

¹ Ecological Network assembly: how the regional metaweb influences
² local food webs

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¹⁰ 4398

¹¹ **Keywords:** Metaweb, ecological network assembly, network assembly model, food web structure, modularity
¹² , trophic coherence, motif, topological roles, null models

¹³ **Running title:** The metaweb influence on local food webs.

14 **Abstract**

- 15 1. Local food webs can be studied as the realisation of a sequence of colonising and extinction events,
16 where a regional pool of species —called the metaweb— acts as a source for new species. Food webs
17 are thus the result of assembly processes that are influenced by migration, habitat filtering, stochastic
18 factors, and dynamical constraints. Therefore, we expect their structure to reflect the action of these
19 influences.
- 20 2. We compared the structure of real local food webs to (1) a metaweb, (2) randomly-constructed webs,
21 and (3) webs resulting from a trophic assembly model. The assembly model had no population dy-
22 namic constraints, but simply required that consumer species have at least one prey present in the
23 local web in order to colonise and remain extant. We compared global properties and network sub-
24 structures—motifs—related to ecological stability, and topological roles that are node-level properties.
25 We hypothesised that the structure of real food webs should differ from other webs in a way that re-
26 flected dynamical stability constraints. Three data-sets were used: (1) the marine Antarctic metaweb,
27 built using a dietary database; (2) the Weddell Sea local food web; and (3) the Potter Cove local food
28 web.
- 29 3. Contrary to our expectation, we found that, while most network global properties of real webs were
30 different from random webs, there were almost no differences between real webs and those resulting
31 from the assembly model. Further, while real webs showed different motif representations compared to
32 the assembly model, these were not motifs associated with increased stability. Species' topological roles
33 showed differences between the metaweb and local food webs that were not explained by the assembly
34 model, suggesting that species in real webs are selected by habitat or dispersal limitations.
- 35 4. Our results suggest that there is not a strong dynamical restriction upon food web structure that
36 operates at local scales. Instead, the structure of local webs is inherited from the metaweb, implying
37 that evolutionary processes acting on large temporal and spatial scales have a more important influence.
- 38 5. Recently, it has been found in competitive and mutualistic networks that structures that are often
39 attributed as causes or consequences of ecological stability are probably a by-product of the assembly
40 processes (i.e. spandrels). We extended these results to trophic networks suggesting that this could be
41 a more general phenomenon.

42 Introduction

43 The characterization of ecological systems as networks of interacting elements has a long history (Cohen &
44 Newman, 1985; May, 1972; Paine, 1966). Much of this work has been devoted to investigate network structure
45 and its effects on dynamics and stability (Thebault & Fontaine, 2010). In recent years a renewed emphasis on
46 structural stability (Grilli et al., 2017; Rohr, Saavedra, & Bascompte, 2014) and new developments in random
47 matrix theory (Allesina et al., 2015) has greatly expanded our capability to analyse ecological networks.
48 However, the effects of ecological dynamical processes on food web structure are not fully understood. One
49 such dynamical process is community assembly: how species from a regional pool colonize a site and build
50 local interactions (Carstensen, Lessard, Holt, Krabbe Borregaard, & Rahbek, 2013). Regional species pools
51 are shaped by evolutionary and biogeographical processes that imply large spatial and temporal scales
52 (Carstensen et al., 2013; Kortsch et al., 2018). More specifically, the assembly of local communities is
53 influenced by dispersal, environmental filters, biotic interactions and stochastic events (HilleRisLambers,
54 Adler, Harpole, Levine, & Mayfield, 2012). These processes have been studied by means of metacommunity
55 theory (Mathew A Leibold, Chase, & Ernest, 2017), where different spatial assemblages are connected
56 through species dispersal.

57 Metacommunity theory provides a framework for assessing the roles of local- and regional-scale processes
58 on network structure (Baiser, Buckley, Gotelli, & Ellison, 2013; M A Leibold et al., 2004). This approach
59 has been applied historically to competitive interactions, whereas trophic interactions have received less
60 attention (Baiser, Elhesha, & Kahveci, 2016). Recently, there has been an increase in food web assembly
61 studies, integrating them with island biogeography (Galiana et al., 2018; Gravel, Massol, Canard, Mouillot,
62 & Mouquet, 2011), metacommunity dynamics (Liao, Chen, Ying, Hiebeler, & Nijs, 2016; Pillai, Gonzalez,
63 & Loreau, 2011) and the effects of habitat fragmentation (Mougi & Kondoh, 2016). Previous attempts to
64 study the food web assembly process have used motifs as building blocks of local communities (Baiser et al.,
65 2016). Motifs are network sub-structures composed of species and links whose frequency deviates from the
66 random expectation (Milo et al., 2002). By comparing motif representation at different spatial scales—from
67 local to regional—the process of assembly of interactions may be revealed (Baiser et al., 2016), e.g. if the
68 same processes structure the food web across scales, motif representation should be the same.

69 Insight into food web assembly can be also gained by assessing the structure of ecological networks at different
70 levels: emergent or global properties that focus on averages over the entire network (e.g. modularity or
71 connectance) and local properties that focus on how one or a group of species are related to the whole.
72 Global properties related to resilience and stability are fundamental to understand the response of ecological

73 networks to global threats like climate change and biological invasions. One of these properties is small-
74 worldness, associated with rapid responses to disturbances and resistance to secondary extinctions (J. M.
75 Montoya & Solé, 2002). The small-world pattern is related to two global properties: the average of the
76 shortest distance between all species, called characteristic path length, and the clustering coefficient, the
77 probability that two species linked to the same species are linked. Then, the small-world pattern implies a
78 short average path length and a high level of clustering compared to random networks (Watts & Strogatz,
79 1998). This pattern comes from the general network theory, beyond ecological networks, and has been
80 recently applied to marine food webs (Bornatowski, Barreto, Navia, & de Amorim, 2017; Gray et al., 2016;
81 Tomás Ignacio Marina et al., 2018; A. F. Navia, Cruz-Escalona, Giraldo, & Barausse, 2016).

82 Since the early studies of May (1972) stating that larger and more connected ecosystems will be unstable,
83 there has been a search for factors that would stabilize complex food webs (Landi, Minoarivelo, Bränström,
84 Hui, & Dieckmann, 2018; K. S. McCann, 2000; Neutel et al., 2007). One of such potential factors is trophic
85 coherence: networks with increasing size and complexity could be stable as long as they are sufficiently
86 coherent (Johnson, Domínguez-García, Donetti, & Muñoz, 2014). Trophic coherence is based on the distances
87 between the trophic positions of species and measures how well species fall into discrete trophic levels.
88 Then, more coherence implies a more hierarchical food web structure, which is directly correlated with local
89 asymptotic stability (Johnson et al., 2014). Trophic coherence is also related to omnivory degree, a perfectly
90 coherent network has zero omnivory degree (Monteiro & Faria, 2016). The advantage of coherence as an
91 index of stability is that it does not make any assumptions about interaction strengths. A property related
92 to coherence is mean trophic level, historically used as an ecosystem health indicator (Pauly, Christensen,
93 Dalsgaard, Froese, & Torres, 1998), predicting that food webs with higher trophic levels are less stable
94 (Borrelli & Ginzburg, 2014).

95 Food webs have structurally complex and highly non-random patterns that contain internal functional units
96 or sub-modules (Grilli, Rogers, & Allesina, 2016). These are groups of prey and predators that interact
97 more strongly with each other than with species belonging to other modules. These modules (also called
98 compartments) act as a buffer to the propagation of perturbations throughout the network, increasing its
99 persistence (D. B. Stouffer & Bascompte, 2011). It is noteworthy to mention that the small-world pattern and
100 modularity act in opposite directions. Whereas a small-world topology favours the spread of perturbations
101 through its rapid dissipation (Gray et al., 2016), the presence of high modularity prevents the dispersal of
102 perturbations (Krause, Frank, Mason, Ulanowicz, & Taylor, 2003; D. B. Stouffer & Bascompte, 2011).

103 Species may participate in different ways with respect to modularity, depending on how many trophic links
104 are conducted within their own module and/or between modules (Roger Guimerà & Nunes Amaral, 2005;

105 Kortsch, Primicerio, Fossheim, Dolgov, & Aschan, 2015). This participation with respect to modularity is
106 called a species' topological role. Theoretical and empirical results suggest these roles are related to species
107 traits, such as wide niche breadth, environmental tolerance, apex position in local communities and high
108 motility (Borthagaray, Arim, & Marquet, 2014; R Guimerà et al., 2010; Kortsch et al., 2015; Rezende, Albert,
109 Fortuna, & Bascompte, 2009). This is a local property at an individual species level.

110 If we consider a subset of linked species inside the food web this forms a sub-network. When the abundance of
111 one of these sub-networks deviates significantly from a null model network, this is called a motif (Milo et al.,
112 2002). Besides this definition, in the ecological literature motif has been used as a synonym of sub-network.
113 We analyse here the three-species sub-networks that have been most studied theoretically and empirically in
114 food webs (Baiser et al., 2016; Prill, Iglesias, & Levchenko, 2005; D. B. Stouffer, Camacho, Jiang, & Nunes
115 Amaral, 2007). Specifically, we focused on four of the thirteen possible three-species sub-networks: apparent
116 competition, exploitative competition, tri-trophic chain, and omnivory (Figure 1).

117 The frequency of motifs (i.e over-represented, under-represented or random) at different spatial scales may
118 reveal aspects about the process behind the assembly of interactions: if the same motif representation is
119 observed across scales, this suggests that the same process may be structuring the network (Baiser et al.,
120 2016). Ecological interactions occur at the local scale so differences may show the importance of local
121 interactions in the assembly of the food web. During the assembly process those motif structures that
122 are less dynamically stable tend to disappear from the food web, which represents a system-level selective
123 force where the ecological interactions are shaped by dynamical constraints rather than Darwinian processes
124 (Borrelli, 2015), this has been called non-adaptative systemic selection (Borrelli et al., 2015).

125 In this study, we measure the network-structural properties (above) in two real local webs: the Weddell
126 Sea food web, which represents 3.5 million km² (Jacob et al., 2011); and the Potter Cove network, which
127 represents 6.8 km² (Tomás I Marina et al., 2018). We compare the real webs to the Antarctic metaweb,
128 built from a dietary database (Raymond et al., 2011), representing an area of 34.8 million km². To provide
129 a baseline for comparison, we compare metrics of the real webs to: (1) random networks, representing an
130 absence of ecological mechanisms; and (2) webs obtained from an assembly model, representing an absence
131 of dynamical stability constraints while preserving species' trophic relationships. If real food web structure
132 reflects dynamical stability constraints, then we should expect to see the structural properties change from
133 the metaweb to the local scale. In particular, we expect global properties related to resilience and stability
134 (i.e. small-worldness, trophic coherence and modularity) to be close to the random model at the metaweb
135 scale, and significantly different at the local scale ; and a greater frequency of stable motifs in the local
136 food webs. In addition, we expect a change in the frequency of topological roles since habitat filtering or

137 dispersal limitation may modify them at the local food web scale. These changes should be also reflected as
138 differences from the metaweb assembly model. On the other hand, if the assembly model also produces webs
139 with stability-enhancing structural attributes, then that indicates that these structures may be spandrels of
140 the metaweb rather than a consequence of some dynamical constraint acting on the local web.

141 Methods

142 The three datasets used in this study encompass a wide range of spatial scales and were collected inde-
143 pendently. The Southern Ocean database compiled by Raymond et al. (2011) was used to construct the
144 Antarctic metaweb selecting only species located at latitudes higher than 60°S. Raymond et al. (2011)
145 compiled information from direct sampling methods of dietary assessment, including gut, scat, and bolus
146 content analysis, stomach flushing, and observed feeding. We considered that the metaweb is the regional
147 pool of species defined by the biogeographic Antarctic region. Next we analysed two local food webs: the
148 Weddell Sea food web dataset includes species situated between 74°S and 78°S with a West-East extension of
149 approximately 450 km, and comprises all information about trophic interactions available for the zone since
150 1983 (Jacob et al., 2011). The Potter Cove dataset comes from a 4 km long and 2.5 km wide Antarctic fjord
151 located at 62°14'S, 58°40'W, South Shetland Islands (Tomás I Marina et al., 2018). These food web datasets
152 comprise benthic and pelagic habitats of the Antarctic ecosystem, few aggregated low-trophic level groups
153 (e.g. detritus, diatoms, phytoplankton, zooplankton) and a high resolution of the macroalgae community
154 (i.e. 24 biological species of red, brown and green macroalgae). The macroalgae community is responsible for
155 the majority of the primary production and supports a large fraction of secondary production in Antarctic
156 fjords (M. L. Quartino & Boraso de Zaixso, 2008, Valdivia, Díaz, Garrido, & Gómez (2015)). Higher trophic
157 levels comprise: invertebrate (e.g. ascidians, sponges, isopods, amphipods, bivalves, gastropods, cephalopods,
158 echinoderms) and vertebrate predator groups (e.g. demersal and pelagic fishes, penguins, seals and whales).
159 For more information about these datasets refer to the original publications. To make datasets compatible,
160 we first checked taxonomic names for synonyms, and second, we added species (either prey or predator)
161 with their interactions to the metaweb when the local food webs contain a greater taxonomic resolution.
162 This resulted in the addition of 258 species to the metaweb, which represent 33% of the total. We removed
163 cannibalistic (self-links) and double arrows (i.d. A eats B and B eats A).

164 We analysed the structure of the networks using properties that focus on different levels: emergent or global
165 properties that take into account the whole network, sub-structural properties that consider several nodes,
166 and properties related to one node. To describe food webs as networks each species is represented as a

node or vertex and the trophic interactions are represented as edges or links between nodes. These links are directed, from the prey to the predator, as the flow of energy and matter. Two nodes are neighbours if they are connected by an edge and the degree k_i of node i is the number of neighbours it has. The food web can be represented by an adjacency matrix $A = (a_{ij})$ where $a_{ij} = 1$ if species j predaes on species i , else is 0. Then $k_i^{in} = \sum_j a_{ji}$ is the number of preys of species i or its in-degree, and $k_i^{out} = \sum_j a_{ij}$ is the number of predators of i or its out-degree. The total number of edges is $E = \sum_{ij} a_{ij}$.

Models

To unravel the mechanisms of network assembly we considered two models: 1) a random network model without any ecological mechanism, and 2) a colonization-extinction model constrained by the network structure, with no consideration of population dynamics and interaction strength. Then we compared the empirical networks with such models using a null model approach: if we observe a deviation from the property obtained with the null model then mechanisms that are excluded from the model may be acting (de Bello, 2012).

The random network model that we used is the Erdős-Rényi random graph (Erdős & Rényi, 1959). An Erdős-Rényi network is constructed fixing the number of edges and nodes and assigning at random the m edges to the n nodes with equal probability (Baiser et al., 2016; Erdős & Rényi, 1959). We restricted the random model by eliminating double arrows and cannibalistic links. In a small number of cases the algorithm generates two separated network components or networks without basal species; we discarded such cases to make possible the calculation of trophic level, trophic coherence (see below) and modularity. We included the random model because it is the baseline model to calculate the small-world structure and motif representations, so it seems logical to apply it to the other properties.

To consider network assembly mechanisms we used a metaweb assembly model (Figure 1), called the trophic theory of island biogeography (Gravel et al., 2011). In this model species migrate from the metaweb to a local web with a uniform 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 can only survive if at least one of its preys is present, or if it is a basal species. When a species goes extinct locally it may produce secondary extinctions; we check that the local predators maintain at least one prey if not they become extinct independent of the probability e . We simulated this model in time and it eventually reaches an equilibrium that depends on the migration and extinction probabilities but also on the structure of the metaweb. The ratio of immigration vs. extinction $\alpha = c/e$ is hypothesized to be inversely related to the

197 distance to the mainland (MacArthur & Wilson, 1967), and as extinction e should be inversely proportional
 198 to population size (Hanski, 1999), the ratio α is also hypothesized to be related to the local area.

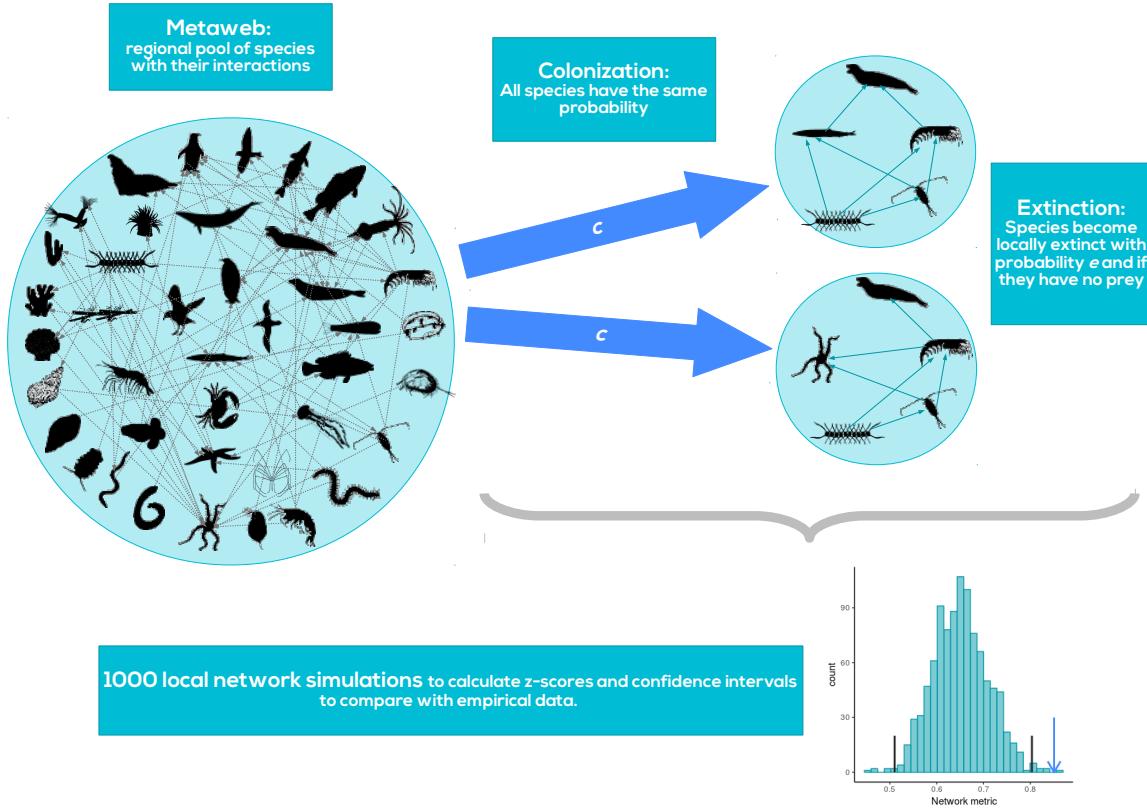


Figure 1: Schematic diagram of the metaweb assembly model: species migrate from the metaweb with a probability c to a local network carrying their potential links to preys; here they have a probability of extinction e . Additionally, predators become extinct if their preys are locally extinct. We simulate 1000 local networks and calculate global properties. From the distribution of these topological properties we calculate 1% confidence intervals to compare with empirical networks

199 For the random model we simulated networks with the same number of nodes n and edges m as the empirical
 200 networks; for the metaweb assembly model we fitted the parameters c and e to obtain networks with n and
 201 m close to the empirical networks. This implies that α should reflect the differences in areas of the two local
 202 food webs. For details of the fitting and simulations see Appendix.

203 Global network properties

204 The first global emergent property we analysed was the small-world pattern, which examines the average of
 205 the shortest distance between nodes and the clustering coefficient of the network (Watts & Strogatz, 1998).

206 This property is associated with an increased resilience and resistance to secondary extinctions (Bornatowski
 207 et al., 2017; Solé & Montoya, 2001). We first calculated the characteristic path length that is the shortest
 208 path between any two nodes. Then L is the mean value of the shortest path length across all pairs of nodes.
 209 The clustering coefficient of node i was defined as

$$cc_i = \frac{2E_i}{k_i(k_i - 1)}$$

210 where E_i is the number of edges between the neighbours of i . The clustering coefficient of the network CC
 211 is the average of cc_i over all nodes. The original definition of small-world networks is conceptual (Watts &
 212 Strogatz, 1998), a network G is small-world when it has a similar mean shortest path length but greater
 213 clustering than an Erdős-Rényi random network with the same number of nodes n and edges m . For the
 214 quantitative version of the small-world pattern we followed Humphries & Gurney (2008); we need to define:

$$\gamma_g = \frac{CC_g}{CC_{null}}$$

215 and

$$\lambda_g = \frac{L_g}{L_{null}}$$

216 where CC_g and L_g are the clustering coefficient and the mean shortest path length of the network of interest
 217 G ; CC_{null} and L_{null} are the same quantities for the null model. Thus, the quantitative small-world-ness is
 218 defined as:

$$S = \frac{\gamma_g}{\lambda_g}$$

219 and to determine if S is statistically significant Monte Carlo methods were used (Crowley, 1992). We built
 220 1000 null model networks with the same number of nodes n and edges m than the empirical network; then
 221 we calculated S for each random network and the lower and higher 99% quantiles of the S distribution are
 222 called ql, qh :

$$CI = \frac{qh - ql}{2}$$

the upper 99% confidence limit is then $CL^{0.01} = 1 + CI$. Thus, if a network has $S > CL^{0.01}$ it is considered a small-world network (Humphries & Gurney, 2008). We also calculated the small-world-ness and the CI using the metaweb assembly model as a null model.

The second global property was 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). We first needed to estimate the trophic level of a node i , defined as the average trophic level of its preys plus 1. That is:

$$tp_i = 1 + \frac{1}{k_i^{in}} \sum_j a_{ij} tp_j$$

where $k_i^{in} = \sum_j a_{ji}$ is the number of preys of species i , basal species that do not have preys (then $k_i^{in} = 0$) are assigned a $tp = 1$. Then the trophic difference associated to each edge is defined as $x_{ij} = tp_i - tp_j$. The distribution of trophic differences, $p(x)$, has a mean $E^{-1} \sum_{ij} a_{ij} x_{ij} = 1$ by definition. Then the trophic coherence is measured by:

$$q = \sqrt{\frac{1}{E} \sum_{ij} a_{ij} x_{ij}^2 - 1}$$

that is the standard deviation of the distribution of all trophic distances. 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 & Jones, 2017; Johnson et al., 2014). To compare coherence and trophic level we generated 1000 null model networks with at least one basal species and the same number of species and links—or approximately the same—than the network of interest. Then we calculated the 99% confidence interval using the 0.5% and 99.5% quantiles of the distribution of q ; we also calculated the confidence interval for the mean trophic level tp . We calculated the z-scores as:

$$z_i = \frac{q_{obs} - q_{null}}{\sigma_{qnull}}$$

where q_{obs} is the observed coherence, q_{null} is the mean coherence from the null model networks and σ_{qnull} is the standard deviation. The same formula is used for tp . The z-score thus measures the significance of deviations of the real network from the null hypothesis. If the distribution of the quantity (q , tp) under the null model is normal, a z-score greater than 2 is evidence that the observed quantity is significantly greater than its random counterpart, and a z-score less than -2 means that the quantity is significantly lower. If the

246 distribution under the null model is skewed this is not necessarily true and thus we must rely on confidence
247 intervals.

248 Another property related to stability is modularity, since the impacts of a perturbation are retained within
249 modules minimizing impacts on the food web (Fortuna et al., 2010; Grilli et al., 2016). It measures how
250 strongly sub-groups of species interact between them compared with the strength of interaction with other
251 sub-groups (Newman & Girvan, 2004). These sub-groups are called compartments. In order to find the
252 best partition we used a stochastic algorithm based on simulated annealing (Reichardt & Bornholdt, 2006).
253 Simulated annealing allows maximizing modularity without getting trapped in local maxima configurations
254 (Roger Guimerà & Nunes Amaral, 2005). The index of modularity was defined as:

$$M = \sum_s \left(\frac{I_s}{E} - \left(\frac{d_s}{2E} \right)^2 \right)$$

255 where s is the number of modules or compartments, I_s is the number of links between species in the module
256 s , d_s is the sum of degrees for all species in module s and E is the total number of links for the network. To
257 assess the significance of our networks we calculate the 99% confidence intervals and z-scores based on 1000
258 null model networks as previously described.

259 Sub-structural properties (motifs)

260 We considered four of the thirteen possible three-species sub-networks: apparent competition, exploitative
261 competition, tri-trophic chain and omnivory (Figure S5). These are the only motifs present in all networks
262 analysed here. We compared the frequency of these motifs to 1000 null model networks using the 99%
263 confidence interval and the z-score as previously described. To determine if the proportions of motifs change
264 across networks we use the Pearson's Chi-squared test with simulated p-value based on 10000 Monte Carlo
265 replicates.

266 Node-level properties (Topological roles)

267 As a local property that reflect the ecological role of each species we determined topological roles using
268 the method of functional cartography (Roger Guimerà & Nunes Amaral, 2005), which is based on module
269 membership (See modularity). The roles are characterized by two parameters: the standardized within-
270 module degree dz and the among-module connectivity participation coefficient PC . The within-module
271 degree is a z-score that measures how well a species is connected to other species within its own module:

$$dz_i = \frac{k_{is} - \bar{k}_s}{\sigma_{ks}}$$

272 where k_{is} is the number of links of species i within its own module s , \bar{k}_s and σ_{ks} are the average and standard
 273 deviation of k_{is} over all species in s . The participation coefficient PC estimates the distribution of the links
 274 of species i among modules; thus it can be defined as:

$$PC_i = 1 - \sum_s \frac{k_{is}}{k_i}$$

275 where k_i is the degree of species i (i.e. the number of links), k_{is} is the number of links of species i to species
 276 in module s . Due to the stochastic nature of the module detection algorithm we made repeated runs of the
 277 algorithm until there were no statistical differences between the distributions of PC_i and dz_i in successive
 278 repetitions; to test such statistical difference we used the k-sample Anderson-Darling test (Scholz & Stephens,
 279 1987). Then we calculated the mean and 95% confidence interval of dz and PC .

280 To determine each species' role the $dz - PC$ parameter space was divided into four areas, modified from
 281 Roger Guimerà & Nunes Amaral (2005), using the same scheme as Kortsch et al. (2015). Two thresholds
 282 were used to define the species' roles: $PC = 0.625$ and $dz = 2.5$. If a species had at least 60% of links within
 283 its own module then $PC < 0.625$, and if it also had $dz \geq 2.5$, thus it was classified as a module hub. This
 284 parameter space defines species with relatively high number of links, the majority within its own module.
 285 If a species had $PC < 0.625$ and $dz < 2.5$, then it was called a peripheral or specialist; this refers to a
 286 species with relatively few links, mostly within its module. Species that had $PC \geq 0.625$ and $dz < 2.5$ were
 287 considered module connectors, since they have relatively few links, mostly between modules. Finally, if a
 288 species had $PC \geq 0.625$ and $dz \geq 2.5$, then it was classified as a super-generalist or hub-connector, because
 289 it has high between- and within-module connectivity. To test if the proportion of species' roles changed
 290 between networks we performed a Pearson's Chi-squared test with simulated p-value based on 10000 Monte
 291 Carlo replicates. Also, we tested if these proportions changed for one realization of the metaweb assembly
 292 model fitted for each local network.

293 All analyses and simulations were made in R version 3.4.3 (R Core Team, 2017), using the igraph pack-
 294 age version 1.1.2 (Csardi & Nepusz, 2006) for motifs and topological role estimations, and NetIndices
 295 (Kones, Soetaert, van Oevelen, & Owino, 2009) for trophic level calculations. Source code and data
 296 is available at figshare https://figshare.com/ADD_URL_HERE and github <https://github.com/lasaravia/MetawebsAssembly/>.

298 **Results**

299 **Global network properties**

300 Based on the random null model, all networks presented the small-world topology as their small-world-ness
301 index was larger than the 99% confidence interval (Table 1 & S1). However, we did not find differences
302 between the local food webs and the assembly model (Figure 2 & Table S2). Regarding trophic coherence,
303 all networks presented negative random z-scores and significantly smaller q values (Table 1 & S1), thus they
304 are more locally stable as they are more coherent. Using the metaweb assembly model, the Weddell Sea
305 food web showed a significative lower value (Figure 2) meaning that it is more stable than the networks
306 generated by the model, and Potter Cove food web exhibited no significant differences (Figure 2 & Table
307 S2). Mean trophic level results were similar among networks and significantly lower than the random null
308 model (Table 1 & S1), though were not significantly different to the metaweb model. Modularity values for
309 the empirical food webs were greater than the random model, but not significantly higher in Potter Cove;
310 and with no differences compared to the metaweb assembly model. This means that networks obtained with
311 the assembly model will have a modularity close to the random model. Overall, networks differed from the
312 random null model though presented similarities with the metaweb assembly model.

Table 1: Network global properties across scales. The *Metaweb* represents the marine predator-prey relationships of Antarctica built from a dietary database, the *Weddell Sea* and *Potter Cove* are the local food webs. Z-scores were calculated against 1000 random model networks. Quantities marked with '*' are significant at 1% level. A negative z-score means that the quantity is smaller than the expectation from null model simulations; a positive z-score means that is greater.

Network	Potter Cove	Weddell Sea	Metaweb
Size	91	437	859
Links	309	1908	9003
Area (Km ²)	6.8	3.5e6	34.8e6
Connectance	0.037	0.010	0.012
PathLength	1.81	2.20	2.57
Clustering	0.10	0.048	0.22
Small-World-ness random	2.75*	4.69*	10.87*
Trophic coherence	0.53	0.45	0.70
Trophic coherence random	-0.54*	-2.08*	-3.54*
z-score			
Mean Trophic level	2.13	1.98	1.91
Trophic level random z-score	-0.27*	-0.86*	-1.60*
Modularity	0.37	0.48	0.45
Modularity random z-score	0.89	18.97*	85.75*

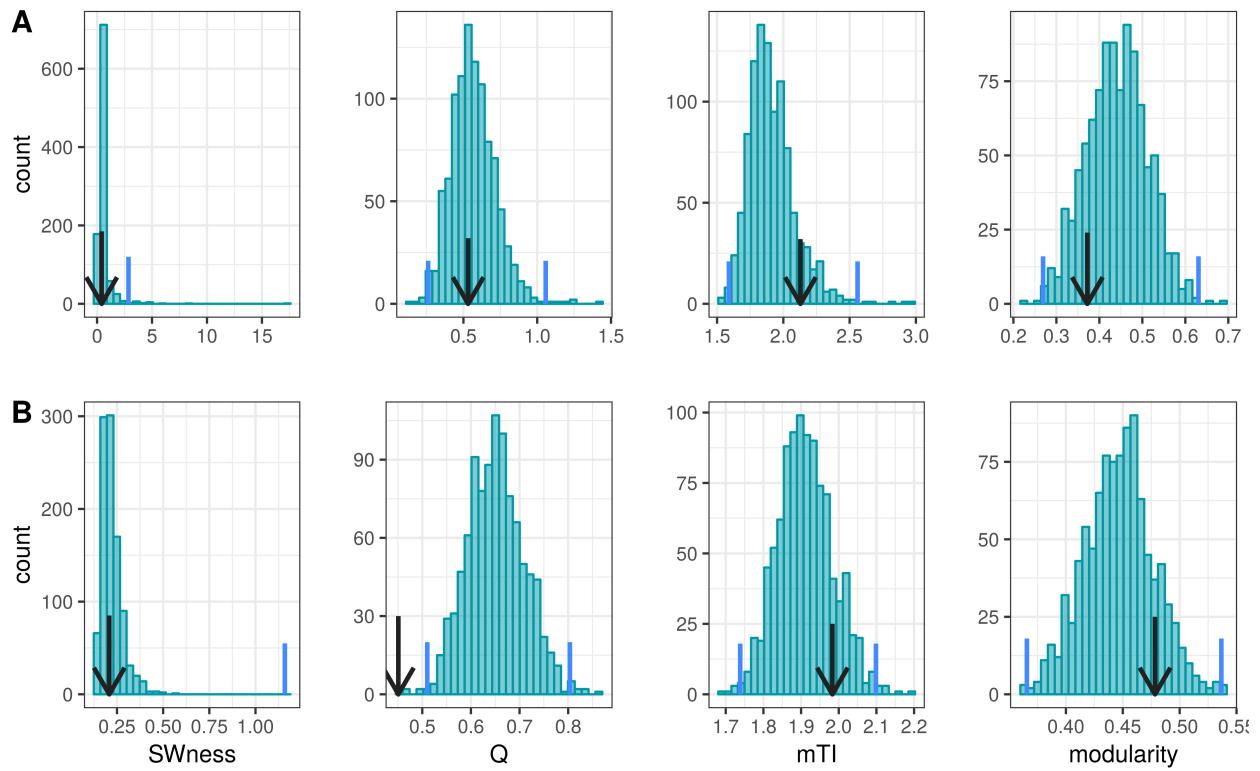


Figure 2: Network global properties compared with the metaweb assembly model for A) Potter Cove and B) Weddell Sea food webs. The properties were: Small-world-ness (SWness), coherence (Q), mean trophic level (mTl) and modularity. We ran 1000 simulations of local networks fitted to Potter Cove and Weddell Sea food webs to build the 99% confidence intervals of a particular property (vertical blue lines) and compare with the empirical calculated value (Black arrows).

313 **Sub-structural properties (motifs)**

314 The representation of three-species sub-networks with respect to the random model showed similar patterns
 315 in all networks (Figure 3A). While exploitative competition, apparent competition, and omnivory were over-
 316 represented, tri-trophic chains were under-represented; all these patterns were significant (Table S3). We
 317 found that motifs proportions for the three examined spatial scales were different (Chi-squared = 12612,
 318 p-value < 1e-04). This means that local networks are not a sample of the metaweb. With respect to the
 319 metaweb assembly model only some of them were significant (Figure 3B, Table S4): tri-trophic chains and
 320 omnivory were under-represented for Weddell Sea, and apparent competition was over-represented for Potter
 321 Cove (Figure 3B). Contrary to our expectations Potter Cove was more similar to the metaweb than Weddell
 322 Sea food web. The under-representation of omnivory in Potter Cove could be related to its low value of
 323 coherence index.

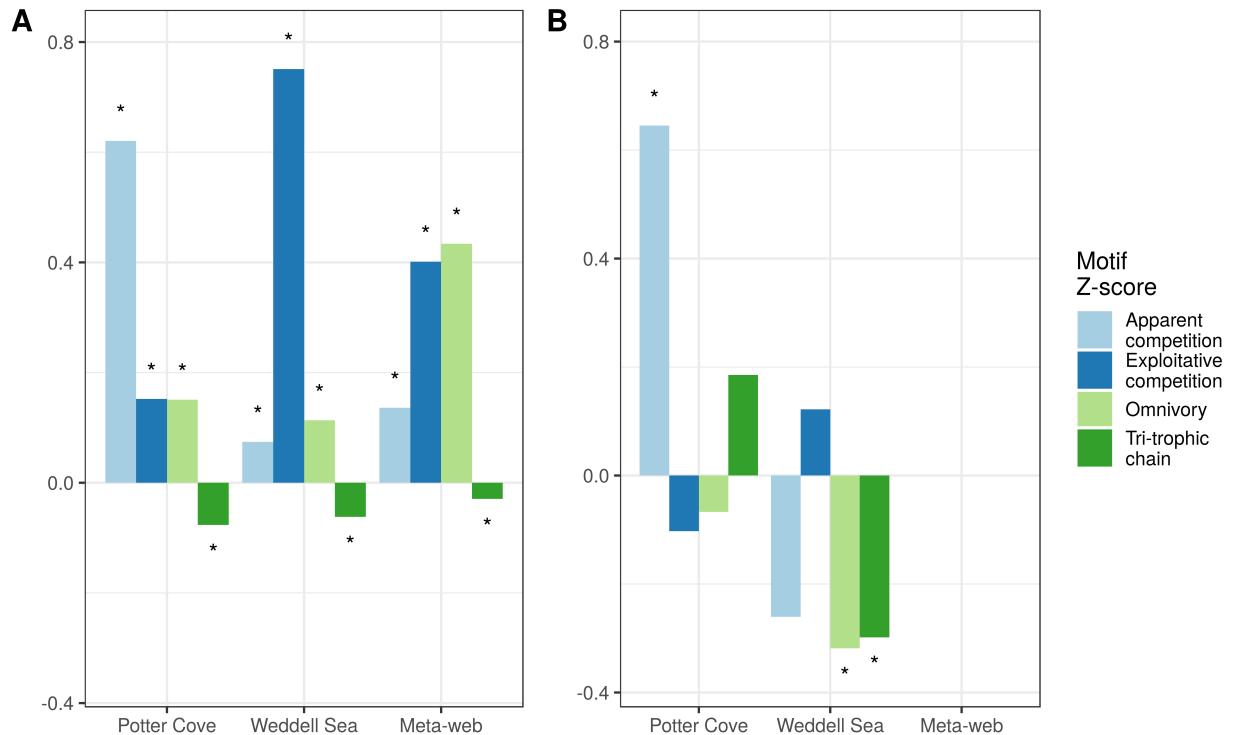


Figure 3: Network motifs z-scores across scales. Motifs are three-node sub-networks counted on each of the networks.: the *Metaweb* represents the marine predator-prey relationships of Antarctica; the *Weddell Sea* and *Potter Cove* are local food webs. A. Z-scores estimated with the random null model. B. Z-scores estimated with the metaweb assembly model. Z-scores were normalized by the square root of the sum of the squared z-scores for that food web, bars marked with '*' are significant at 1% level.

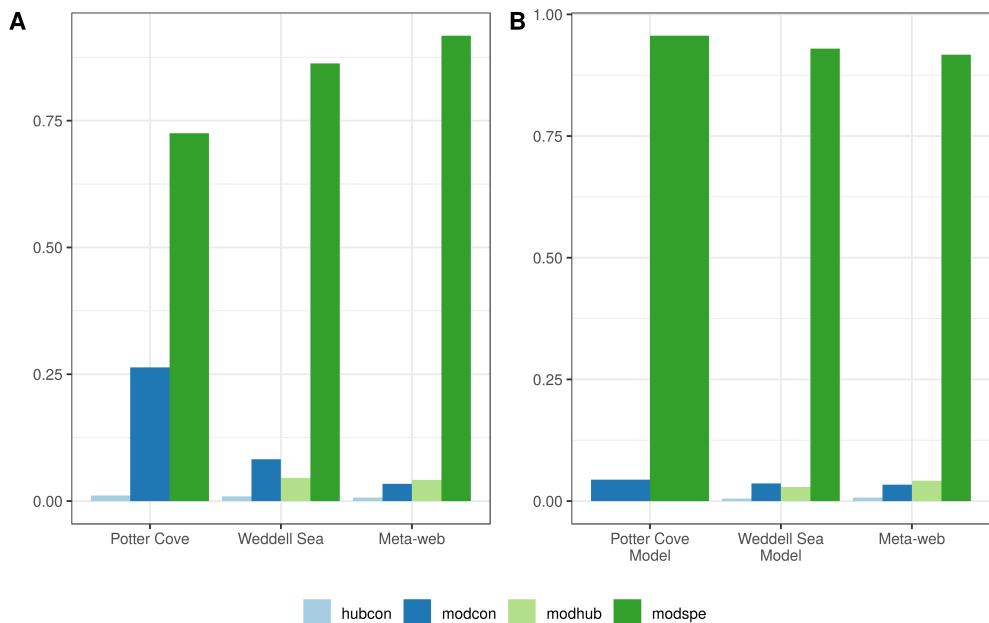


Figure 4: Proportion of topological roles across scales., the *Metaweb* represents the marine predator-prey relationships of Antarctica; the *Weddell Sea* and *Potter Cove* are local food webs. The topological roles are: *Hub connectors*, high number of between-module links; *Module connectors*, low number of links mostly between modules; *Module hubs*, high number of links within its module; *Module specialists*, low number of links within its module. A. Observed proportions for each food web; significant differences were found between them ($\text{Chi-squared} = 79.31$, $p\text{-value} = 1\text{e-}04$). B. Proportions for local networks obtained from the metaweb assembly model; no differences were found ($\text{Chi-squared} = 5.95$, $p\text{-value} = 0.41$)

³²⁴ **Node-level properties (Topological roles)**

³²⁵ The proportion of species displaying the four topological roles was different among networks (Chi-squared =
³²⁶ 79.31, p-value = 1e-04). A higher presence of module connectors (few links, mostly between modules) was
³²⁷ observed in Weddell Sea, while a lack of module hubs (high number of links inside its module) was found
³²⁸ in Potter Cove (Figure 3 A), which can be related to its low modularity value (Table 1). The proportions
³²⁹ obtained with the metaweb assembly model were not different across the simulated networks (Chi-squared
³³⁰ = 5.95, p-value = 0.41)(Figura 3 B).

³³¹ The plot of topological roles combined with trophic levels and modularity revealed important details of
³³² the food webs (Figure 5): the metaweb presents densely connected compartments but some of them have
³³³ few low-connected species (module connectors or module specialists). Additionally, we observed in the
³³⁴ Weddell Sea food web hub connectors with a basal trophic level (Table S5). These are aggregated nodes that
³³⁵ represent generic prey, e.g. fish or zooplankton, they only have incoming links or predators and they cannot
³³⁶ have outgoing links or prey because they comprise several species. Different fish species are present in the
³³⁷ Weddell Sea food web with detailed information about prey and predators, but for some predators there is
³³⁸ insufficient knowledge of its prey and aggregated nodes must be added. Thus the existence of these basal
³³⁹ hub connectors is a spurious result of aggregating prey species. The other non-aggregated hub connectors
³⁴⁰ are highly mobile species with an intermediate trophic level like krill (Table S5). The variation of maximum
³⁴¹ trophic levels is evidenced in Figure 5, where both Potter Cove and Metaweb networks have similar values
³⁴² and Weddell Sea food web exhibit a lower maximum trophic level.

³⁴³ **Discussion**

³⁴⁴ By definition, the metaweb structure should reflect the evolutionary constraints of the species interactions,
³⁴⁵ and the local networks should be influenced and determined by the assembly processes and the local en-
³⁴⁶ vironment. Our results showed that the structure of the metaweb does not differ from local food webs in
³⁴⁷ many properties as the spatial scale changes. We did not find a clear pattern in the properties expected to
³⁴⁸ be maximized by dynamical assembly and local stability (modularity, coherence, motifs), though we found
³⁴⁹ clear differences in the properties influenced by habitat filtering and dispersal limitation (motif, topological
³⁵⁰ roles). These suggest that food webs would be mainly shaped by evolutionary forces and local environment
³⁵¹ drivers and less constrained by dynamical and assembly processes.

³⁵² Global level network properties showed a similar pattern across scales; most of them were significantly
³⁵³ different from the random null model but not from the assembly model. Modularity for Potter Cove food

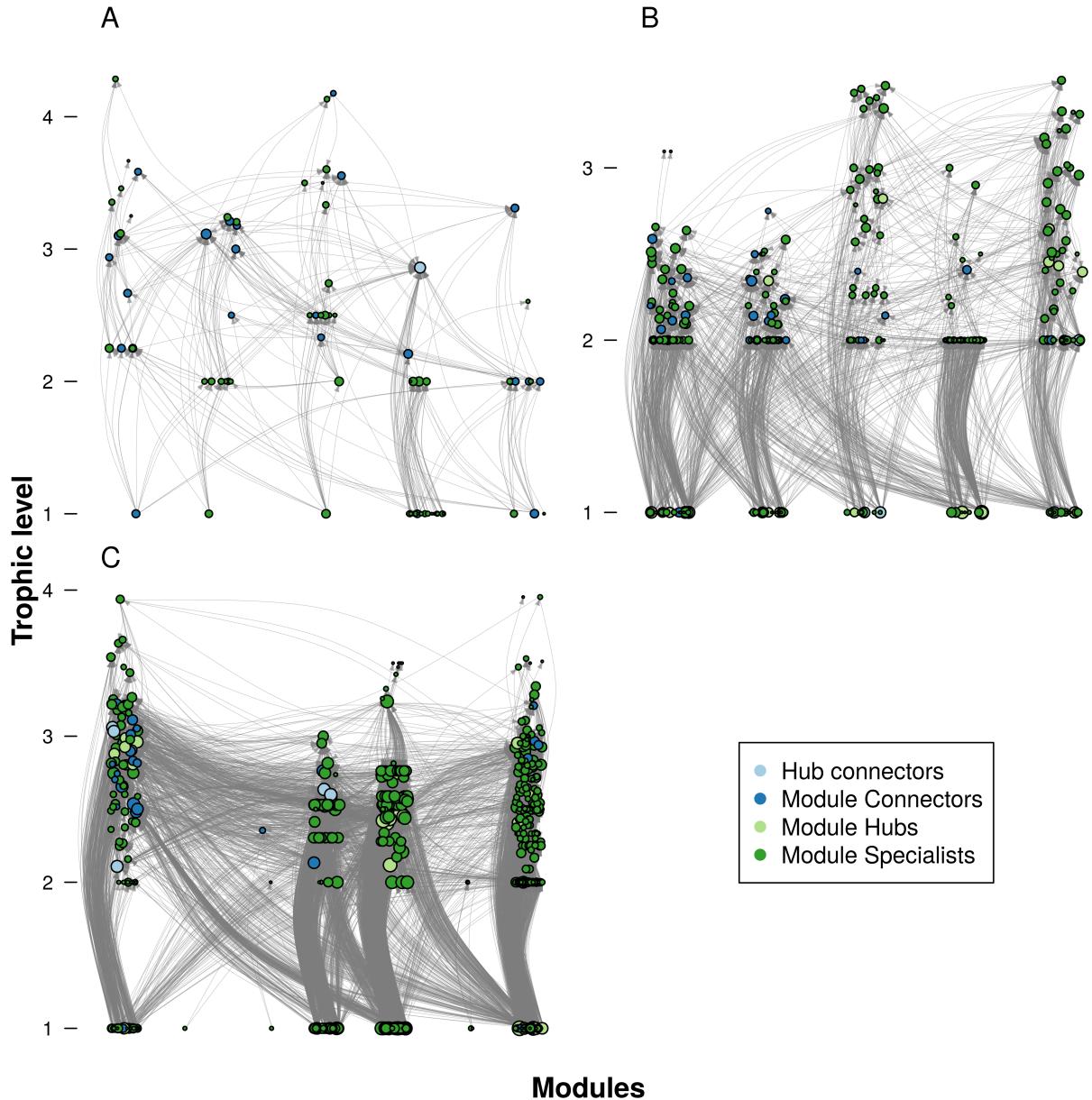


Figure 5: Plot of topological roles combined with trophic levels and modularity for each food web (A) Potter Cove, (B) Weddell Sea (C) the Metaweb. The topological roles are: *Hub connectors* have a high number of between module links, *Module connectors* have a low number of links mostly between modules, *Module hubs* have a high number of links inside its module. *Module specialists* have a low number of links inside its module. Size of the nodes is proportional to the log of the species degree.

354 web was the only property that is similar to the random model. The existence of a modular structure could
355 be related to different habitats (Krause et al., 2003; Rezende et al., 2009) —in marine environments, these
356 could be benthic with different depths and pelagic with different extensions. Even though Potter Cove has
357 a small extent (6.8 Km^2) studies suggest there exist different habitats (Wölfel et al., 2014), then the lack of
358 significant modularity compared to random and to the assembly model could be a sampling effect. Recent
359 studies suggest that modularity enhances local stability and this effect is stronger the more complex the
360 network is (D. B. Stouffer & Bascompte, 2011), even though the effect on stability strongly depends on
361 the interaction strength configuration (Grilli et al., 2016) and on the existence of external perturbations
362 (Gilarranz, Rayfield, Liñán-Cembrano, Bascompte, & Gonzalez, 2017). We found that modularity is not
363 different from the assembly model and we observed that the modular structure is present in the metaweb.
364 This suggests that modularity is not produced by maximization of local stability and could be a spandrel of
365 assembly.

366 Biotic interactions are expected to be more important at the finest scales (Araújo & Rozenfeld, 2014), thus
367 dynamical stability represented in trophic coherence is expected to be maximized at Potter Cove, but we
368 only found that Weddell Sea exhibited a greater trophic coherence than the assembly model. Thus, although
369 this evidence is not conclusive with regard to the importance of dynamical processes in the assembly of food
370 webs, the structure of the local food webs examined here seem to be a consequence of the metaweb structure.

371 All networks have a significant value of small-world-ness compared with the random model and both local
372 food webs are not different from the assembly model. In general, food webs do not show the small-world
373 topology (Dunne, Williams, & Martinez, 2002; Tomás Ignacio Marina et al., 2018), which suggests that
374 the small-world property is inherited from the metaweb and is less influenced by the greater percentage of
375 realized interactions in local food webs. If small-world-ness was determinant for an increased resilience and
376 robustness to secondary extinctions (Bornatowski et al., 2017), local food webs should reflect significantly
377 higher values than those obtained from the metaweb assembly models.

378 Motifs have the same representation patterns across networks against the random model. If food web struc-
379 ture is influenced by dynamical constraints, then we would expect real food webs to have a higher frequency
380 of stability-enhancing motifs than assembled model webs. The expected pattern is an over-representation
381 tri-trophic chains, exploitative and apparent competition (Borrelli, 2015), and the omnivory motif could
382 enhance or diminish stability (Monteiro & Faria, 2016). Instead, our real webs had an under-representation
383 tri-trophic chains while the other motifs matched expectation, and omnivory was over-represented. The
384 motif structure observed in the metaweb is not maintained in local food webs: apparent competition is
385 over-represented in Potter Cove, which would enhance stability, and both omnivory and tri-trophic chains

386 are under-represented in Weddell Sea which seems to have a neutral effect on stability. Thus, the assembly
387 process is not random, there are differences in the frequencies of motifs as the scale change, but the selection
388 of motifs due to its dynamical stability is not the main driver. This implies that other processes that influ-
389 ence the presence or absence of species like habitat filtering or dispersal limitation are acting and probably
390 modifying motif frequencies in empirical food webs.

391 As expected, all the networks have a short mean trophic level (Borrelli & Ginzburg, 2014; Williams, Berlow,
392 Dunne, Barabási, & Martinez, 2002) compared with the random model. Different hypotheses have been posed
393 to explain this pattern: the low efficiency of energy transfer between trophic levels, predator size, predator
394 behaviour, and consumer diversity (Young et al., 2013). These have contradictory support, reviewed by
395 Ward & McCann (2017). Recently, it has been proposed that maximum trophic level could be related to
396 productivity and ecosystem size depending on the context but related to energy fluxes that promote omnivory
397 (Ward & McCann, 2017). A different mechanism based on dynamic stability of the whole web was proposed:
398 food webs with shorter trophic levels (between 2 and 4) that have more omnivore chains are more likely to
399 be stable, which increase the probability of being observed in nature (Borrelli & Ginzburg, 2014). We found
400 that mean trophic level of the local food webs was not different from the assembly model, and omnivory was
401 under-represented. This combination suggests that the trophic level could also be a spandrel of assembly,
402 inherited from the metaweb structure.

403 Topological roles are valuable to detect the existence of functional roles of species, like super-generalists (or
404 hub connectors). These roles may change as the scale changes. A simple explanation is that modules also
405 change. It was demonstrated in Arctic and Caribbean marine food webs that modules are usually associated
406 with habitats (Kortsch et al., 2015; Rezende et al., 2009). For example, the Antarctic cod (*Notothenia*
407 *coriiceps*) is a super-generalist for Potter Cove and a module hub—a species with most of their links within
408 its module—for the metaweb. This means that the same species can have different influences on the food
409 web depending on the type or extension of the habitat considered. Although the networks based on metaweb
410 assembly model showed no change in the frequency of topological roles, we found a change in topological
411 roles with the scale. That means that as in smaller areas there will be different proportions and different
412 kinds of habitats, and probably as a product of habitat filtering, there should be a change in the frequency
413 of species that represent a particular topological role.

414 The spatial scales involved in our study do not represent a continuity; the metaweb and the Weddell sea web
415 have a 10 to 1 ratio but the local web is 10^6 smaller, besides that most of the global network properties and
416 the motif structure showed no changes relative to the null model. We did not find evidence that the structure
417 of the food web was influenced by dynamical constraints. Instead, we hypothesise that other local processes,

418 that limit which species from the metaweb can colonise the local web, are influencing the assembly process.
419 Although our results are limited to Antarctic marine food webs, our findings suggest that future studies
420 about food webs should give more attention to evolutionary and assembly processes, and less emphasis to
421 local dynamics. This kind of analysis needs to be expanded to different regions and other kinds of habitats
422 (e.g. terrestrial, freshwater, etc.) to confirm if this is a general pattern or not.

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