

## RESEARCH ARTICLE

# Ecological network assembly: How the regional metaweb influences local food webs

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## Abstract

1. Local food webs result from a sequence of colonisations and extinctions by species from the regional pool or metaweb, that is, the assembly process. Assembly is theorised to be a selective process: whether or not certain species or network structures can persist is partly determined by local processes including habitat filtering and dynamical constraints. Consequently, local food web structure should reflect these processes.
2. The goal of this study was to test evidence for these selective processes by comparing the structural properties of real food webs to the expected distribution given the metaweb. We were particularly interested in ecological dynamics; if the network properties commonly associated with dynamical stability are indeed the result of stability constraints, then they should deviate from expectation in the direction predicted by theory.
3. To create a null expectation, we used the novel approach of randomly assembling model webs by drawing species and interactions from the empirical metaweb. The assembly model permitted colonisation and extinction, and required a consumer species to have at least one prey, but had no habitat type nor population dynamical constraints. Three datasets were used: (a) the marine Antarctic metaweb, with two local food webs; (b) the 50 lakes of the Adirondacks; and (c) the arthropod community from Florida Keys' classic defaunation experiment.
4. Contrary to our expectations, we found that there were almost no differences between empirical webs and those resulting from the null assembly model. Few empirical food webs showed significant differences with network properties, motif representations and topological roles. Network properties associated with stability did not deviate from expectation in the direction predicted by theory.
5. Our results suggest that—for the commonly used metrics we considered—local food web structure is not strongly influenced by dynamical nor habitat restrictions. Instead, the structure is inherited from the metaweb. This suggests that the network properties typically attributed as causes or consequences of ecological stability are instead a by-product of the assembly process (i.e. spandrels), and may potentially be too coarse to detect the true signal of dynamical constraint.

**KEYWORDS**

ecological network assembly, food web structure, Metaweb, modularity, motif, network assembly model, null models, topological roles

## 1 | INTRODUCTION

What determines the structure of a food web? The characterisation of ecological systems as networks of interacting elements has a long history (Cohen & Newman, 1985; May, 1972; Paine, 1966); however, the effects of ecological dynamical processes on network structure are not fully understood. Structure is the result of community assembly, which is a repeated process of species arrival, colonisation and local extinction (Cornell & Harrison, 2014). That implies there are two major components that determine food web structure: the composition of the regional pool, from which the species are drawn; and a selective process, which determines which species can arrive and persist in the local web. The selective process is very complex and involves multiple mechanisms (Mittelbach & Schemske, 2015). However, we should in theory be able to detect the signal of this process by comparing local webs to the regional pool from which they were drawn.

The structure of a food web is ultimately constrained by the species and potential interactions that exist in the regional pool, that is, the metaweb. The regional pool is shaped by evolutionary and biogeographical processes that imply large spatial and temporal scales (Carstensen et al., 2013; Kortsch et al., 2018), and it generally extends over many square kilometres and contains a large number of habitats and communities (Mittelbach & Schemske, 2015). Each of the local communities that make up the metaweb can have different food web structures, both in terms of the species present and interactions between them. Consequently, the metaweb includes many species co-occurrence and interaction possibilities that do not occur in reality.

Within the ultimate constraint imposed by the metaweb, the composition of the local community is determined by metacommunity processes. Which regional species can arrive and persist in a web is influenced by dispersal, environmental filters, biotic interactions and stochastic events (HilleRisLambers et al., 2012). These processes have been studied using metacommunity theory, where different spatial assemblages are connected through species dispersal (Leibold et al., 2017). Recently, there has been an increase in food web assembly studies, integrating them with island biogeography (Gravel et al., 2011), metacommunity dynamics (Liao et al., 2016; Pillai et al., 2011) and the effects of habitat fragmentation (Mougi & Kondoh, 2016). As an extension of the species-area relationship (SAR) approach, one can derive a network-area relationship (NAR) using theoretical models (Galiana et al., 2018). However, this approach assumes that ecological dynamics (e.g. stability) will have no influence. Compared to the body of metacommunity theory, there are very few studies that have analysed the assembly process using experimental or empirical data, and none of them focuses on topological network properties that could be related to different

assembly processes. Piechnik et al. (2008) found that the first to colonise are trophic generalists followed by specialists, supporting the hypothesis that biotic interactions are important in the assembly process (Holt et al., 1999). Baiser et al. (2013) showed that habitat characteristics and dispersal capabilities were the main drivers of the assembly. Fahimipour and Hein (2014) also found that colonisation rates were an important factor.

On top of metacommunity processes, local dynamical processes play a role in determining food web structure, and the potential for stability to constrain food web structure has received plenty of theoretical attention (May, 1972; McCann, 2000). Some theorists conceive of assembly as a non-Darwinian selection process (Borrelli, 2015), whereby species and structures that destabilise the web will be lost and stabilising structures persist (Borrelli, 2015; Pawar, 2009). Typically, assembly simulations produce large webs that are both stable in the dynamical sense and relatively resistant to further invasions (Drake, 1990; Law & Morton, 1996; Luh & Pimm, 1993). Therefore, we expect that particular structural properties that confer stability will be over-represented in real food webs (Borrelli et al., 2015), as these are the webs that are able to persist in time (Grimm et al., 1992).

There is some evidence that real food webs possess stabilising structural properties. A classic finding is that dynamical models parametrised with realistic species interaction strength patterns have higher stability than randomised alternatives (de Ruiter et al., 1995; Neutel et al., 2002). The frequency of three-node sub-networks, called motifs (Milo et al., 2002), is correlated with the stability in ecological (Borrelli, 2015) and other biological (Prill et al., 2005) networks. However, stability-enhancing structural features can also arise for non-dynamical reasons. For example, the nested structure of mutualistic networks can arise as a spandrel of adaptive radiation (Maynard et al., 2018; Valverde et al., 2018), and low connectance may occur as a consequence of restricted diet breadth and adaptive foraging behaviour (Beckerman et al., 2006). Furthermore, it is niche models—which are typically interpreted in terms of physiological constraints on predation relationships and do not rely upon population dynamic mechanisms—that have been most successful at reproducing realistic food web structure (Loeuille & Loreau, 2005; Williams & Martinez, 2000). This raises the possibility that the structural attributes typically measured in real webs can be explained by other processes, or may be too coarse to detect a subordinate influence of dynamics.

To test the hypothesis that dynamical selective processes are responsible for food web structure, we need an appropriate null model (Lau et al., 2017). Here, we propose that the metaweb itself can be used to create that baseline for comparison. We conceive of the metaweb as the source of food web structural diversity, from which local food web structure is drawn, and upon which local processes

can act. Although the metaweb is also a consequence of local assembly processes (being the sum of local webs), it contains species co-occurrences and network structures that never occur in a local web, including those presumably precluded by local dynamics. Therefore, if there are local selective processes that determine the structure of local food webs, then comparing local webs to the metaweb may allow us to separate the larger evolutionary and biogeographical processes from the theorised local selective process. For example, we would expect to find that the structural properties that confer stability are over-represented in local food webs compared to the metaweb.

In this study, we developed a null model independent of dynamic stability processes and compared the resulting structure to real food webs using network properties. We cannot directly compare the metaweb properties with the local web properties since they are dependent on size, number of links and/or connectance (Dunne et al., 2002; Poisot & Gravel, 2014). Therefore, we compared the real networks to networks generated by the null model, which takes into account this issue. To create null food webs, we made the most minimal assumption possible about the metacommunity process: any species from the metaweb can colonise and persist in a local web given at least one prey (food) item available. Thus the model considers colonisation–extinction and secondary extinctions events constrained by network structure, so it does not include dynamical stability and local habitat constraints that are thought to drive the assembly process. If the real food web structure differs from null models and in the direction predicted by theory, then that is evidence in favour of the hypothesis that food web structure is constrained by dynamics.

## 2 | MATERIALS AND METHODS

We compiled three metawebs with their corresponding local food webs, with a total of 58 local food webs from a variety of regions and ecosystems. We built the first metaweb from the Southern Ocean database compiled by Raymond et al. (2011), selecting only species located at latitudes higher than 60°S. Raymond et al. (2011) compiled information from direct sampling methods of dietary assessment, including gut, scat and bolus content analysis, stomach flushing, and observed feeding. We considered that the metaweb is the regional pool of species defined by the biogeographic Antarctic region. As local food webs we included two of the most well-resolved datasets publicly available for the region: Weddell Sea and Potter Cove food webs. The first includes species situated between 74°S and 78°S with a west–east extension of approximately 450 km and comprises all information about trophic interactions available for the zone since 1983 (Jacob et al., 2011), this dataset was obtained from Brose et al. (2005). The Potter Cove food web comes from a 4 km long and 2.5 km wide Antarctic fjord located at 62°14'S, 58°40'W, South Shetland Islands (Marina et al., 2018). To make datasets compatible, we firstly checked taxonomic names for synonyms, and secondly added species (either prey or predator) with their interactions

to the metaweb when the local food webs contain a greater taxonomic resolution. This resulted in the addition of 258 species to the metaweb, which represent 33% of the total. We named this the Antarctic metaweb, which has 846 species (S), 6,897 links (L) and a connectance ( $L/S^2$ ) of 0.01.

The second metaweb was collected from pelagic organisms of 50 lakes of the Adirondacks region (Havens, 1992), which were sampled once during summer 1984 (Sutherland, 1989). Havens (1992) determined the potential predator–prey interactions among 211 species from previous diet studies; species that lacked a trophic link were deleted and feeding links were assumed when the species involved were present in a particular lake. The so-called Lakes metaweb considers 211 species, 8,426 links and a connectance of 0.19, this was obtained from the GATEWAY database (Brose et al., 2019).

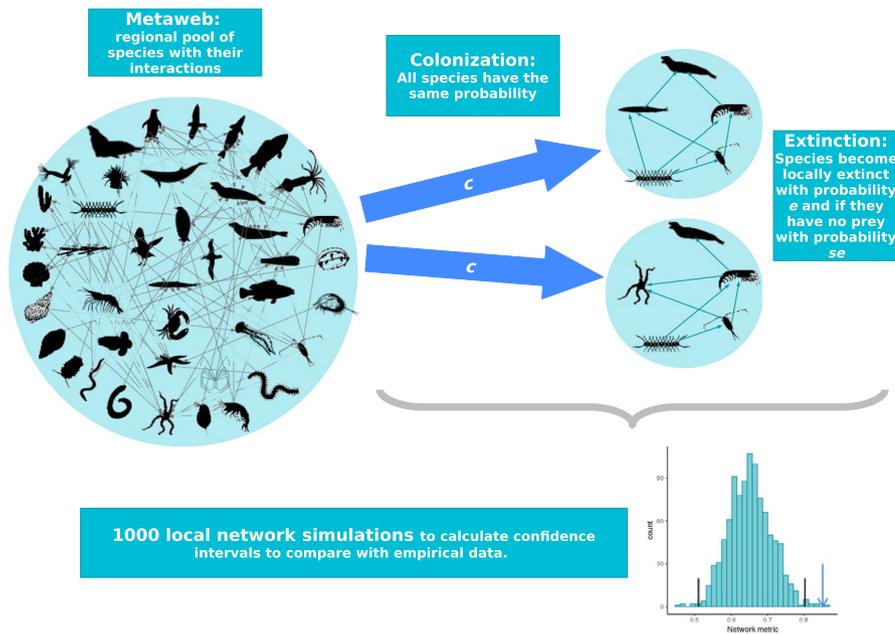
The third metaweb comes from a well-known defaunation experiment performed in the Florida Keys in the 1960s (Piechnik et al., 2008; Simberloff & Wilson, 1969), where six islands of 11–25 m in diameter were defaunated with insecticide. The arthropods were censused before the experiment and after it approximately once every 3 weeks during the first year and again 2 years after defaunation. For the metaweb and local webs we used only the first census that represent a complete community. Piechnik et al. (2008) determined the trophic interactions among 155 species (5,114 links, connectance 0.21) using published information and expert opinions. This dataset was obtained directly from the authors of Gravel et al. (2011). As this is a modelling study that uses already published data no ethical approval was needed.

### 2.1 | Metaweb assembly null model

To consider network assembly mechanisms we used a metaweb assembly model (Figure 1), similar to the trophic theory of island biogeography (Gravel et al., 2011). In this model species migrate from the metaweb to a local web with a probability  $c$ , and become extinct from the local web with probability  $e$ ; a reminiscence of the theory of island biogeography (MacArthur & Wilson, 1967), but with the addition of network structure. Species migrate with their potential network links from the metaweb, then in the local web, species have a probability of secondary extinction  $se$  if none of its preys are present, which only applies to non-basal species. When a species goes extinct locally it may produce secondary extinctions modulated by  $se$  (Figure 1).

Then there are three possible events: colonisation, extinction and secondary extinction. After a colonisation event with probability  $c$ , the species is present in the local community and two other events are possible:

1. if it is a basal species it does not need predators to survive, then it persists until an extinction event with probability  $e$ ;
2. if it is a non-basal species it could become extinct with probability  $e$  but if it has no prey it could also become extinct with probability  $se$ .



**FIGURE 1** Schematic diagram of the metabweb assembly null model: species migrate from the metabweb with a probability  $c$  to a local network carrying their potential links; here they have a probability of extinction  $e$ . Additionally, predators become extinct if their preys are locally extinct with probability  $se$ . We simulate 1,000 local networks and calculate network properties. From the distribution of these topological properties we calculate 1% confidence intervals to compare with empirical networks

These events could happen at random if the necessary conditions are fulfilled, to simulate the model we use the Gillespie (1976) algorithm that produces a statistically exact trajectory of the stochastic process (Black & McKane, 2012).

We simulated this model in time and it eventually reached a steady state that depends on the migration and extinction probabilities but also on the structure of the metabweb. The ratio of immigration versus extinction  $\alpha = c/e$  is hypothesised to be inversely related to the distance to the mainland (MacArthur & Wilson, 1967), and as extinction should be inversely proportional to population size (Hanski, 1999), the ratio  $\alpha$  is also hypothesised to be related to the local area.

For the model used in Gravel et al. (2011), simulations with the same ratio  $\alpha = c/e$  should give the same results, but as our model incorporates  $se$  as an additional parameter this might not be the case. We checked this performing simulations with different combinations of  $c$ ,  $e$  and  $se$  keeping  $\alpha$  constant for different metabwebs. We found differences for some of the combinations (Figure S6), thus we performed the fitting using the three parameters.

To fit the model to each metabweb we performed 150,000 simulations with a wide range of parameters (Table S1) using latin hypercube sampling (Fang et al., 2005). We simulated the model for 1,000 time steps and use the last 100 time steps to calculate averages for the number of species  $S_m$ , the number of links  $E_m$  and the connectance  $C_m = E_m/S_m^2$ . Then we calculated a relative distance to the number of species  $S_e$  and connectance  $C_e$  of the empirical food webs:

$$\text{distance} = \sqrt{\left(\frac{S_e - S_m}{S_e}\right)^2 + \left(\frac{C_e - C_m}{C_e}\right)^2}.$$

Then we used the parameters with the minimal distance to simulate the model and compare with the network properties described in the following section. The fitted parameters for all local food webs are presented in Table S2.

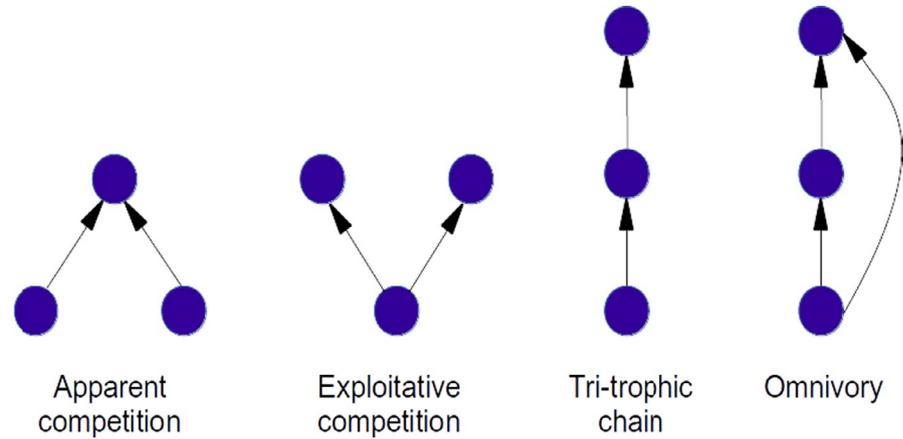
In summary, this model considers colonisation–extinction and secondary extinctions events constrained by network structure, with no consideration of population dynamics and interaction strength. Then, this simple model acts as a null model: if we observe a deviation from a network property obtained with the null model then those mechanisms that are excluded from the model may be acting (de Bello, 2012).

## 2.2 | Structural network properties

We first calculated trophic coherence (Johnson et al., 2014), that is related to stability in the sense that small perturbations could get amplified or vanished, which is called local linear stability (May, 1972; Rohr et al., 2014). A food web is more coherent when  $Q$  is closer to zero, thus the maximal coherence is achieved when  $Q = 0$ , and corresponds to a layered network in which every node has an integer trophic level (Johnson et al., 2014; Johnson & Jones, 2017). A related metric is mean trophic level, historically used as an ecosystem health indicator (Pauly et al., 1998), predicting that food webs with higher trophic levels are less stable (Borrelli & Ginzburg, 2014). To compare coherence and trophic level we generated 1,000 null model networks with the fitted parameters of the metabweb assembly model. Then we calculated the 99% confidence interval using the 0.5% and 99.5% quantiles of the distribution of  $Q$ . We also calculated the CI for the mean trophic level.

Another property related to stability is modularity, since the impacts of a perturbation are retained within modules minimising impacts on the food web (Fortuna et al., 2010; Grilli et al., 2016). It measures how strongly sub-groups of species interact between them compared with the strength of interaction with other sub-groups (Newman & Girvan, 2004). These sub-groups are called modules. To find the best partition, we used a stochastic algorithm based

**FIGURE 2** The four three-species motifs analysed: apparent competition, exploitative competition, tri-trophic chain and omnivory. Motifs are three-node sub-networks. These four motifs have been explored both theoretically and empirically in ecological networks and are the most common found in food webs



on simulated annealing (Reichardt & Bornholdt, 2006). Simulated annealing allows maximising modularity without getting trapped in local maxima configurations (Guimerá & Nunes Amaral, 2005). As the simulated annealing algorithm is stochastic we estimated modularity as the mean of 100 repetitions. To assess the significance of our networks we calculated the 99% confidence intervals based on 1,000 null model networks as previously described.

Finally, we calculated the average of the maximal real part of the eigenvalues of the jacobian (Grilli et al., 2016) for randomly parametrised systems, keeping fixed the predator–prey (sign) structure. This is a measure related to quasi sign-stability (QSS) that is the proportion of randomly parametrised systems that are locally stable (Allesina & Pascual, 2008). We sampled 1,000 jacobians to estimate the maximal real part of the eigenvalues and withhold the average, we repeat this procedure for each of the 1,000 null model networks and estimated the 99% confidence intervals as described earlier.

To show the results graphically we calculated the deviation for each metric, which correspond to the 99% confidence intervals for the metric's value in the assembly null model. We define the mid-point

$$\text{metric}_{\text{mid}} = \text{metric}_{\text{low}} + \frac{\text{metric}_{\text{high}} - \text{metric}_{\text{low}}}{2}.$$

Then the deviation of the observed value of the real web is calculated.

$$\text{deviation} = \frac{\text{metric}_{\text{observed}} - \text{metric}_{\text{mid}}}{\text{metric}_{\text{high}} - \text{metric}_{\text{low}}}.$$

A deviation value outside of  $[-0.5, 0.5]$  indicates that the value is outside of the 99% confidence interval. See the Supporting Information for formulas and more details about these metrics.

### 2.3 | Motifs

We considered the abundance of sub-networks that deviates significantly from a null model network, which are called motifs (Milo

et al., 2002). In practice, sub-networks are generally called motif without taking into account the mentioned condition. During the assembly process, motifs that are less dynamically stable tend to disappear from the food web (Borrelli, 2015; Borrelli et al., 2015). Furthermore, different motifs patterns could also be the result of habitat filtering (Baldassano & Bassett, 2016; Dekel et al., 2005).

We analysed here the four three-species motifs that have been most studied theoretically and empirically in food webs (Baiser et al., 2016; Prill et al., 2005; Stouffer et al., 2007) (Figure 2). The four three-species motifs are: apparent competition, where two preys share a predator; exploitative competition, where two predators consume the same prey; omnivory, where predators feed at different trophic levels; and tri-trophic chain, where the top predator consumes an intermediate predator that consumes a basal prey (Figure 2). These are the most common motifs present in food webs (Borrelli, 2015; Monteiro & Del Bianco Faria, 2017). We compared the frequency of these motifs to 1,000 null model networks using the 99% confidence intervals, and deviation as previously described.

### 2.4 | Topological roles

To detect the process of habitat filtering or dispersal limitation in local food webs we calculated topological roles, which characterise how many trophic links are conducted within their module and/or between modules (Guimerá & Nunes Amaral, 2005; Kortsch et al., 2015). Theoretical and empirical results suggest these roles are related to species traits, such as niche breadth, environmental tolerance, apex position in local communities and motility (Dupont & Olesen, 2009; Rezende et al., 2009; Guimerá et al., 2010; Borthagaray et al., 2014; Kortsch et al., 2015).

We determined topological roles using the method of functional cartography (Guimerá and Nunes Amaral, 2005), which is based on module membership (see Supporting Information for more details). There are four roles: *Hub connectors* have a high number of between module links; *Module connectors* have a low number of links mostly between modules; *Module hubs* have a high number of links inside its module; and *Module specialists* have a low number of links inside its module.

We estimated the roles for empirical networks and for 20 realisations of each assembly model network. To test if the proportion of species' roles changed between the empirical and each of the realisations of the model we performed a Pearson's Chi-square test with simulated  $p$ -value based on 10,000 Monte Carlo replicates.

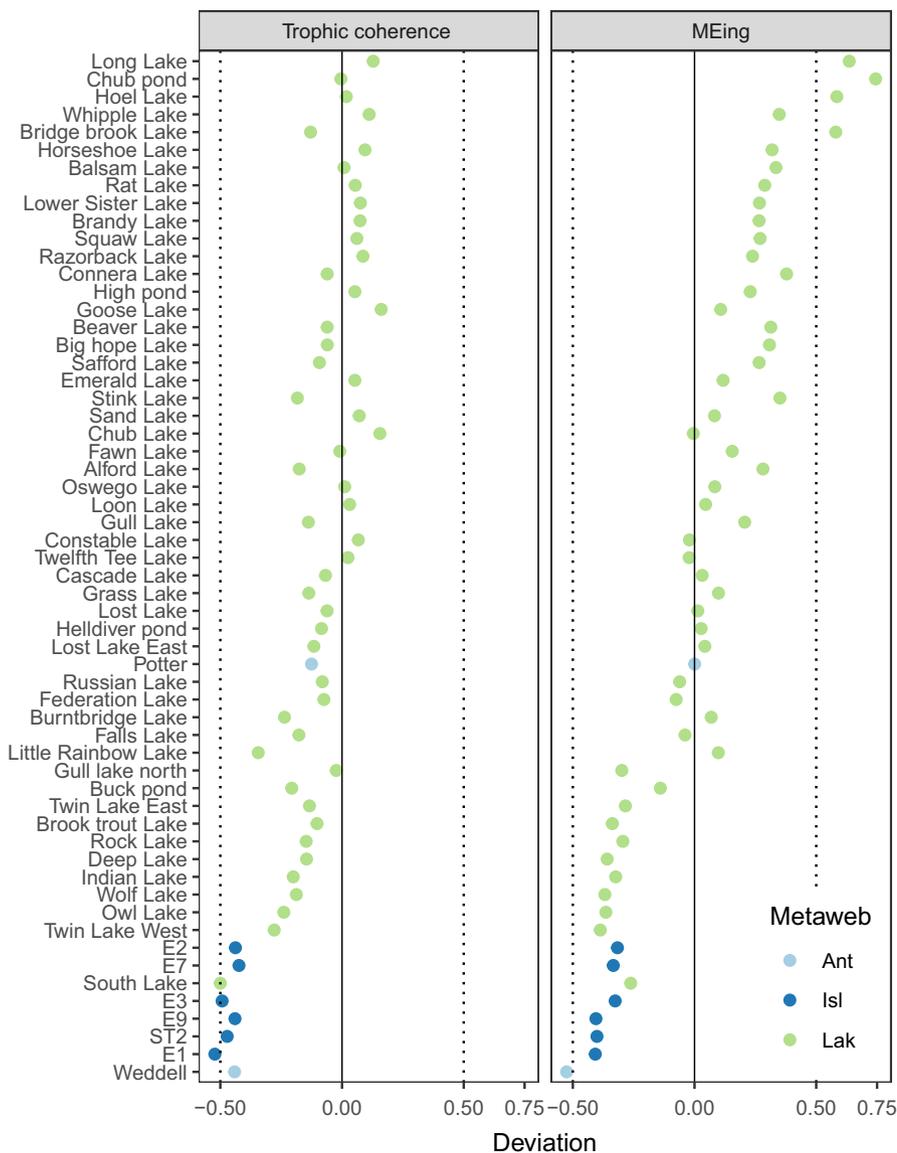
All analyses and simulations were performed in R version 4.1.1 (R Core Team, 2017), using the IGRAPH package version 1.2.6 (Csardi & Nepusz, 2006) for motifs, the package MULTIWEB for topological roles,  $Q$  and other network metrics (Saravia, 2019) and the package MEWEASMO for the metaweb assembly model (Saravia, 2020).

### 3 | RESULTS

A general description of all networks using the structural properties including metawebs is presented in Table S3. For the Antarctic metaweb, the differences in the number of species (size) between local food webs and the metaweb are greater than for the other

metawebs. The metawebs of Florida Islands and Adirondacks' Lakes have similar sizes and both are smaller and have higher connectance than the Antarctic metaweb. Thus there is a wide range of local food web sizes (13–435), number of links (17–1,978) and connectance (0.01–0.29) in our dataset.

We found almost no differences between the assembly null model and the local food webs for trophic coherence ( $Q$ ) except for E1 Island, which exhibited a lower value, hence, more stable (Figure 3, Table S5). The mean maximal eigenvalue ( $MEing$ ) was also not different except for Weddell Sea, which has a lower value resulting in an increased local stability, and four local webs from the Lakes dataset (Bridgeway Lake, Chub Pond, Hoel Lake and Long Lake) which have a higher  $MEing$  and lower stability than the model (Figure 3, Table S5). Only Weddell Sea and E1 Island were significantly different for mean trophic level (TL) (Figure 4, Table S4), only E1 Island have a lower TL, this should be the expected pattern if dynamical stability constraints were acting. For modularity we found only two local food webs different, Chub Pond, from Lakes



**FIGURE 3** Trophic coherence ( $Q$ ) and mean of maximal eigenvalue ( $MEing$ ) comparison for local empirical networks (dots) and assembly null model networks. We ran 1,000 simulations of the metaweb assembly model fitted to local networks to build the 99% confidence intervals of the metric and calculated the deviation; a value outside  $-0.5, 0.5$  interval (vertical dotted lines) indicates that the value is outside of the 99% confidence interval. Colours represent metawebs to which local food webs belong, where *Ant* is the Antarctic, *Isl* is the Islands and *Lak* is the Lakes metaweb

metaweb, that is less modular than the model and Island E9 which is more modular (Figure 4, Table S5).

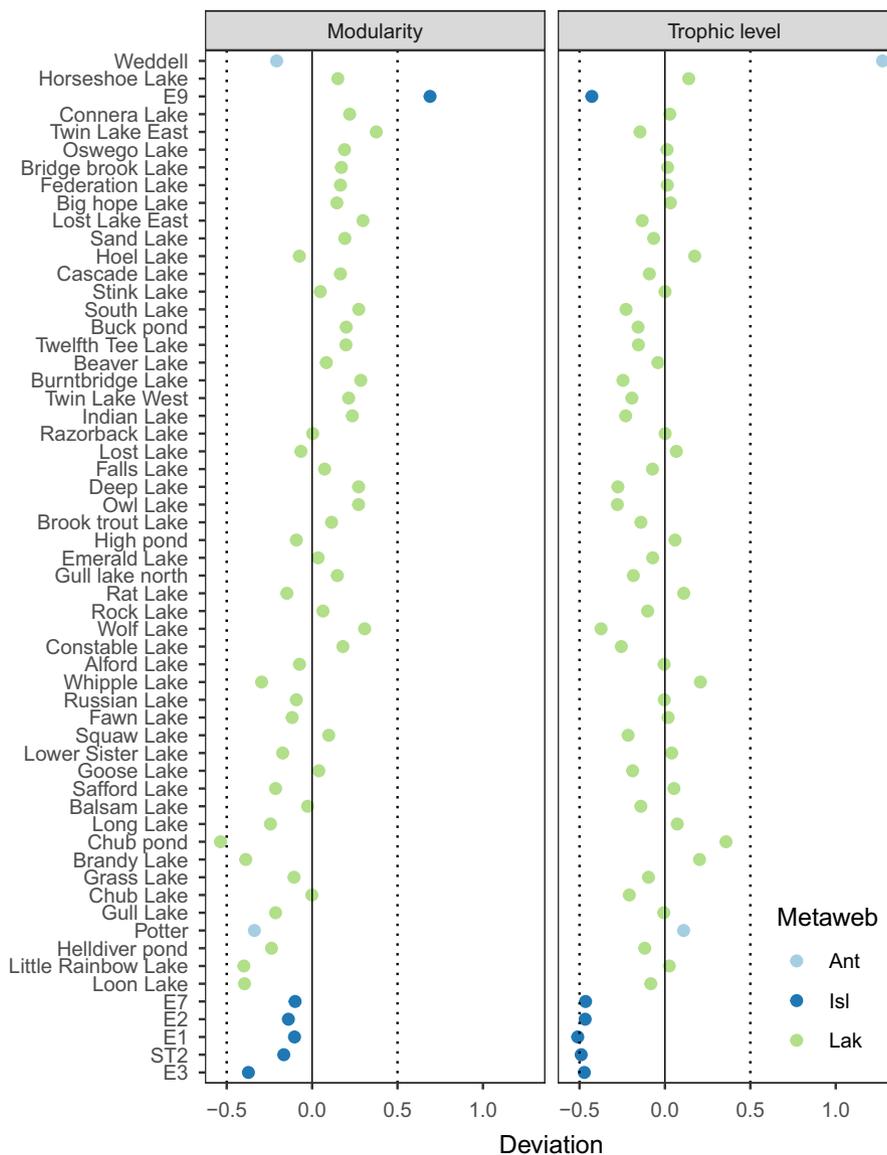
Comparing the motifs generated from the metaweb assembly null model, 9 of 58 (16%) networks showed at least one significant motif over-representation and only one (Weddell Sea) showed motifs under-representation (Figure 5, Table S6). The Hoel Lake network was the only one that showed over-representation for all motifs. Long Lake showed only omnivory over-representation, and five more have only one motif (not omnivory) over-representation. Apparent competition and exploitative competition were the most over-represented motifs (six and five times).

The proportions of topological roles were similar to the metaweb assembly model; across the 20 realisations of the assembly model, between 3 and 10 out of 58 local (5%–17%) were different at 1% significant level (Table S8). Figure 6 shows the proportions for the Antarctic and Islands metawebs for one realisation of the model and Figure S5 shows the proportions for the Lakes metaweb; we added the topological role proportions for the corresponding metaweb in

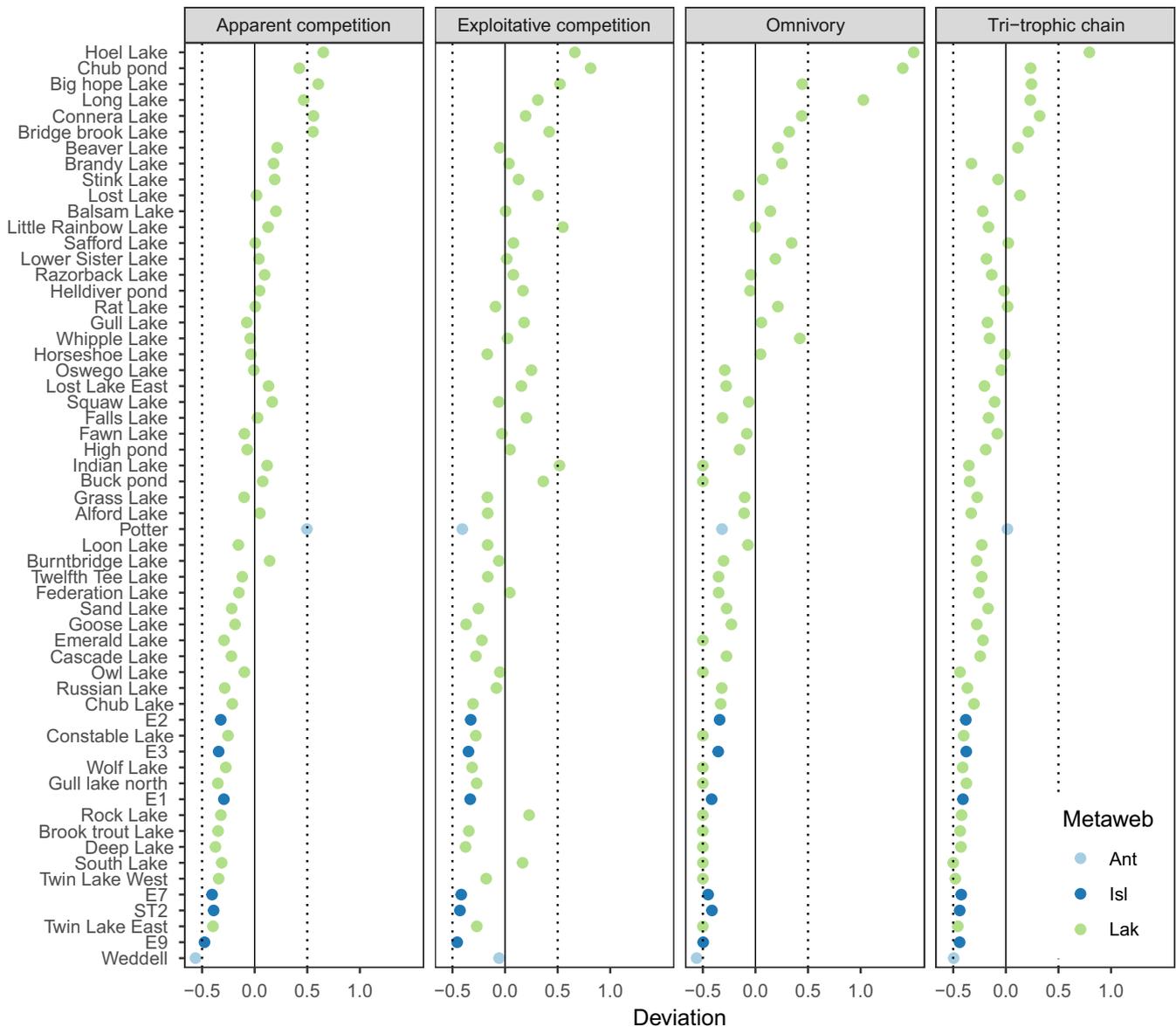
each case to visually compare with both the empirical and model food webs. The only food web that showed consistent differences with the model was Potter Cove (100% of the realisations), the second the Island E9 with 60% and the third the Weddell Sea food web that showed differences 50% of the time (Table S9).

## 4 | DISCUSSION

We hypothesised that, if local processes like dynamical stability determine food web structure, then we should observe a consistent difference in network properties between real webs and model webs randomly assembled from the regional metaweb. Contrary to our expectations, we found that most structural properties did not differ significantly between real and randomly assembled webs. We investigated network properties associated with dynamical stability (trophic coherence, modularity,  $MEing$  and motifs). Although we found differences for some local food webs, there was not a general



**FIGURE 4** Modularity and mean trophic level comparison for local empirical networks (dots) and assembly null model networks. We ran 1,000 simulations of the metaweb assembly model fitted to local networks to build the 99% confidence intervals of the metric and calculated the deviation; a value outside  $-0.5, 0.5$  interval (vertical dotted lines) indicates that the value is outside of the 99% confidence interval. Colours represent metawebs to which local food webs belong, where *Ant* is the Antarctic, *Isl* is the Islands and *Lak* is the Lakes metaweb



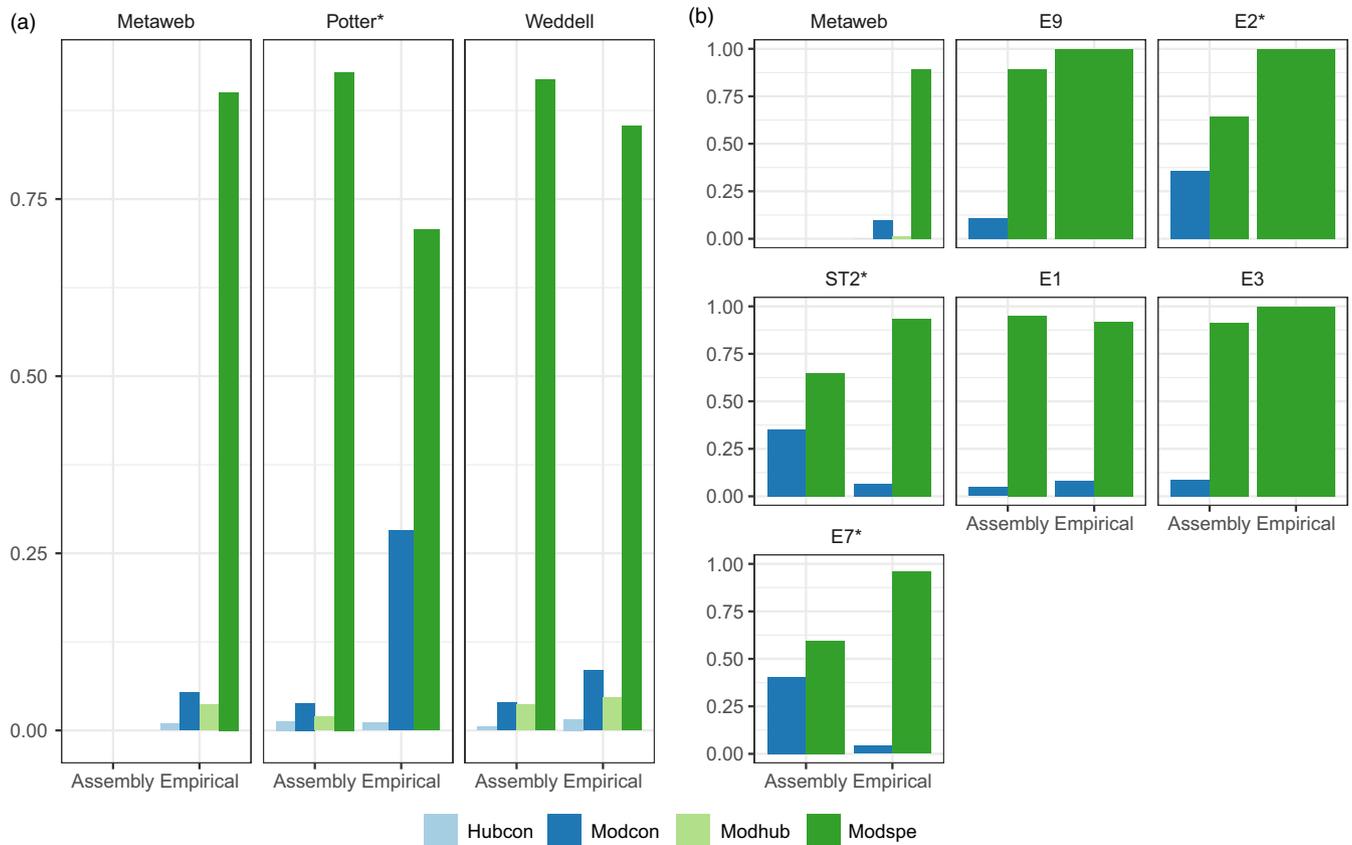
**FIGURE 5** Motifs' abundance comparison for local empirical networks (dots) and assembly null model networks. We ran 1,000 simulations of the metaweb assembly model fitted to local networks to build the 99% confidence intervals of the metric and calculated the deviation; a value outside  $-0.5, 0.5$  interval (vertical dotted lines) indicates that the value is outside of the 99% confidence interval. Colours represent metawebs to which local food webs belong, where *Ant* is the Antarctic, *Isl* is the Islands and *Lak* is the Lakes metaweb

pattern, and real web properties did not display a consistent tendency to deviate in the direction predicted by theory. We also investigated topological roles, which we expected to change due to habitat filtering and dispersal limitation. However, with the exception of the two Antarctic webs, we found a similar lack of difference between real and model webs. These results suggest that—for the metrics we considered—food webs are mainly shaped by metaweb structure, and we did not find good evidence for the influence of local dynamics.

Local food webs are expected to have relatively few trophic levels (Borrelli & Ginzburg, 2014; Williams et al., 2002). Different hypotheses have been posed to explain this pattern: the low efficiency of energy transfer between trophic levels, predator size, predator behaviour and consumer diversity (Young et al., 2013).

Recently, it has been proposed that maximum trophic level could be related to productivity and ecosystem size depending on the context but related to energy fluxes that promote omnivory (Ward & McCann, 2017). Our results of mostly no differences with the randomly assembled webs, do not invalidate these previous hypotheses but point out that the mechanisms may not be acting at the scale of the assembly process.

We expected modularity to differ between real and randomly assembled webs both due to the influence of habitat heterogeneity (Krause et al., 2003; Rezende et al., 2009) and modularity's stability-enhancing effects. Recent studies suggest that modularity increases local stability, and this effect is stronger the more complex the network is (Stouffer & Bascompte, 2011). This suggests that modularity should be higher in real webs than random webs. However, the



**FIGURE 6** Topological roles proportions for local empirical networks and metawebs compared with assembly null model for the Antarctic (a) and Islands metawebs (b). The topological roles are: *Hub connectors* have a high number of between module links; *Module connectors* have a low number of links mostly between modules; *Module hubs* have a high number of links inside its module; and *Module specialists* have a low number of links inside its module. Plots marked with “\*” are different from the null model at 1% level

effect on stability also strongly depends on the interaction strength configuration (Grilli et al., 2016) and the existence of external perturbations (Gilarranz et al., 2017). We found in most cases no significant difference in modularity, which means that the species participating in the modules could change due to differences in habitats, but the strength of the modules in terms of number of within and between interactions is the same as the observed in the assembly model.

Due to dynamical stability constraints, we expected real webs to have a lower maximum eigenvalue ( $MEing$ ) and higher trophic coherence ( $Q$ ) than randomly assembled webs. However, only the Weddell Sea followed this expectation (i.e. greater stability, lower  $MEing$ ), and four local food webs belonging to the Lakes metaweb showed the opposite pattern (i.e. lower stability, higher  $MEing$ ). Thus, although this evidence is not conclusive concerning the importance of dynamical stability in the assembly of food webs, the structure of the local food webs examined here seems to be a consequence of the metaweb structure.

We also expected real webs to have a higher frequency of stability-enhancing motifs than randomly assembled webs. Specifically, we expected an over-representation of tri-trophic chains, exploitative competition, and apparent competition (Borrelli, 2015). Some Lakes food webs had an over-representation of stability-enhancing motifs, but there was not a consistent pattern. Furthermore, Lakes

webs with an over-representation of stability-enhancing motifs often had low local stability (measured as high  $MEing$ ). The omnivory motif can either enhance or diminish stability, depending on the context (Monteiro & Faria, 2016). In our study, omnivory seemed to be destabilising: food webs with an over-representation of it (Chub Pond, Hoel Lake and Long Lake) were also those with significant lower local stability (higher  $MEing$ ); and Weddell Sea, which had the most significant higher local stability result, also had the most significant under-representation of omnivory. Food webs are more than the sum of their three-species modules (Cohen et al., 2009), which is exemplified by the contradictory results for the Weddell Sea food web: high mean trophic level, enhancing stability, but an under-representation of omnivory and apparent competition motifs.

The relative proportions of topological roles were similar between real and randomly assembled webs except in two Antarctic food webs (Weddell Sea and Potter Cover) and some from the Islands metaweb (E2, E5 and E9). These differences could reflect real differences between the habitats of the local webs and the metaweb. For example, in the metaweb, the Antarctic cod *Notothenia coriiceps* is a module hub (a species with most of its links within its module), but in Potter Cove, it is a super-generalist. In the Antarctic web, similar to observations in other Arctic and Caribbean marine

food webs (Kortsch et al., 2015; Rezende et al., 2009), modules typically correspond to a particular habitat, for example, a benthic module, a pelagic module, etc. Consequently, given that local webs are smaller than the metaweb and could cover a particular habitat, habitat filtering (a local process that is not included in the random assembly model) could play a large role. In contrast, the Lakes local food webs seem to be covered by similar local habitats.

The lack of difference between real and randomly assembled webs raises the possibility that, for these commonly used metrics that we measured, the values they take in local food webs merely reflect the properties of the metaweb. That does not mean that they are indeed the result of random assembly, nor that local processes like dynamical constraints do not act in reality. Rather, it suggests that, without further evidence, one cannot take for granted that these metrics reflect dynamical constraints (see Zhang (2020) for a similar argument regarding species co-occurrence patterns). This is particularly true given that the metrics associated with dynamical constraints can also be subordinate to other more fundamental structure-determining forces. For example, high trophic coherence means that the trophic levels are fairly distinct and there is little to no omnivory. Trophic coherence is associated with high stability; however, it has also been modelled as a consequence of the relative strength of competition versus width of consumption niche, all mediated by a physiological trait such as body size (Loeuille & Loreau, 2005). Furthermore, adaptive foraging (Heckmann et al., 2012) also leads to the emergence of trophic coherence in theoretical assembly models (Drossel et al., 2001), which has the side effect of lowering connectance and hence increasing stability (Beckerman et al., 2006).

Assuming that population dynamics does indeed play some role in determining food web structure, why then did we not observe its signal? One possible reason is that the effect of dynamics on the local network properties also manifests on regional scales. The metaweb structure is an aggregation of local webs (Ricklefs, 1987; Araújo & Rozenfeld, 2014); therefore, if dynamical constraints prevent certain network structures from occurring in local webs, then they are also prevented in the metaweb. However, while it is obviously true that local processes influence metaweb structure, we still expected to see differences between real webs and those randomly assembled from the metaweb. Local food webs differ from one another due to, for example, historical contingencies, like the stochastically determined order of arrival of species. These differences between local webs provide the species and structural diversity in the metaweb upon which non-Darwinian selection process is theorised to act (Borrelli, 2015). It is important to note that a species that is stabilising in one food web can be destabilising in another. In contrast, the metaweb describes species co-occurrences and interaction possibilities that do not occur in reality, including those that are presumably precluded due to dynamical constraints. Therefore, if the non-Darwinian selection process is true, we should expect to see differences between real and randomly assembled webs, not only due to these historical contingencies, but also due to subsequent dynamical constraints

that precluded certain co-occurrences and interactions from occurring.

Another possible reason why we did not observe the expected difference between real and randomly assembled webs is that these commonly used metrics are too coarse to detect the signal of dynamical constraint. We chose popular structural metrics that have been associated with stability in the literature; however, stability also depends on interaction strengths. For example, generalisations about the relationship between modularity and stability cannot be made without first characterising the distribution of interaction strengths (Grilli et al., 2016), which were unknown for our webs. Furthermore, given that most predator-prey interactions are weak (McCann et al., 1998; Neutel et al., 2002), the structure of the species-rich food webs we investigated might mask the importance of the few strong links. Theoretical predictions relating stability to structure also depend on the particulars of the community and the type of perturbation considered (Cenci et al., 2018). It is known that small changes in network structure can have large effects on food web stability (Fox, 2006). It is also known that the sum of effects of positive and negative feedback loops that determine stability can interact in counterintuitive ways (Hosack et al., 2009). Therefore, it may not be possible to reduce those complex interactions into simple structural metrics.

In conclusion, we found that the commonly used metrics of network structure do not differ between real food webs and model webs randomly assembled from the regional metaweb. This suggests that evolutionary and metacommunity assembly processes are more important to these aspects of food web structure than local dynamics. However, this kind of analysis needs to be expanded to other regions and habitat types to confirm whether or not this is a general pattern.

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#### CONFLICT OF INTEREST

All authors declare no conflict of interest.

#### AUTHORS' CONTRIBUTIONS

L.A.S., T.I.M., M.D.T. and F.R.M. conceived the ideas and designed the methodology; T.I.M. and L.A.S. collected the data; L.A.S. wrote the code; L.A.S., T.I.M. and N.P.K. analysed the data; N.P.K., L.A.S. and T.I.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

#### DATA AVAILABILITY STATEMENT

The source code and data are available at Zenodo <https://doi.org/10.5281/zenodo.5783873> (Saravia, 2021) and Github <https://github.com/lSaravia/MetawebsAssembly/>.

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