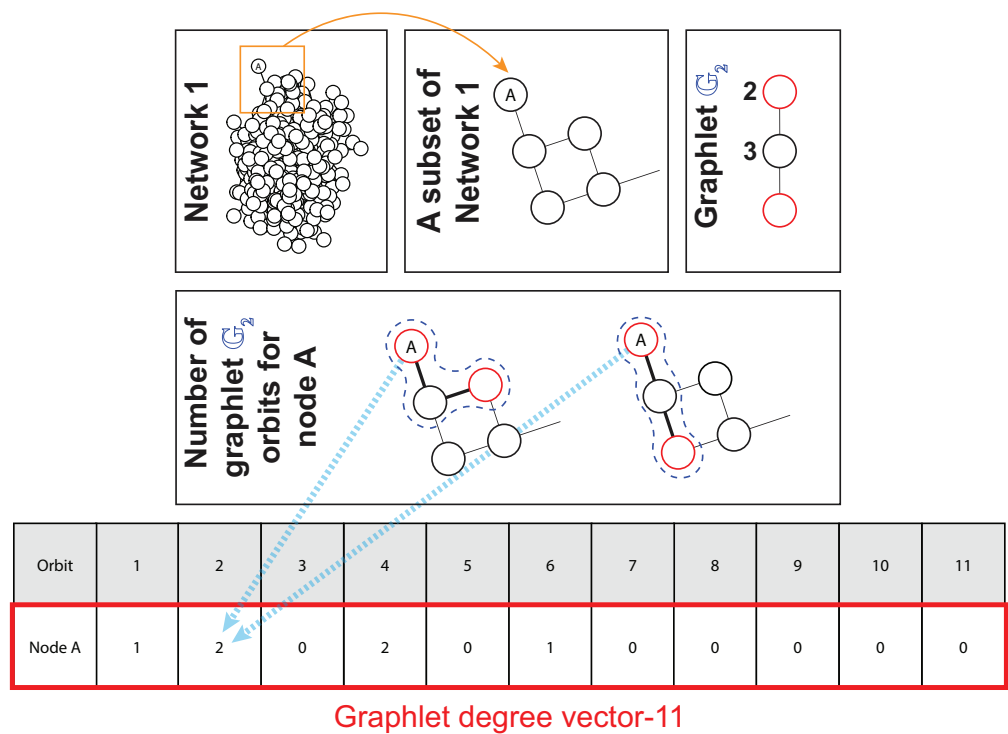
Figure S6.2. Example calculation of the counts for orbit 2 in a graphlet degree vector-11 for node A of Network 1.
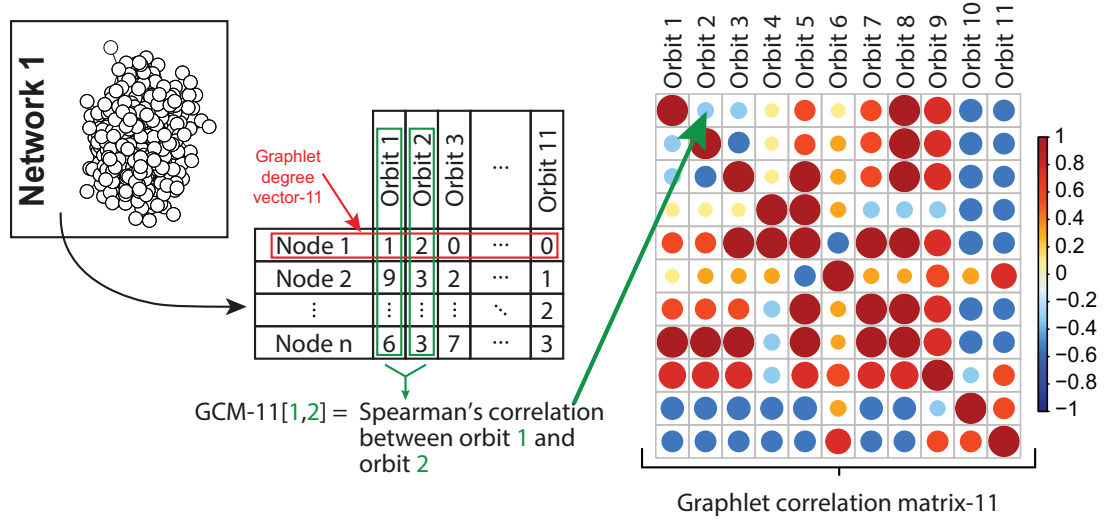
Figure S6.3. Example calculation of a graphlet correlation matrix-11 (GCM-11) for Network 1 using the 11 orbits that comprise the graphlet correlation distance-11 method. First, graphlet degree vector-11s for each node in the network are calculated (a single vector is highlighted in red). Next, Spearman's correlations are calculated between all pairs of orbits using the number of times each node occupies each orbit (an example of the vectors used in a single correlation is highlighted in green). The resulting correlations form entries within the GCM-11.
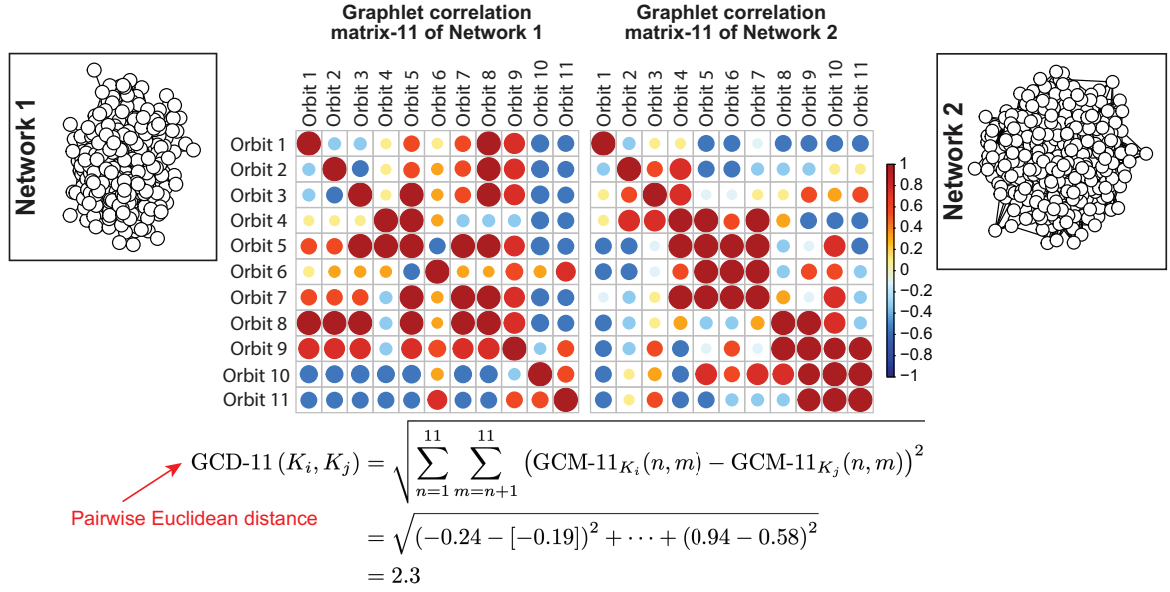
Figure S6.4. The formula and an example calculation of the pairwise graphlet correlation distance-11 (pairwise GCD-11) using the two graphlet correlation matrix-11s of Network 1 and Network 2.

Graphlet correlation matrix-11 of Network 1 and **Graphlet correlation matrix-11 of Network 2**, with axes labeled Orbit 1 through Orbit 11.

$$\text{GCD-11}\,(K_i, K_j) = \sqrt{\sum_{n=1}^{11} \sum_{m=n+1}^{11} \left(\text{GCM-11}_{K_i}(n,m) - \text{GCM-11}_{K_j}(n,m)\right)^2}$$

Pairwise Euclidean distance

$$= \sqrt{(-0.24 - [-0.19])^2 + \cdots + (0.94 - 0.58)^2}$$

$$= 2.3$$
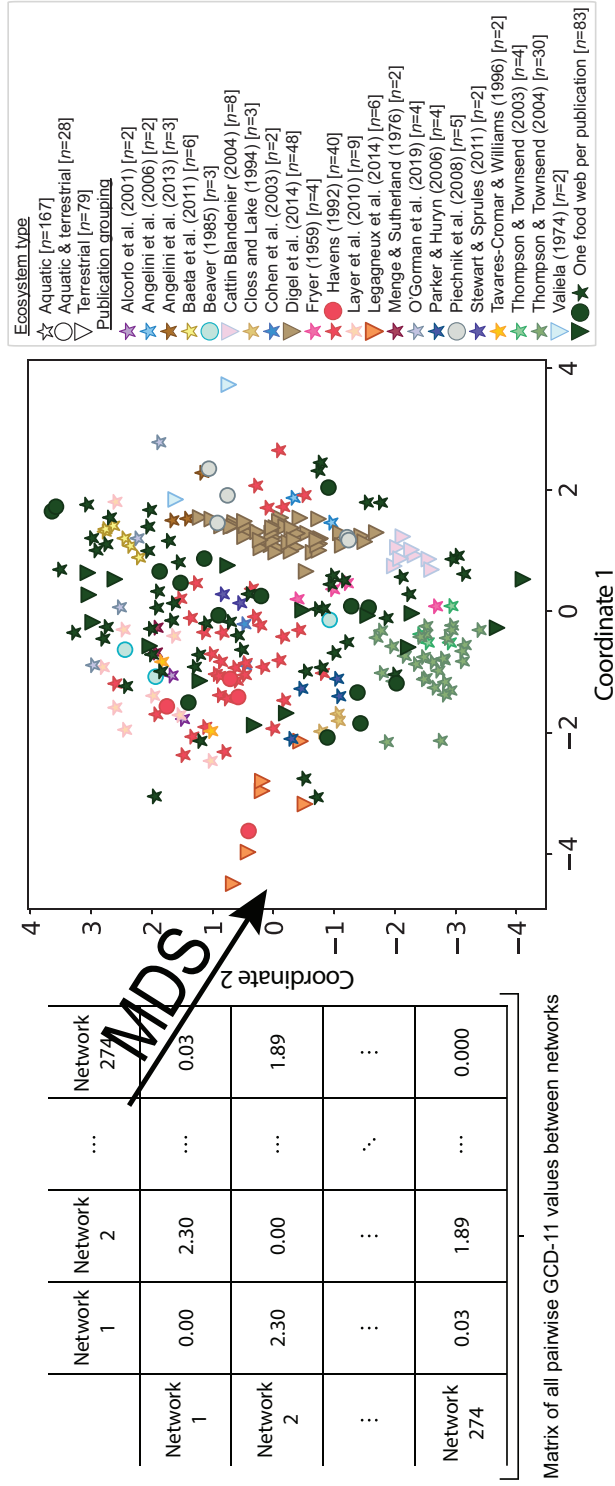
Figure S6.5. Multidimensional scaling (MDS) projection of all pairwise GCD-11s between the 274 food webs, as also shown in Figure 6.3.

S6.10.3 Example of mean pairwise GCD-11 as a dispersion metric

In Figure S6.6, we provide a toy example of how the mean pairwise GCD-11 between defined sets of food webs (i.e., green circles and purple squares) can be used as a metric of dispersion within those sets of webs. We note that the distances represented in the multidimensional scaling plot of Figure S6.6 are only a 2-dimensional best approximation to the true pairwise distances between all 7 food webs using pairwise GCD-11s (as calculated via eq. 6.1). We used the "true" pairwise GCD-11s between food webs (i.e., the pairwise input data used to perform a multidimensional scaling) throughout the manuscript for all quantitative measurements.

	a	b	c	d	e	f	g
a	0	6.3	6.3	3.5	9.6	12.8	12.5
b	6.3	0	4.6	7.2	3.6	6.6	6.2
c	6.3	4.6	0	4.5	7.8	10.3	8.5
d	3.5	7.2	4.5	0	10.8	13.8	12.7
e	9.6	3.6	7.8	10.8	0	3.2	4.3
f	12.8	6.6	10.3	13.8	3.2	0	3.4
g	12.5	6.2	8.5	12.7	4.3	3.4	0

"True" pairwise GCD-11s between all 7 food webs prior to visualizing in multidimensional scaling

Mean pairwise GCD-11: (6.3+4.6+4.5+3.5+6.3+7.2)/6=5.4

Mean pairwise GCD-11: (3.2+3.4+4.3)/3≈3.6
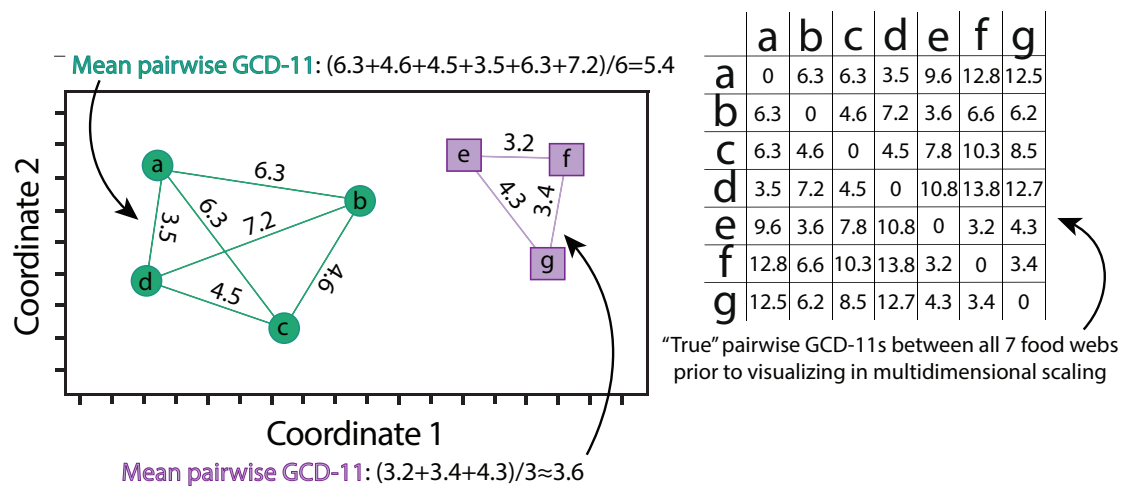
Figure S6.6. Example multidimensional scaling (MDS) [plot on left] of all pairwise graphlet correlation distance-11s (GCD-11) [matrix on right] between food webs ($n = 7$) mapped in 2-dimensional space. Lines are drawn on the MDS to convey the pairwise distances between symbols/webs (but distances are obtained from the matrix). Each symbol in the plot is a single food web, where colour and shape reflects the respective food web's grouping. Distances between webs of opposite groupings are not drawn on plot for the sake of simplicity.

S6.10.4   Distribution of all pairwise GCD-11 values

In Figure S6.7, we provide the distribution of all $n = 37401$ pairwise GCD-11 values between the 274 food webs used in this study, where total pairwise distances are defined by

$$\frac{\text{number of networks} \cdot (\text{number of networks} - 1)}{2} = \frac{274 \cdot 273}{2} = 37401 \, . \qquad \text{(S6.1)}$$

The total number of pairwise distances between: (i) the 83 food webs sourced from a publication that produced only a single network was $n = 3403$, (ii) the 191 food webs sourced from 22 publications that each produced multiple networks was $n = 2487$, and (iii) all other webs (i.e., between two food webs sourced from two different publications that produced multiple networks or a food web from a publication that produced only a single network and a food web from a publication that produced multiple networks) was $n = 31511$.

Strikingly, the low pairwise GCD-11s between food webs analyzed in our study were dominated by those webs that shared a publication source. In particular, the majority (i.e., about 62%) of the smallest pairwise GCD-11s (i.e., those ≤ 1.5) measured between all food webs were only between those webs sourced from the same publication that produced multiple networks, despite only making up 7% of the total pairwise distances (i.e., 2487/37401). Moreover, 87% of all pairwise GCD-11s recorded between food webs that shared a publication source were ≤ 2.5. In comparison, only about 30% and 27% of food webs from publications that produced only a single network, and all other pairwise distances between webs, were ≤ 2.5.

These results show that it would be extremely difficult—if not impossible—to categorize food webs using the same number of webs ($n = 191$) to maximize structural similarity, other than by the publication groupings presented in this manuscript (i.e., food webs sourced from the same publication that produced multiple networks). Given that the majority of small pairwise GCD-11s are already categorized as food webs that share a publication source, there are very few pairwise GCD-11s that remain which could be categorized to further maximize structural similarity. Moreover, these categorizations would need to be based on a priori rules rooted in ecological theory, rather than categorizing food webs simply based on small GCD-11s.
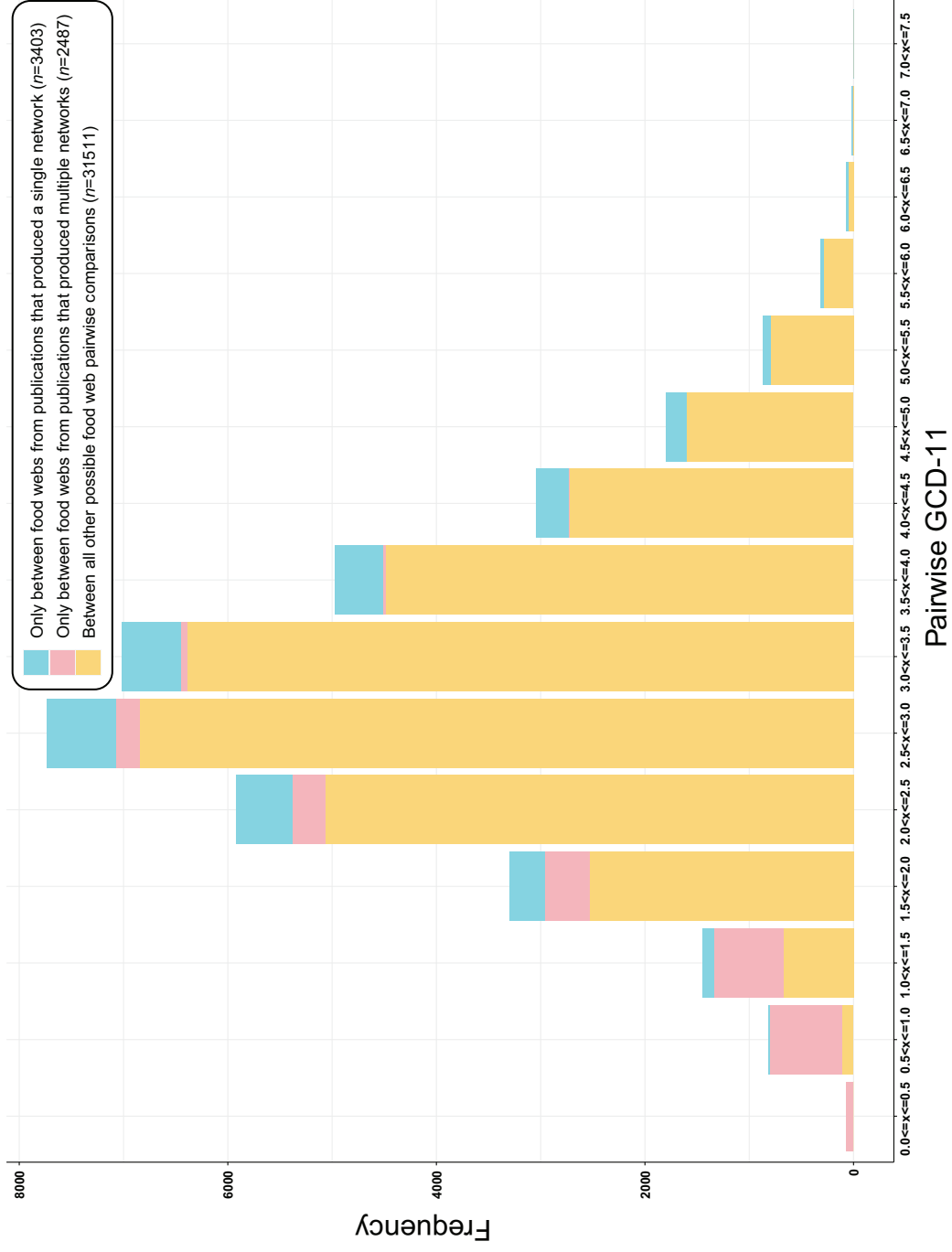
Figure S6.7. The distribution of all pairwise graphlet correlation distance-11s (GCD-11s) between 247 food webs. n in legend corresponds to the number of pairwise GCD-11s for each category, where all total pairwise distances is $n = 37401$ [i.e., $\frac{\text{number of networks} \cdot (\text{number of networks} - 1)}{2} = \frac{274 \cdot 273}{2}$].

S6.10.5   No substantial evidence of increased structurally similarity between the "aquatic" food webs of "lake", "marine", "river", and "stream"

Here, we test whether "aquatic" food webs—when further identified down to either "lake", "marine", "river", and "stream"—have increased structurally similarity (i.e., smaller mean pairwise GCD-11). Note: we omitted the single food web sampled from a "spring" ecosystem (i.e., WEB45_) in this analysis, since it is impossible to evaluate mean pairwise GCD-11 with only a single network.

S6.10.5.1   Analysis

Since food webs sourced from the same publication are already known to be highly similar to each other (i.e., mean pairwise GCD-11 of 1.51 [Table 6.2]), we removed the publication effect from this analysis by only using a single web from a publication that provided multiple networks. As a means of reducing the burden of sampling across all possible different and unique combinations of taking a single web from each of the publications that provided multiple networks for the "aquatic" food web ecosystem, we simply randomly chose a single web from each of these publication. We refer to a collated combination of randomly chosen webs (each one from a unique publication source that provided multiple networks), and all webs sourced from publications that each provided only a single network, as a single realization. When analyzing the mean pairwise GCD-11 between food webs from the same "aquatic" ecosystem (e.g., "lake"), we averaged all mean pairwise GCD-11 values across 200 realizations between webs only from the same "aquatic" ecosystem. When analyzing the mean pairwise GCD-11 between food webs across "aquatic" ecosystems (e.g., "lake" and "marine"), we averaged all mean pairwise GCD-11 values across 200 realizations between food webs only from the two *different* "aquatic" ecosystems. Below we list the number of food webs in a realization from each of these "aquatic" ecosystems.

S6.10.5.2   Data

Of the "lake" food webs available from our dataset, 7 webs were sourced from publications that each provided only a single network, while 49 webs were sourced from 6 publications that each provided multiple networks (see Table S6.7 for list). Specifically, 3 webs were sourced from Angelini et al. (2013), 2 webs were sourced from Stewart and Sprules (2011), 2 webs were sourced from Alcorlo et al. (2001), 2 webs were sourced from Cohen et al. (2003), 4 webs were sourced from Fryer (1959), and 36 webs were sourced from Havens (1992). A given realization then consisted of 13 "lake" food webs.

Of the "marine" food webs available from our dataset, 27 webs were sourced from publications that each provided only a single network, while 8 webs were sourced from 2 publications that each provided multiple networks (see Table S6.7 for list). Specifically, 6 webs were sourced from Baeta et al. (2011), and 2 webs were sourced from Menge and Sutherland (1976). A given realization then consisted of 29 "marine" food webs.

Of the "river" food webs available from our dataset, 6 webs were sourced from publications that each provided only a single network, while 2 webs were sourced from 1 publication that provided multiple networks (see Table S6.7 for list). Specifically, 2 webs were sourced from Angelini et al. (2006). A given realization then consisted of 7 "river" food webs.

Of the "stream" food webs available from our dataset, 11 webs were sourced from publications that each provided only a single network, while 56 webs were sourced from 7 publication that provided multiple networks (see Table S6.7 for list). Specifically, 3 webs were sourced from Closs and Lake (1994), 9 webs were sourced from Layer et al. (2010), 4 webs were sourced from O'Gorman et al. (2019), 4 webs were sourced from Parker and Huryn (2006), 2 webs were sourced from Tavares-Cromar and Williams (1996), 4 webs were sourced from Thompson and Townsend (2003), and 30 webs were sourced from Thompson and Townsend (2004). A given realization then consisted of 18 "stream" food webs.

S6.10.5.3 Findings

Altogether, there is no substantial evidence that "aquatic" food webs further identified to "lake", "marine", "river", or "stream" are more structurally similar (i.e., smaller mean pairwise GCD-11 between webs from the same "aquatic" ecosystem) [Table S6.2]. While "lake" food webs were moderately more structurally similar to each other (i.e., mean pairwise GCD-11: 2.58)—as compared to any other non-publication type grouping studied for this paper—food webs sourced from the same publication were much more structurally similar to each other (i.e., mean pairwise GCD-11: 1.51), especially those published after the 1990s (i.e., mean pairwise GCD-11: 1.28) [Table 6.2]. Moreover, the other three types of "aquatic" food webs had considerably larger mean pairwise GCD-11 than "lakes" (i.e., "marine": 3.16, "river": 2.87, and "stream" 3.21).

Table S6.2. Mean pairwise graphlet correlation distance-11 (GCD-11) between food webs sampled from the same type or different "aquatic" ecosystem. Number of webs from each "aquatic" ecosystem are identified in parentheses.

	Lake	Marine	River	Stream
Lake	2.58 ($n = 13$)			
Marine	2.96	3.16 ($n = 29$)		
River	2.71	3.17	2.87 ($n = 7$)	
Stream	2.93	3.24	2.97	3.21 ($n = 18$)

S6.10.6 Median pairwise GCD-11

Table S6.3. Median pairwise graphlet correlation distance-11 (GCD-11) between food webs sampled from the same type of ecosystem or different type of ecosystem. Number of webs from each ecosystem are identified in parentheses. "Aquatic" food webs include those from marine, lakes, rivers, streams, and springs, "aquatic and terrestrial" food webs include those from salt marshes, ponds, bogs, mudflats, pitcher plants, and tree holes filled with water, and "terrestrial" food webs include those from sand dunes, forests, meadows, prairie, and farmlands.

	Aquatic	Aquatic and terrestrial	Terrestrial
Aquatic	3.01 ($n = 167$)		
Aquatic and terrestrial	3.06	3.09 ($n = 28$)	
Terrestrial	3.00	2.86	2.33 ($n = 79$) 3.72 ($n = 31$)[†]

[†]After removing all $n = 48$ "terrestrial" food webs sourced from Digel et al. (2014).

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Table S6.4. Median pairwise graphlet correlation distance-11 (GCD-11) between food webs sourced from the same publication grouping. Multiple food webs sourced from the same publication are termed "multiple food webs per publication" and food webs sourced from publications that each produced only a single network are termed "one food web per publication". See Table S6.6 for a list of publications that provided more than one food web and each publication's mean pairwise GCD-11.

Publication grouping	Median pairwise GCD-11	Number of food webs	Number of publications
One food web per publication	3.02	83	83
Multiple food webs per publication	1.15‡	191	22
Multiple food webs per publication (before or during 1990s)	2.00‡	56	7
Multiple food webs per publication (after 1990s)	1.08‡	135	15

‡Calculated by taking the median of the median pairwise GCD-11s between food webs from the same publication.

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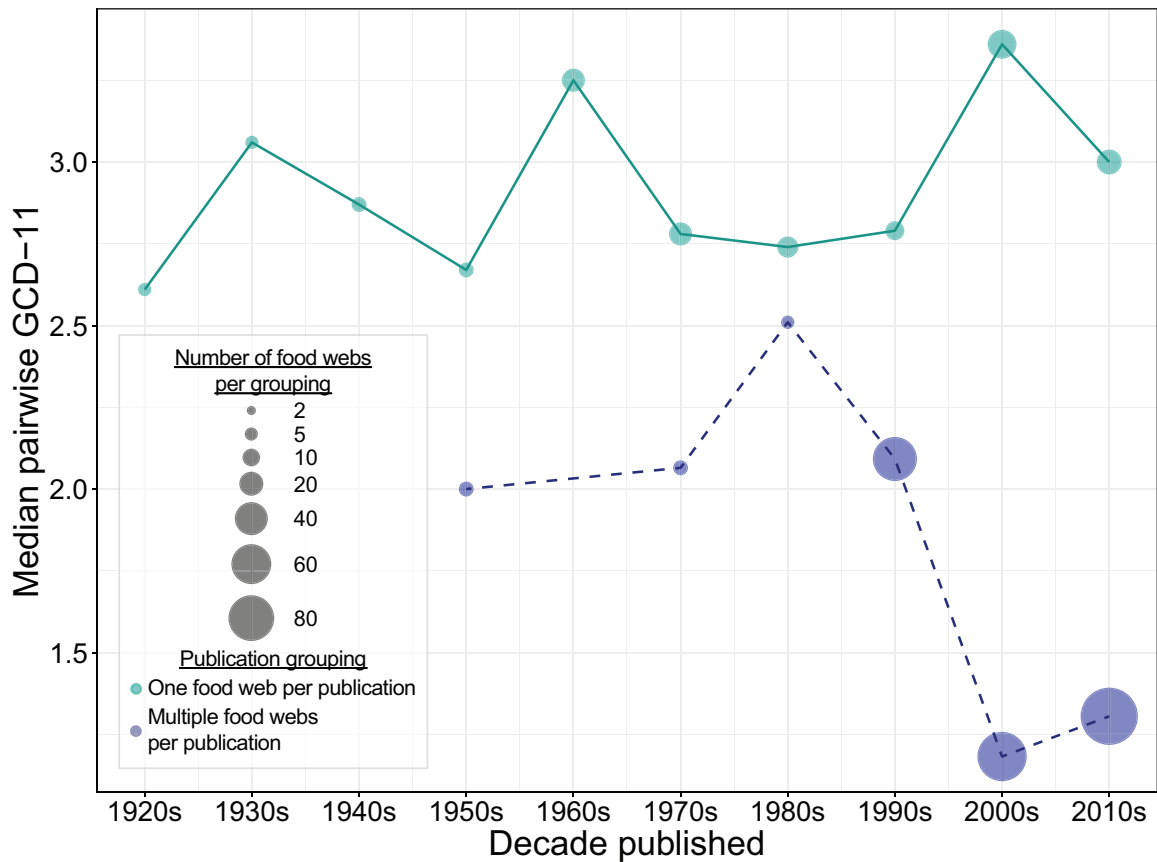
Figure S6.8. Median pairwise graphlet correlation distance-11 (GCD-11) by decade published between food webs sourced from publications that each produced only a single network (teal solid line) and, multiple food webs sourced from the same publication, weighted by the number of networks produced by each publication (blue dashed line). Circle size corresponds to the number of food webs published in the decade.

S6.10.7 No evidence that the number of nodes or standard deviation in the number of nodes influences pairwise GCD-11

Here, we test whether the number of nodes (i.e., web size) or standard deviation in the number of nodes (i.e., standard deviation of web size) in food webs influenced both mean and individual pairwise GCD-11.

S6.10.7.1 Mean pairwise GCD-11 between food webs from publications that produced only a single network

We divided webs sourced from publications that each provided only a single network into quartiles based on their number of nodes (Table S6.5). With respect to these quartiles (labelled Q1, Q2, Q3, and Q4), we found that although both web size (mean number of nodes for Q1: 12.52, Q2: 19.57, Q3: 28.89, and Q4: 117.95) and standard deviation in web size (mean standard deviation of nodes for Q1: 1.59, Q2: 3.09, Q3: 3.05, and Q4: 108.76) differed greatly between the quartiles, there were no large differences between their respective mean pairwise GCD-11 (mean pairwise GCD-11 for Q1: 2.70, Q2: 2.90, Q3: 3.04, and Q4: 3.05). Hence, neither web size or standard deviation in web size influenced mean pairwise GCD-11.

S6.10.7.2 Mean pairwise GCD-11 between food webs from publications that produced multiple networks

To keep publication a factor rather than separate webs into quartiles as was done above for webs sourced from publications that each provided only a single network, we chose to instead evaluate the regressions of both mean web size and standard deviation in web size across publications to explain mean pairwise GCD-11 (Figure S6.9). In both cases, neither web size nor the standard deviation in web size explained mean pairwise GCD-11 across publication ($p > 0.34$, and $p > 0.55$, respectively).

S6.10.7.3 Pairwise GCD-11 between all food webs

Regardless of publication source, we compared all pairwise graphlet correlation distance-11s (GCD-11s) between the 274 food webs in this study. This amounts to a total of 37401 pairwise distances:

$$\frac{\text{number of networks} \cdot (\text{number of networks} - 1)}{2} = \frac{274 \cdot 273}{2} = 37401 \, . \qquad \text{(S6.2)}$$

In both cases, neither web size ($R^2 = 0.02$) nor standard deviation in web size ($R^2 = 0.02$) meaningfully explained pairwise GCD-11s (Figure S6.10).

Table S6.5. Mean pairwise graphlet correlation distance-11 (GCD-11) between food webs sourced from publications that each produced only a single network (i.e., one food per publication) when partitioned into quartiles based the number of nodes.

Quartile number of nodes	Mean pairwise GCD-11	Mean number of nodes	S.D. number of nodes	Number of food webs
1	2.70	12.52	1.59	23
2	2.90	19.57	3.09	21
3	3.04	28.89	3.05	19
4	3.05	117.95	108.76	20
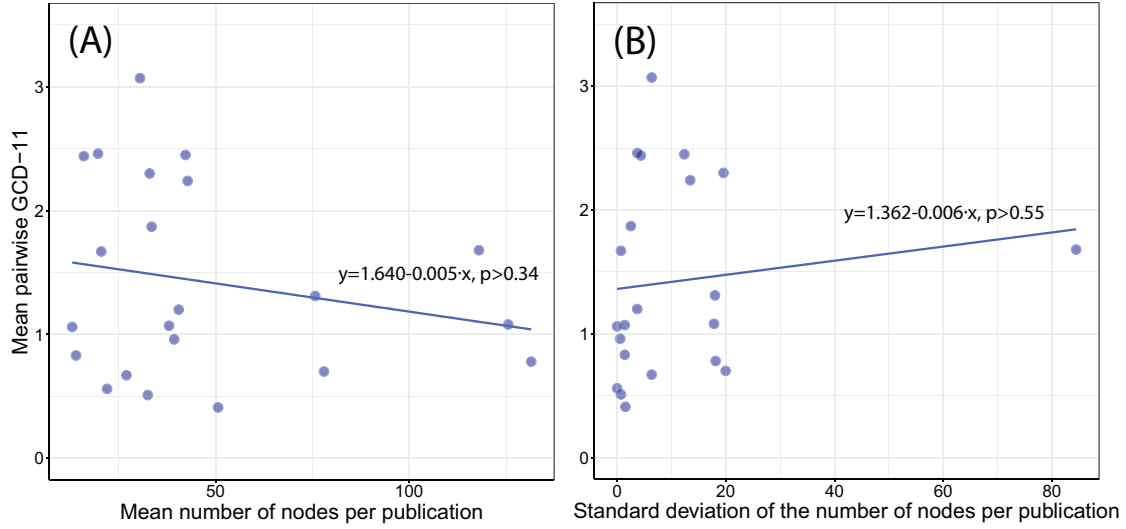
Figure S6.9. **(A)** Mean pairwise graphlet correlation distance-11 (GCD-11) as a function of the mean number of nodes between food webs sourced from the same publication ($n = 22$). **(B)** Mean pairwise GCD-11 as a function of the standard deviation in the number of nodes between food webs sourced from the same publication ($n = 22$). See Table S6.6 for exact values for the mean pairwise GCD-11, the mean number of nodes, and the standard deviation in the number of nodes between food webs sourced from the same publication.
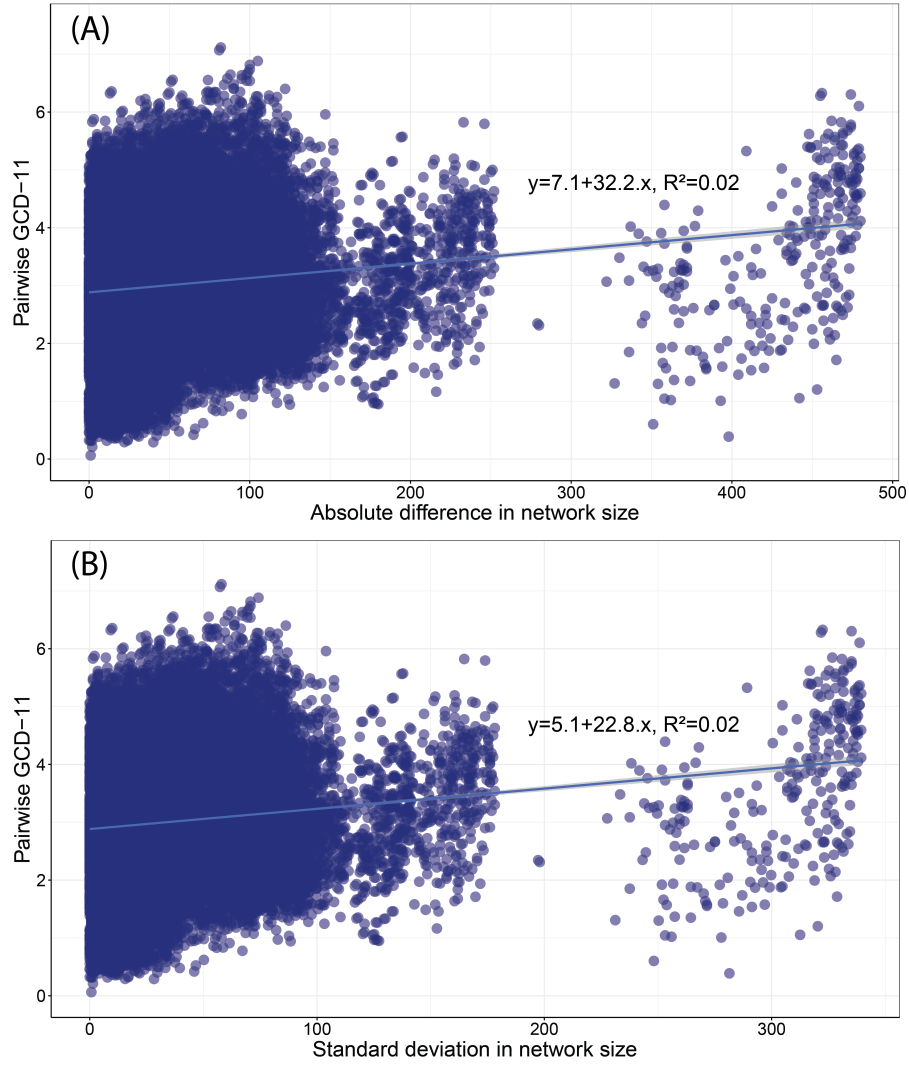
Figure S6.10. **(A)** All possible $n = 37401$ pairwise graphlet correlation distance-11s (GCD-11s) between the 274 food webs as a function of the absolute difference in network size (i.e., number of nodes), where each point is a pairwise GCD-11 measure between two webs. **(B)** All possible $n = 37401$ pairwise graphlet correlation distance-11s (GCD-11s) between the 274 food webs as a function of the standard deviation in network size (i.e., number of nodes), where each point is a pairwise GCD-11 measure between two webs.

Table S6.6. Mean pairwise graphlet correlation distance-11 (GCD-11) between food webs from the same publication grouping. Each food web sourced from a publication that produced only a single network belong to the grouping "one food web per publication", while multiple food webs sourced from the same publication belong to that publication's grouping.

Publication grouping	Mean pairwise GCD-11	Mean number of nodes	S.D. number of nodes	Number of food webs
Closs and Lake (1994)	0.41	50.67	1.53	3
Angelini et al. (2006)	0.51	32.50	0.71	2
Stewart and Sprules (2011)	0.56	22.00	0.00	2
Baeta et al. (2011)	0.67	27.00	6.36	6
Thompson and Townsend (2003)	0.70	78.00	19.98	4
Cattin Blandenier (2004)	0.78	131.50	18.13	8
Alcorlo et al. (2001)	0.83	14.00	1.41	2
Angelini et al. (2013)	0.96	39.33	0.58	3
Menge and Sutherland (1976)	1.06	13.00	0.00	2
Tavares-Cromar and Williams (1996)	1.07	38.00	1.41	2
Digel et al. (2014)	1.08	125.56	17.83	48
Parker and Huryn (2006)	1.20	40.50	3.70	4
Thompson and Townsend (2004)	1.31	75.73	18.01	30
Cohen et al. (2003)	1.67	20.50	0.71	2
Piechnik et al. (2008)	1.68	118.00	84.46	5
Fryer (1959)	1.87	33.50	2.52	4
Havens (1992)	2.24	42.80	13.45	40
Layer et al. (2010)	2.30	33.00	19.58	9
Beaver (1985)	2.44	16.00	4.36	3
O'Gorman et al. (2019)	2.45	42.25	12.37	4
Legagneux et al. (2014)	2.46	19.67	3.72	6
Valiela (1974)	3.07	30.50	6.36	2
One food web per publication	3.13	43.46	67.55	83

S6.10.8 No substantial evidence "aquatic" food webs constructed via Ecopath are more structurally similar than "aquatic" food webs not constructed via Ecopath

Overall, there is no substantial improvement in structural similarity when food webs were built using similar *network construction methodology*. As illustrated in Subsubsections S6.10.8.1 and S6.10.8.2, the mean pairwise graphlet correlation distance-11 (GCD-11) between "aquatic" webs constructed via Ecopath is marginally reduced/improved as compared to non-Ecopath "aquatic" webs (2.78 vs. 3.02, respectively). In contrast, the mean pairwise GCD-11 between food webs sourced from the same publication is much smaller and more similar, i.e., mean pairwise GCD-11: 1.51 (Table 6.2).

Of the non-Ecopath "aquatic" webs available from our dataset, 37 webs were sourced from publications that each provided only a single network, while 102 webs were sourced from 12 publications that each provided multiple networks (see Table S6.7 for list). Specifically, 3 webs were sourced from Closs and Lake (1994), 4 webs were sourced from Thompson and Townsend (2003), 2 webs were sourced from Alcorlo et al. (2001), 2 webs were sourced from Menge and Sutherland (1976), 2 webs were sourced from Tavares-Cromar and Williams (1996), 4 webs were sourced from Parker and Huryn (2006), 30 webs were sourced from Thompson and Townsend (2004), 2 webs were sourced from Cohen et al. (1993), 4 webs were sourced from Fryer (1959), 36 webs were sourced from Havens (1992), 9 were sourced from Layer et al. (2010), and 4 were sourced from O'Gorman et al. (2019).

S6.10.8.1 Structural similarity between "aquatic" food webs not constructed via Ecopath

Here, we evaluated the mean pairwise GCD-11 between all "aquatic" food webs not constructed using Ecopath. Since food webs sourced from the same publication were already known to be very highly structurally similar to each other (i.e., mean pairwise GCD-11 of 1.51 [Table 6.2]), we needed to remove publication effect from this Ecopath network analysis. To do so, we only included in our analyses, webs that each had unique publication sources. As a means of reducing the burden of sampling across all possible different and unique combinations of taking a single web from each of the 12 publications that provided multiple networks, we simply randomly chose 12 webs. We refer to a collated combination of 12 randomly chosen webs (each one from a unique publication source that provided multiple networks), and all 37 webs sourced from publications that each provided only a single network, as a single realization, which consisted of 49 webs. Across 200 realizations, we found the average mean pairwise GCD-11 between "aquatic" webs not constructed via Ecopath was 3.02.

S6.10.8.2 Structural similarity between "aquatic" food webs constructed via Ecopath

To test for the possible improvement in food web structural similarity when limiting one's analysis to only those that have been constructed using similar methodology, we also evaluated the mean pairwise GCD-11 between "aquatic" food webs constructed using Ecopath. Of the 28 "aquatic" food webs constructed using Ecopath (see Table S6.7 for list), 15 webs were sourced from publications that each produced only a single network, while 13 webs were sourced from 4 publications that each produced multiple networks. Specifically, 2 webs were sourced from Angelini et al. (2006), 3 webs were sourced from Angelini et al. (2013), 6 webs were sourced from Baeta et al. (2011), and 2 webs were sourced from Stewart and Sprules (2011).

Again, since food webs sourced from the same publication were very highly structurally similar to each other, we needed to remove this publication effect in order to effectively evaluate the structural similarity between the 28 "aquatic" webs constructed using Ecopath. To do so, we only included in our analyses webs that each had unique publication sources. Thus, we evaluated the mean pairwise GCD-11 between food webs sourced from publications that each produced only a single network, along with all 72 different unique combinations when including four chosen webs, one from each of the publications that produced multiple networks. We refer to a single unique combination of 4 webs each chosen from a different publication that produced multiple networks and the 15 webs sourced from publications that each produced a single network, as a single realization, which consisted of 19 webs. Across all 72 realizations, we found the average mean pairwise GCD-11 between "aquatic" food webs constructed via Ecopath was 2.78.

S6.10.9 Food web citations

Table S6.7. The list of 148 food webs used in this study. Webs are classified as belonging to type aquatic ("A"), aquatic and terrestrial ("A&T"), or terrestrial ("T").

#	Name	Type	Refined aquatic type	Publication grouping	Ecopath	Citation
1	WEB3_	A&T		One network per publication	NA	Woodwell (1967)
2	WEB4_	A&T		One network per publication	NA	Johnston (1956)
3	WEB6_	A&T		One network per publication	NA	MacGinitie (1935)
4	WEB12_	A	Marine	Menge & Sutherland (1976)	NA	Menge and Sutherland (1976)
5	WEB13_	A	Marine	Menge & Sutherland (1976)	NA	Menge and Sutherland (1976)
6	WEB17_	A	Marine	One network per publication	NA	Hiatt and Strasburg (1960)
7	WEB18_	A&T		One network per publication	NA	Niering (1963)
8	WEB22_	A&T		One network per publication	NA	Summerhayes and Elton (1923)
9	WEB28_	T		One network per publication	NA	Paviour-Smith (1956)
10	WEB29_	A	Marine	One network per publication	NA	Dunbar (1953)
11	WEB33_	A	Lake	Fryer (1959)	NA	Fryer (1959)
12	WEB204_	A	Lake	Fryer (1959)	NA	Fryer (1959)
13	WEB38_	A	Lake	Fryer (1959)	NA	Fryer (1959)
14	WEB39_	A	Lake	Fryer (1959)	NA	Fryer (1959)
15	WEB34_	A	Stream	One network per publication	NA	Erichsen Jones (1949)
16	WEB35_	A	Stream	One network per publication	NA	Minshall (1967)
17	WEB37_	A	Marine	One network per publication	NA	Clarke et al. (1967)
18	WEB40_	T		One network per publication	NA	Harrison (1962)
19	WEB42_	A	Marine	One network per publication	NA	Vinogradov and Shushkina (1978)
20	WEB43_	A	Marine	One network per publication	NA	Rosenthal et al. (1974)

Table continued . . .

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... Continuation of Table S6.7.

#	Name	Type	Refined aquatic type	Publication grouping	Ecopath	Citation
21	WEB45_	A	Spring	One network per publication	NA	Tilly (1968)
22	WEB58_	A&T		One network per publication	NA	Smirnov (1961)
23	WEB59_	T		One network per publication	NA	Twomey (1945)
24	WEB63_	A	River	One network per publication	NA	Erichsen Jones (1950)
25	WEB67_	A&T		One network per publication	NA	Carlson (1968)
26	WEB72_	A	Lake	One network per publication	NA	Baril (1983)
27	WEB84_	A&T		One network per publication	NA	Wilbur (1972)
28	WEB87_	A	Marine	One network per publication	NA	Bradstreet and Cross (1982)
29	WEB88_	A	River	One network per publication	NA	Kuusela (1979)
30	WEB89_	A	River	One network per publication	NA	Hartley (1948)
31	WEB98_	T		One network per publication	NA	Holm and Scholtz (1980)
32	WEB104_	A	Marine	One network per publication	NA	Menge et al. (1986)
33	WEB105_	A	Marine	One network per publication	NA	Edwards et al. (1982)
34	WEB107_	A	Marine	One network per publication	NA	Peterson (1979)
35	WEB108_	A	Marine	One network per publication	NA	Hewatt (1937)
36	WEB117_	A	Lake	One network per publication	NA	Zaret and Paine (1973)
37	WEB121_	A	Marine	One network per publication	NA	van Es (1977)
38	WEB123_	T		One network per publication	NA	Harris (2016)
39	WEB131_	A&T		Beaver (1985)	NA	Beaver (1985)
40	WEB132_	A&T		Beaver (1985)	NA	Beaver (1985)
41	WEB134_	A&T		Beaver (1985)	NA	Beaver (1985)
42	WEB151_	T		One network per publication	NA	Richards (1926)
43	WEB152_	T		One network per publication	NA	Whittaker (1984)

Table continued ...

#	Name	Type	Refined aquatic type	Publication grouping	Ecopath	Citation
44	WEB154_	T		One network per publication	NA	Mayse and Price (1978)
45	WEB155_	T		One network per publication	NA	Askew (1975)
46	WEB199_	T		One network per publication	NA	Valiela (1969)
47	WEB200_	T		Valiela (1974)	NA	Valiela (1974)
48	WEB201_	T		Valiela (1974)	NA	Valiela (1974)
49	WEB205_	A	Stream	One network per publication	NA	Hildrew et al. (1985)
50	WEB207_	A	Stream	One network per publication	NA	Koslucher and Minshall (1973)
51	WEB208_	A	Stream	One network per publication	NA	Minckley (1963)
52	WEB210_	A	Stream	One network per publication	NA	Percival and Whitehead (1929)
53	WEB211_	A	Stream	One network per publication	NA	Ricker (1934)
54	WEB213_	A	Stream	One network per publication	NA	Badcock (1949)
55	WEB214_	A	Stream	Thompson & Townsend (2003)	NA	Thompson and Townsend (2003)
56	WEB215_	A	Stream	Thompson & Townsend (2003)	NA	Thompson and Townsend (2003)
57	WEB216_	A	Stream	Thompson & Townsend (2003)	NA	Thompson and Townsend (2003)
58	WEB217_	A	Stream	Thompson & Townsend (2003)	NA	Thompson and Townsend (2003)
59	WEB218_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
60	WEB219_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
61	WEB220_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
62	WEB221_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
63	WEB222_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
64	WEB223_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
65	WEB224_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
66	WEB225_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)

#	Name	Type	Refined aquatic type	Publication grouping	Ecopath	Citation
67	WEB226_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
68	WEB227_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
69	WEB228_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
70	WEB229_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
71	WEB230_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
72	WEB231_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
73	WEB232_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
74	WEB233_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
75	WEB234_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
76	WEB235_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
77	WEB236_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
78	WEB237_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
79	WEB238_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
80	WEB239_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
81	WEB240_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
82	WEB241_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
83	WEB242_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
84	WEB243_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
85	WEB244_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
86	WEB245_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
87	WEB246_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
88	WEB247_	A	Stream	Thompson & Townsend (2004)	NA	Thompson and Townsend (2004)
89	WEB248_	A&T		One network per publication	NA	Thompson et al. (2005)

Table continued ...

... Continuation of Table S6.7.

#	Name	Type	Refined aquatic type	Publication grouping	Ecopath	Citation
90	WEB249_	A	River	One network per publication	Yes	Angelini and Agostinho (2005)
91	WEB250_	A	River	Angelini et al. (2006)	Yes	Angelini et al. (2006)
92	WEB251_	A	River	Angelini et al. (2006)	Yes	Angelini et al. (2006)
93	WEB252_	A	River	One network per publication	Yes	Angelini et al. (2010)
94	WEB253_	A	Marine	One network per publication	Yes	Angelini and Vaz-Velho (2011)
95	WEB254_	A	Lake	Angelini et al. (2013)	Yes	Angelini et al. (2013)
96	WEB255_	A	Lake	Angelini et al. (2013)	Yes	Angelini et al. (2013)
97	WEB256_	A	Lake	Angelini et al. (2013)	Yes	Angelini et al. (2013)
98	WEB257_	A	Marine	Baeta et al. (2011)	Yes	Baeta et al. (2011)
99	WEB258_	A	Marine	Baeta et al. (2011)	Yes	Baeta et al. (2011)
100	WEB259_	A	Marine	Baeta et al. (2011)	Yes	Baeta et al. (2011)
101	WEB260_	A	Marine	Baeta et al. (2011)	Yes	Baeta et al. (2011)
102	WEB261_	A	Marine	Baeta et al. (2011)	Yes	Baeta et al. (2011)
103	WEB262_	A	Marine	Baeta et al. (2011)	Yes	Baeta et al. (2011)
104	WEB263_	A&T		One network per publication	NA	Schneider (1997)
105	WEB264_	A	Stream	One network per publication	NA	Stagliano and Whiles (2002)
106	WEB265_	A	Marine	One network per publication	Yes	Lin et al. (2006)
107	WEB266_	A	Marine	One network per publication	Yes	Cornejo-Donoso and Antezana (2008)
108	WEB267_	A	Marine	One network per publication	Yes	Zetina-Rejón et al. (2003)
109	WEB268_	A	Marine	One network per publication	Yes	Cruz-Escalona et al. (2007)
110	WEB269_	A	Lake	One network per publication	Yes	Liu et al. (2021)
111	WEB270_	A	Marine	One network per publication	NA	Filgueira and Castro (2011)

Table continued ...

#	Name	Type	Refined aquatic type	Publication grouping	Ecopath	Citation
112	WEB271_	A	Lake	One network per publication	NA	Amundsen et al. (2013)
113	WEB273_	A	Stream	Parker & Huryn (2006)	NA	Parker and Huryn (2006)
114	WEB274_	A	Stream	Parker & Huryn (2006)	NA	Parker and Huryn (2006)
115	WEB275_	A	Stream	Parker & Huryn (2006)	NA	Parker and Huryn (2006)
116	WEB276_	A	Stream	Parker & Huryn (2006)	NA	Parker and Huryn (2006)
117	WEB278_	A	Lake	Stewart & Sprules (2011)	Yes	Stewart and Sprules (2011)
118	WEB279_	A	Lake	Stewart & Sprules (2011)	Yes	Stewart and Sprules (2011)
119	WEB281_	A	Stream	Tavares-Cromar & Williams (1996)	NA	Tavares-Cromar and Williams (1996)
120	WEB285_	A	Stream	Tavares-Cromar & Williams (1996)	NA	Tavares-Cromar and Williams (1996)
121	WEB288_	A	Marine	One network per publication	Yes	Christian and Luczkovich (1999)
122	WEB289_	A	Lake	One network per publication	Yes	Fetahi et al. (2011)
123	WEB295_	A&T		One network per publication	NA	Preston et al. (2012)
124	WEB296_	A&T		One network per publication	NA	Ratsirarson and Silander (1996)
125	WEB306_	A	Stream	Closs & Lake (1994)	NA	Closs and Lake (1994)
126	WEB307_	A	Stream	Closs & Lake (1994)	NA	Closs and Lake (1994)
127	WEB308_	A	Stream	Closs & Lake (1994)	NA	Closs and Lake (1994)
128	WEB309_	A	Marine	One network per publication	NA	Gontikaki et al. (2011)
129	WEB310_	A	River	One network per publication	Yes	Khan and Panikkar (2009)
130	WEB311_	T		One network per publication	NA	Memmott et al. (2000)
131	WEB334_	A	Lake	Alcorlo et al. (2001)	NA	Alcorlo et al. (2001)
132	WEB335_	A	Lake	Alcorlo et al. (2001)	NA	Alcorlo et al. (2001)

Table continued ...

... Continuation of Table S6.7.

#	Name	Type	Refined aquatic type	Publication grouping	Ecopath	Citation
133	WEB338_	A	Marine	One network per publication	Yes	Torres et al. (2013)
134	WEB340_	A	Marine	One network per publication	NA	Smith et al. (2020)
135	WEB343_	A&T		One network per publication	NA	Kitching (1987)
136	WEB344_	T		One network per publication	NA	Hodkinson and Coulson (2004)
137	WEB345_	A	Lake	One network per publication	NA	Boit et al. (2012)
138	WEB347_	A	Stream	One network per publication	NA	Motta and Ueda (2005)
139	WEB350_	A	Marine	One network per publication	NA	Douglass et al. (2011)
140	WEB351_	A&T		One network per publication	NA	Warren (1989)
141	WEB353_	A	Stream	One network per publication	Yes	Poepperl (2003)
142	WEB354_	T		One network per publication	NA	Goldwasser and Roughgarden (1993)
143	WEB355_	A	Lake	Cohen et al. (2003)	NA	Cohen et al. (2003)
144	WEB356_	A	Lake	Cohen et al. (2003)	NA	Cohen et al. (2003)
145	WEB357_	A	Marine	One network per publication	NA	Yodzis (1998)
146	WEB358_	T		One network per publication	NA	Schröter et al. (2003)
147	carpinteria_	A&T		One network per publication	NA	Lafferty et al. (2006)
148	FW_008_	A	Marine	One network per publication	Yes	Bascompte and Jordano (2007)
149	mown_Clmown1_	T		Cattin Blandenier (2004)	NA	Cattin Blandenier (2004)
150	mown_Clmown2_	T		Cattin Blandenier (2004)	NA	Cattin Blandenier (2004)
151	mown_Scmown1_	T		Cattin Blandenier (2004)	NA	Cattin Blandenier (2004)
152	mown_Scmown2_	T		Cattin Blandenier (2004)	NA	Cattin Blandenier (2004)
153	not_mown_ClControl1_	T		Cattin Blandenier (2004)	NA	Cattin Blandenier (2004)

Table continued ...

... Continuation of Table S6.7.

#	Name	Type	Refined aquatic type	Publication grouping	Ecopath	Citation
154	not_mown_ ClControl2_	T		Cattin Blandenier (2004)	NA	Cattin Blandenier (2004)
155	not_mown_ ScControl1_	T		Cattin Blandenier (2004)	NA	Cattin Blandenier (2004)
156	not_mown_ ScControl2_	T		Cattin Blandenier (2004)	NA	Cattin Blandenier (2004)
157	AEW01_	T		Digel et al. (2014)	NA	Digel et al. (2014)
158	AEW02_	T		Digel et al. (2014)	NA	Digel et al. (2014)
159	AEW03_	T		Digel et al. (2014)	NA	Digel et al. (2014)
160	AEW04_	T		Digel et al. (2014)	NA	Digel et al. (2014)
161	AEW05_	T		Digel et al. (2014)	NA	Digel et al. (2014)
162	AEW06_	T		Digel et al. (2014)	NA	Digel et al. (2014)
163	AEW07_	T		Digel et al. (2014)	NA	Digel et al. (2014)
164	AEW08_	T		Digel et al. (2014)	NA	Digel et al. (2014)
165	AEW09_	T		Digel et al. (2014)	NA	Digel et al. (2014)
166	AEW11_	T		Digel et al. (2014)	NA	Digel et al. (2014)
167	AEW17_	T		Digel et al. (2014)	NA	Digel et al. (2014)
168	AEW18_	T		Digel et al. (2014)	NA	Digel et al. (2014)
169	AEW25_	T		Digel et al. (2014)	NA	Digel et al. (2014)
170	AEW27_	T		Digel et al. (2014)	NA	Digel et al. (2014)
171	AEW30_	T		Digel et al. (2014)	NA	Digel et al. (2014)
172	AEW49_	T		Digel et al. (2014)	NA	Digel et al. (2014)
173	HEW01_	T		Digel et al. (2014)	NA	Digel et al. (2014)

Table continued ...

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#	Name	Type	Refined aquatic type	Publication grouping	Ecopath	Citation
174	HEW02_	T		Digel et al. (2014)	NA	Digel et al. (2014)
175	HEW03_	T		Digel et al. (2014)	NA	Digel et al. (2014)
176	HEW04_	T		Digel et al. (2014)	NA	Digel et al. (2014)
177	HEW05_	T		Digel et al. (2014)	NA	Digel et al. (2014)
178	HEW06_	T		Digel et al. (2014)	NA	Digel et al. (2014)
179	HEW10_	T		Digel et al. (2014)	NA	Digel et al. (2014)
180	HEW11_	T		Digel et al. (2014)	NA	Digel et al. (2014)
181	HEW12_	T		Digel et al. (2014)	NA	Digel et al. (2014)
182	HEW13_	T		Digel et al. (2014)	NA	Digel et al. (2014)
183	HEW16_	T		Digel et al. (2014)	NA	Digel et al. (2014)
184	HEW17_	T		Digel et al. (2014)	NA	Digel et al. (2014)
185	HEW21_	T		Digel et al. (2014)	NA	Digel et al. (2014)
186	HEW22_	T		Digel et al. (2014)	NA	Digel et al. (2014)
187	HEW36_	T		Digel et al. (2014)	NA	Digel et al. (2014)
188	HEW47_	T		Digel et al. (2014)	NA	Digel et al. (2014)
189	SEW01_	T		Digel et al. (2014)	NA	Digel et al. (2014)
190	SEW02_	T		Digel et al. (2014)	NA	Digel et al. (2014)
191	SEW03_	T		Digel et al. (2014)	NA	Digel et al. (2014)
192	SEW04_	T		Digel et al. (2014)	NA	Digel et al. (2014)
193	SEW05_	T		Digel et al. (2014)	NA	Digel et al. (2014)
194	SEW06_	T		Digel et al. (2014)	NA	Digel et al. (2014)
195	SEW07_	T		Digel et al. (2014)	NA	Digel et al. (2014)
196	SEW08_	T		Digel et al. (2014)	NA	Digel et al. (2014)

Table continued ...

... Continuation of Table S6.7.

#	Name	Type	Refined aquatic type	Publication grouping	Ecopath	Citation
197	SEW09_	T		Digel et al. (2014)	NA	Digel et al. (2014)
198	SEW18_	T		Digel et al. (2014)	NA	Digel et al. (2014)
199	SEW35_	T		Digel et al. (2014)	NA	Digel et al. (2014)
200	SEW36_	T		Digel et al. (2014)	NA	Digel et al. (2014)
201	SEW37_	T		Digel et al. (2014)	NA	Digel et al. (2014)
202	SEW41_	T		Digel et al. (2014)	NA	Digel et al. (2014)
203	SEW43_	T		Digel et al. (2014)	NA	Digel et al. (2014)
204	SEW48_	T		Digel et al. (2014)	NA	Digel et al. (2014)
205	Alford_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
206	Balsam_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
207	Beaver_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
208	Big_Hope_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
209	Brandy_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
210	Bridge_Brook_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
211	Burntbridge_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
212	Cascade_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
213	Chub_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
214	Connera_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
215	Constable_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
216	Emerald_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
217	Falls_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
218	Fawn_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)

Table continued ...

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... Continuation of Table S6.7.

#	Name	Type	Refined aquatic type	Publication grouping	Ecopath	Citation
219	Federation_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
220	Goose_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
221	Grass_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
222	Gull_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
223	Hoel_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
224	Horseshoe_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
225	Little_Rainbow_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
226	Long_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
227	Loon_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
228	Lost_Lake_East_	A	Lake	Havens (1992)	NA	Havens (1992)
229	Lost_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
230	Lower_Sister_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
231	Oswego_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
232	Rat_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
233	Razorback_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
234	Russian_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
235	Safford_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
236	Sand_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
237	Squaw_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
238	Stink_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)

Table continued . . .

... Continuation of Table S6.7.

#	Name	Type	Refined aquatic type	Publication grouping	Ecopath	Citation
239	Twelfth_Tee_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
240	Whipple_Lake_	A	Lake	Havens (1992)	NA	Havens (1992)
241	Buck_Pond_	A&T		Havens (1992)	NA	Havens (1992)
242	Chub_Pond_	A&T		Havens (1992)	NA	Havens (1992)
243	Helldiver_Pond_	A&T		Havens (1992)	NA	Havens (1992)
244	High_Pond_	A&T		Havens (1992)	NA	Havens (1992)
245	Afon_Hafren_2005_	A	Stream	Layer et al. (2010)	NA	Layer et al. (2010)
246	Allt_a_Mharcaidh_	A	Stream	Layer et al. (2010)	NA	Layer et al. (2010)
247	Broadstone_Stream_	A	Stream	Layer et al. (2010)	NA	Layer et al. (2010)
248	Dargall_Lane_	A	Stream	Layer et al. (2010)	NA	Layer et al. (2010)
249	Duddon_Pike_Beck_	A	Stream	Layer et al. (2010)	NA	Layer et al. (2010)
250	Hardknott_Gill_	A	Stream	Layer et al. (2010)	NA	Layer et al. (2010)
251	Mill_Stream_	A	Stream	Layer et al. (2010)	NA	Layer et al. (2010)
252	Mosendale_Beck_	A	Stream	Layer et al. (2010)	NA	Layer et al. (2010)
253	Old_Lodge_	A	Stream	Layer et al. (2010)	NA	Layer et al. (2010)
254	Alert_	T		Legagneux et al. (2014)	NA	Legagneux et al. (2014)
255	Bylot_	T		Legagneux et al. (2014)	NA	Legagneux et al. (2014)
256	Herschel_	T		Legagneux et al. (2014)	NA	Legagneux et al. (2014)

Table continued ...

... Continuation of Table S6.7.

#	Name	Type	Refined aquatic type	Publication grouping	Ecopath	Citation
257	Nenetsky_	T		Legagneux et al. (2014)	NA	Legagneux et al. (2014)
258	Yamal_	T		Legagneux et al. (2014)	NA	Legagneux et al. (2014)
259	Zackenberg_	T		Legagneux et al. (2014)	NA	Legagneux et al. (2014)
260	Iceland_Stream_ IS7_April_2009_	A	Stream	O'Gorman et al. (2019)	NA	O'Gorman et al. (2019)
261	Iceland_Stream_ IS7_August_2008_	A	Stream	O'Gorman et al. (2019)	NA	O'Gorman et al. (2019)
262	Iceland_Stream_ IS8_April_2009_	A	Stream	O'Gorman et al. (2019)	NA	O'Gorman et al. (2019)
263	Iceland_Stream_ IS8_August_2008_	A	Stream	O'Gorman et al. (2019)	NA	O'Gorman et al. (2019)
264	Lake_Malawi_	A	Lake	One network per publication	Yes	Nsiku (1999)
265	Ythan_Estuary_	A	Marine	One network per publication	NA	Cohen et al. (2009)
266	Kongsfjorden_	A	Marine	One network per publication	NA	Eklöf et al. (2013)
267	Weddell_Sea_	A	Marine	One network per publication	NA	Jacob et al. (2011)
268	Skipwith_Pond_	A&T		One network per publication	NA	Warren (1990)
269	Gearagh_	T		One network per publication	NA	McLaughlin et al. (2010)
270	FloridaIslandE1_	A&T		Piechnik et al. (2008)	NA	Piechnik et al. (2008)
271	FloridaIslandE2_	A&T		Piechnik et al. (2008)	NA	Piechnik et al. (2008)
272	FloridaIslandE3_	A&T		Piechnik et al. (2008)	NA	Piechnik et al. (2008)
273	FloridaIslandE7_	A&T		Piechnik et al. (2008)	NA	Piechnik et al. (2008)
274	FloridaIslandE9_	A&T		Piechnik et al. (2008)	NA	Piechnik et al. (2008)

Chapter 7

Final remarks

Species interactions are fundamental to the functioning of our planet. For example, interactions influence the evolution of species via community stability (Landi et al., 2018), species abundances, and ecosystem functioning (Barraclough, 2015). Moreover, species interactions also have substantial economic value. Among the most obvious are pollination services, estimated to enhance annual global crop output by \$235–577 billion USD in 2015 (Potts et al., 2016), a figure that has surely increased since.

Despite their importance, effectively measuring the impact of species interactions on ecological communities is enormously difficult. Given the large number of species and interactions that make up an ecological community, simply amassing and keeping track of all the constituent components is challenging (Morales-Castilla et al., 2015; de Aguiar et al., 2019). Beyond this characterization, accurately assessing how species interactions affect community functioning remains elusive. Although communities are commonly modelled as species interaction networks—whose topology (or structure) is defined by their configuration of nodes (i.e., species) and edges (i.e., interactions)—many network metrics that measure this structure lack any known biological function (Thompson et al., 2012; Dormann, 2023). For instance, while high nestedness in plant-pollinator networks has been touted as a stabilizing mechanism for communities in seasonal environments (Song et al., 2017), no such study has rigorously tested this claim. Certainly more work is needed to develop biologically meaningful network metrics and test when species interaction networks effectively model their respective ecological communities.

The aims of my thesis were to help resolve the drivers of topology in species interaction networks and to evaluate the utility of networks for informing about ecological communities. This was achieved through investigating the dynamics in the structure of species interaction networks, and the formulation of a framework for understanding these structural drivers. In short, I uncovered large and natural changes to species interactions in time and space. This includes invoking seasonality to explain temporal changes of stream fish communities across the eastern United States, and attempting to use seasonality to understand the topology of ecological communities across the globe. I also explored how my proposed three classes of *biological and environmental factors*, *sampling strategies*, and *network construction methodologies* determine the topology of ecological communities. In combination, these three classes strongly influence the structure of species interaction networks, which likely make comparing networks built by different researchers problematic.

7.1 Thesis summary and future directions

7.1.1 Synthesis of thesis

Undoubtedly, the effects of seasonality on community topology have been largely overlooked relative to their potential impact (White and Hastings, 2020). This is especially true for communities consisting of large-bodied organisms, primarily due to the practical difficulty in characterizing these organisms and their trophic interactions (Brimacombe et al., 2021). To address this, in Chapter 2, I adopted an inferential method that inferred interactions when the abundance of one species affected the abundance of another. This method was applied to build two seasonal species interaction networks from stream fish abundances measured in the Fall and Spring at long-term ecological research stations. In general, I uncovered that the topology of stream fish communities changes considerably across these seasons, comparable to that found in plant-pollinator communities (CaraDonna et al., 2021). Notably, most of these seasonal network changes were due to differences in interactions between species present in both seasons, rather than seasonal species turnover. In concert, these findings highlight that species interaction networks that do not account for natural temporal changes in their communities, both in terms of their species composition and interactions, risk obscuring true ecological dynamics.

Of the few studies that have evaluated the influence of seasonality on ecological networks, many have done so by reusing species interaction networks to test their hypotheses (Brimacombe et al., 2022b). These networks were constructed by previous researchers for their own studies, and made freely available (i.e., *open*) after publication. However, studies that reuse open networks are typically limited to testing their hypothesis using a small number of networks (i.e., $n < 30$) across a small spatial extent [e.g., Olesen and Jordano (2002); Schleuning et al. (2014); Dalsgaard et al. (2017)]. In both Chapters 3 and 4, I used large datasets of open bipartite species interaction networks to evaluate if seasonality explains network topology across the globe. Contrary to previous conclusions, I found no substantive evidence that community topology was a function of seasonality. Instead, a control variable for the amount of effort used to build each open network, *sampling intensity* (Schleuning et al., 2012), almost always explained network topology better than any combination of abiotic variables. Hence, open species interaction networks built by different researchers may be inadequate for testing ecological hypotheses due to significant structural differences among them.

Clearly, topological differences among open networks are necessary for investigating their drivers. However, open species interaction networks sourced from various publications likely exhibit substantial topological differences, posing challenges for their comparison (May, 1983). These disparities stem from the diverse (i) *sampling strategies*, and (ii) *network construction methodologies* employed across the studies that build them (Dunne, 2006). Moreover, the communities represented by these open networks are (iii) exposed to various *biological and environmental factors*. Using a subgraph technique, I quantified topological heterogeneity across commonly adopted open bipartite networks (e.g., plant-pollinator, host-parasite; in Chapter 5), and open food webs (in Chapter 6). In both Chapters, I found no compelling evidence that the environment, sampling strategies, or network construction methods alone clearly explained network topology. Instead, the topology of open networks appears to be primarily determined by the publication source of each network, as networks sourced from the same publication are very topologically similar. It is likely that *biological and environmental factors*, *sampling strategies*, and *network construction methodologies* act

similarly on networks sourced from the same publication to make them structurally similar. These findings highlight the potential pitfalls of interpreting community structure through aggregated open networks without appropriate controls for how they were built.

7.1.2 Future directions

In ecology, species interaction networks frequently serve as models to represent ecological communities (Poisot et al., 2016b; Delmas et al., 2019). However, a significant gap persists in our understanding of how effectively these types of networks accurately reflect real ecological communities. Researchers who build networks to investigate the topology of communities, frequently fail to validate their networks or their network metrics (Blüthgen, 2010; Dormann, 2023). Consequently, inferences drawn from these potentially flawed representations—for instance, how food webs are influenced by land-use intensity Brimacombe et al. (2024)—likely lead to misleading conclusions. To ensure the optimal evolution of network ecology, it is crucial that we develop better approaches to link the biology of the systems we are trying to model and the corresponding network structure.

An ambitious approach to improve this connection involves testing predictions derived from these models. Predictive test, or forecasts, are considered a more rigorous test of hypotheses than traditional significance tests (Dietze et al., 2018), and thus offer greater confidence in models that demonstrate good predictive capabilities. By comparing predictions to empirical observation, we can measure a network's accuracy, reliability and transparency, including assumptions, and model choice (Bodner et al., 2020). Prediction is by no means a fool-proof approach to choose useful models, after all, even a broken clock is right twice a day. Therefore, careful consideration must be given to plausible conclusions that can be drawn from the data and approaches used (Shadish et al., 2002). For example, while a few plant-pollinator networks may inform about the functioning of their local ecosystem, generalizing these results requires caution.

To model communities effectively, we must consider them as dynamic through space and time (Pellissier et al., 2018; CaraDonna et al., 2021). While it has become commonplace to model communities as static networks (Cirtwill et al., 2019), such models will likely not produce as many fruitful insights as possible since these networks do not capture spatial and temporal realities (Vázquez et al., 2022). For example, community structure is known to vary across days, weeks, months, and years (Schwarz et al., 2020), and across the amount of area used to encapsulate the community (Galiana et al., 2022). If we hope to understand community dynamics using networks, we must account for these spatial and temporal dimensions.

Of course, the availability of large amounts of high-quality empirical data is a prerequisite for improving ecological community representation as networks (Valdovinos, 2019). However, collecting this data is an incredibly arduous and expensive task (McLeod et al., 2021). After all, determining species' presences and absences is known to be challenging, but collecting interaction data is even harder. Specifically, observing a trophic interaction between two species requires detecting both species *and* witnessing an interaction between them (Jordano, 2016). Without sufficient effort, an ecological community will be misrepresented as a network when species and their interactions are missed during *in situ* sampling (Pringle and Hutchinson, 2020). Acknowledging this difficulty is important as it underscores that building networks without adequate data is insufficient for understanding complex ecological systems. However, addressing the shortfall in high quality

community data—the Eltonian shortfall—is essential for advancing network ecology.

Given the expense of collected data, many communities and areas across the globe remain poorly characterized (Poisot et al., 2021). Fortunately, cheaper methods to overcome this limitation are now increasingly available. In particular, camera traps have become popular as instruments to observe biological and environmental phenomena quickly and less intrusively (Smith et al., 2020; Fisher, 2023). Paired with machine learning and artificial intelligence, camera traps are likely to be influential in many different areas of ecology, including species identification and monitoring, ecosystem management, and ecological modelling (Christin et al., 2019). Also potentially transformative for network science is species identification using DNA collected from environmental samples (eDNA) by applying the metabarcoding procedure (Deiner et al., 2017). For example, the metabarcoding of eDNA collected from water samples has been used to reconstruct species co-occurrence networks (Seymour et al., 2020). By identifying the co-occurrence of many species using a single environmental sample, metabarcoding can significantly reduce the cost burden of characterizing a community (Corlett, 2017). Additionally, metabarcoding of gut contents and feces can be applied to finely resolve species eaten (i.e., the trophic interactions in a food web), which might otherwise be incomprehensible to decipher by traditional methods such as a microscope (Pringle and Hutchinson, 2020). Although promising, relatively few studies have implemented camera traps or metabarcoding to study species interaction networks, and so their effectiveness in this context will need to be continuously tested.

Long-term monitoring stations also offer invaluable insights into ecological communities (Gonzalez et al., 2016), albeit at a premium cost. These initiatives are particularly useful as they enable long-term studies to reveal trends not uncovered by shorter observational experiments (Magnuson, 1990). Combined with the many additional measurements taken, these long-term monitoring stations contribute to a holistic understanding of ecology (Collins and Childers, 2014). For example, one of the most prominent initiatives in North America is the National Ecological Observatory Network (NEON), which monitors biotic and abiotic variables across many sites in the United States (Thorpe et al., 2016). Since the empirical observations at NEON are collected using standardized protocols across sites, they can be more easily compared across wide spatial and temporal extents, relating biological response variables to abiotic measurements. Beyond the many findings already made using this data source (listed here: `https://neon.dimensions.ai/discover/publication`), including those presented in Chapter 2, many more discoveries that involve long-term monitoring stations are likely to be made in the future (Vanderbilt and Gaiser, 2017).

Currently, we rely heavily on reusing open species interaction networks from previous published studies to understand ecological communities, due to the impracticality of sampling communities across space and time (Poisot et al., 2021). However, the diverse *biological and environmental factors*, *sampling strategies*, and *network construction methodologies* that strongly influence the structure of networks sourced from different publications complicate drawing meaningful inferences from them (Brimacombe et al., 2023). Perhaps unsurprisingly due to many influences, open networks often resemble the structure of random network null models (Banville et al., 2023). Indeed, many questions surround the utility of these open networks (Dunne, 2006), and whether approaches can be adopted to make them more commensurable. For instance, how can we effectively compare the structure of open networks representing a dung food web and a forest food web to further our

understanding of community ecology? Clearly, networks constructed for vastly different environments are collected in very different ways, with different sets of organisms in mind (May, 1983; Paine, 1988). Further research is needed to develop effective methods to compare these networks. Nevertheless, improvements to network data will likely be a necessity (Winemiller, 1990). This includes establishing protocols to record the sampling procedures (e.g., amount of time and area used to monitor an in situ community), network construction methodologies (e.g., all nodes represent species), and environmental and biological factors that influence the studied community by the researchers that build networks (Poisot et al., 2016*b*; Kita et al., 2022).

In addition to their intrinsic value, studying communities as species interaction networks could hold important conservation implications amid the sixth mass extinction. Many species are experiencing rapid declining population sizes (Ceballos et al., 2017), a crisis exacerbated by climate change (IPCC, 2021). Addressing this loss will require informed policy that combines the effort of both decision makers and scientists (Bodner et al., 2021*b*). Holistic approaches, such as viewing a community as a network of interacting species, offer promising avenues to inform scientists. For instance, identifying keystone species within food webs may pinpoint species for targeted conservation efforts that, if conserved, may avoid cascading species loss (Vázquez et al., 2022). Of course, other insights will be gained from adopting additional methodologies, but leveraging networks may be another tool for effective conservation management.

7.2   Conclusion

Ecological communities are complex systems, commonly modelled as networks where species are represented as nodes and their trophic interactions as edges. Undoubtedly, the network approach has uncovered many properties regarding communities, but it has also likely missed others. My thesis has highlighted some of these shortcomings. In particular, I have demonstrated how a static representation of an ecological community fails to capture important temporal dynamics between species and their interactions, which perhaps can be better captured by modelling the same community across time using multiple networks. Additionally, I have explored how the three classes of *sampling strategies*, *network construction methodologies*, and *biological and environmental factors* holistically influence the topology of species interaction networks. While these three classes induce a publication effect in the structure of networks sourced from the same publication, this result suggests effective comparison can be made if networks are sampled and constructed using similar approaches. By addressing these criticisms and embracing the suggested fixes, my thesis attempts to enhance our understanding of ecological communities using networks.

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