

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

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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 (Daniel B Stouffer & Bascompte, 2011). It is noteworthy to mention that the small-world
100 pattern and modularity act in opposite directions. Whereas a small-world topology favours the spread of
101 perturbations through its rapid dissipation (Gray et al., 2016), the presence of high modularity prevents
102 the dispersal of perturbations (Krause, Frank, Mason, Ulanowicz, & Taylor, 2003; Daniel B Stouffer &
103 Bascompte, 2011).

104 Species may participate in different ways with respect to modularity, depending on how many trophic links

105 are conducted within their own module and/or between modules (Roger Guimerà & Nunes Amaral, 2005;
106 Kortsch, Primicerio, Fossheim, Dolgov, & Aschan, 2015). This participation with respect to modularity is
107 called a species' topological role. Theoretical and empirical results suggest these roles are related to species
108 traits, such as wide niche breadth, environmental tolerance, apex position in local communities and high
109 motility (Borthagaray, Arim, & Marquet, 2014; R Guimerà et al., 2010; Kortsch et al., 2015; Rezende, Albert,
110 Fortuna, & Bascompte, 2009). This is a local property at an individual species level.

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

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

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

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

142 Methods

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

165 We analysed the structure of the networks using properties that focus on different levels: emergent or global
166 properties that take into account the whole network, sub-structural properties that consider several nodes,

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 $E = \sum_{ij} a_{ij}$.

174 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

197 metaweb. The ratio of immigration vs. extinction $\alpha = c/e$ is hypothesized to be inversely related to the
 198 distance to the mainland (MacArthur & Wilson, 1967), and as extinction e should be inversely proportional
 199 to population size (Hanski, 1999), the ratio α is also hypothesized to be related to the local area.

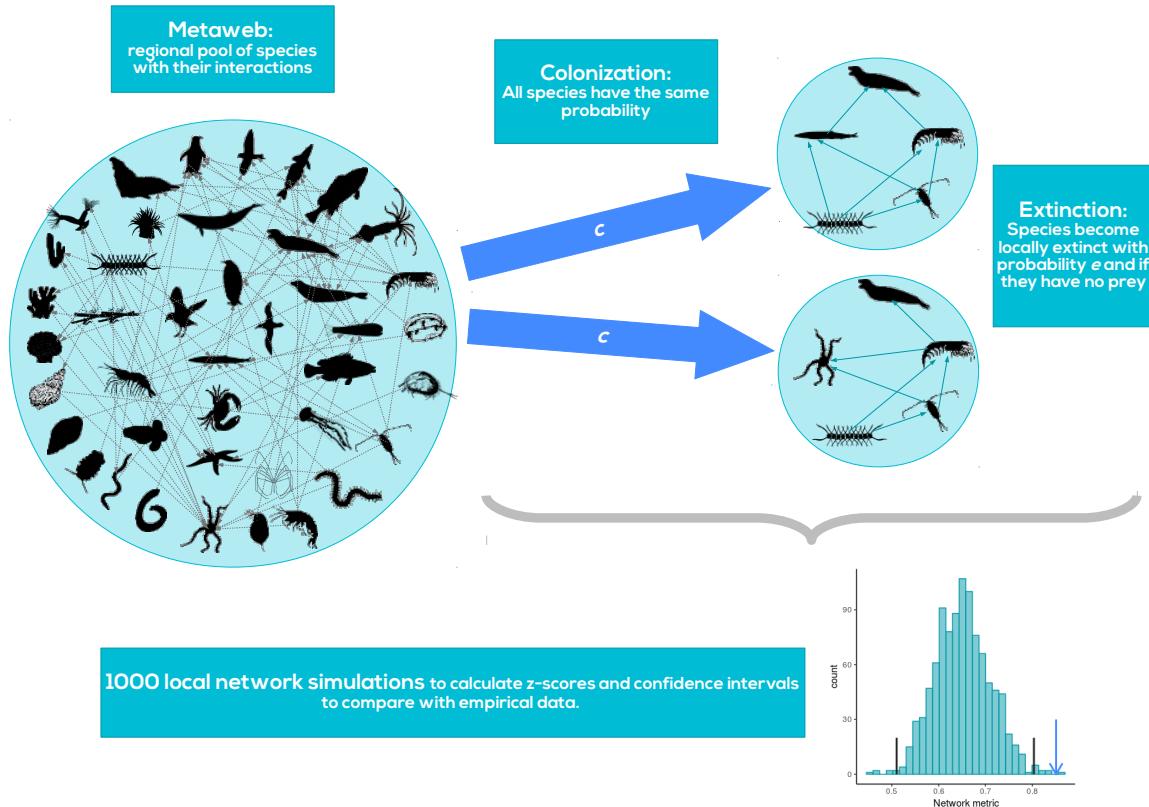


Figure 1: Schematic diagram of the metaweb assembly model: species migrate from the metaweb with a probability c to a local network carrying their potential links to preys; here they have a probability of extinction e . Additionally, predators become extinct if their preys are locally extinct. We simulate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

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

204 **Global network properties**

205 The first global emergent property we analysed was the small-world pattern, which examines the average of
 206 the shortest distance between nodes and the clustering coefficient of the network (Watts & Strogatz, 1998).
 207 This property is associated with an increased resilience and resistance to secondary extinctions (Bornatowski
 208 et al., 2017; Solé & Montoya, 2001). We first calculated the characteristic path length that is the shortest
 209 path between any two nodes. Then L is the mean value of the shortest path length across all pairs of nodes.
 210 The clustering coefficient of node i was defined as

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

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

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

216 and

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

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

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

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

223 called ql, qh :

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

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

227 The second global property was trophic coherence (Johnson et al., 2014), that is related to stability in the
228 sense that small perturbations could get amplified or vanished, which is called local linear stability (May,
229 1972; Rohr et al., 2014). We first needed to estimate the trophic level of a node i , defined as the average
230 trophic level of its preys plus 1. That is:

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

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

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

235 that is the standard deviation of the distribution of all trophic distances. A food web is more coherent
236 when q is closer to zero, thus the maximal coherence is achieved when $q = 0$, and corresponds to a layered
237 network in which every node has an integer trophic level (Johnson & Jones, 2017; Johnson et al., 2014). To
238 compare coherence and trophic level we generated 1000 null model networks with at least one basal species
239 and the same number of species and links—or approximately the same—than the network of interest. Then
240 we calculated the 99% confidence interval using the 0.5% and 99.5% quantiles of the distribution of q ; we
241 also calculated the confidence interval for the mean trophic level tp . We calculated the z-scores as:

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

242 where q_{obs} is the observed coherence, q_{null} is the mean coherence from the null model networks and $\sigma_{q_{null}}$

243 is the standard deviation. The same formula is used for tp . The z-score thus measures the significance of
244 deviations of the real network from the null hypothesis. If the distribution of the quantity (q, tp) under the
245 null model is normal, a z-score greater than 2 is evidence that the observed quantity is significantly greater
246 than its random counterpart, and a z-score less than -2 means that the quantity is significantly lower. If the
247 distribution under the null model is skewed this is not necessarily true and thus we must rely on confidence
248 intervals.

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

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

256 where s is the number of modules or compartments, I_s is the number of links between species in the module
257 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
258 assess the significance of our networks we calculate the 99% confidence intervals and z-scores based on 1000
259 null model networks as previously described.

260 Sub-structural properties (motifs)

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

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

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

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

273 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
274 deviation of k_{is} over all species in s . The participation coefficient PC estimates the distribution of the links
275 of species i among modules; thus it can be defined as:

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

276 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
277 in module s . Due to the stochastic nature of the module detection algorithm we made repeated runs of the
278 algorithm until there were no statistical differences between the distributions of PC_i and dz_i in successive
279 repetitions; to test such statistical difference we used the k-sample Anderson-Darling test (Scholz & Stephens,
280 1987). Then we calculated the mean and 95% confidence interval of dz and PC .

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

292 Carlo replicates. Also, we tested if these proportions changed for one realization of the metaweb assembly
293 model fitted for each local network.

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

299 Results

300 Global network properties

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

Network	Potter Cove	Weddell Sea	Metaweb
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*

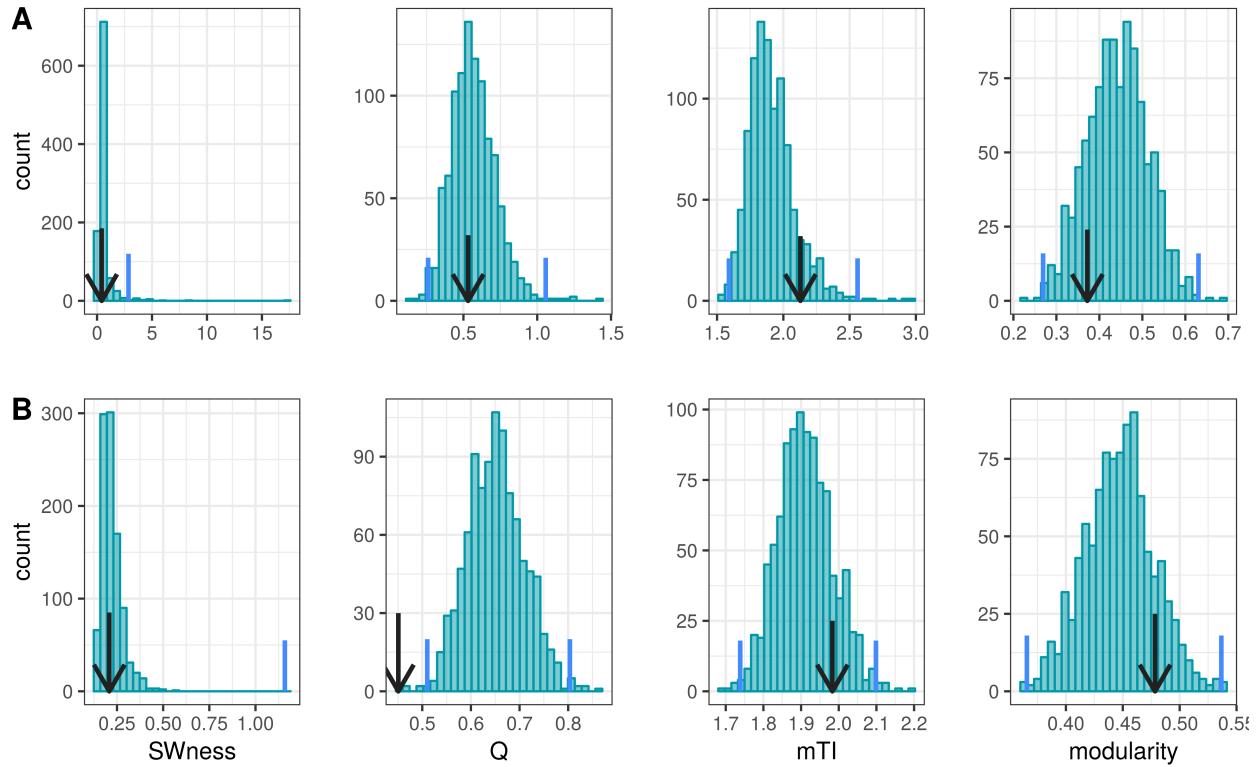


Figure 2: Network global properties compared with the metaweb assembly model for A) Potter Cove and B) Weddell Sea food webs. The properties were: Small-world-ness (SWness), coherence (Q), mean trophic level (mTL) and modularity. We ran 1000 simulations of local networks fitted to Potter Cove and Weddell 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.

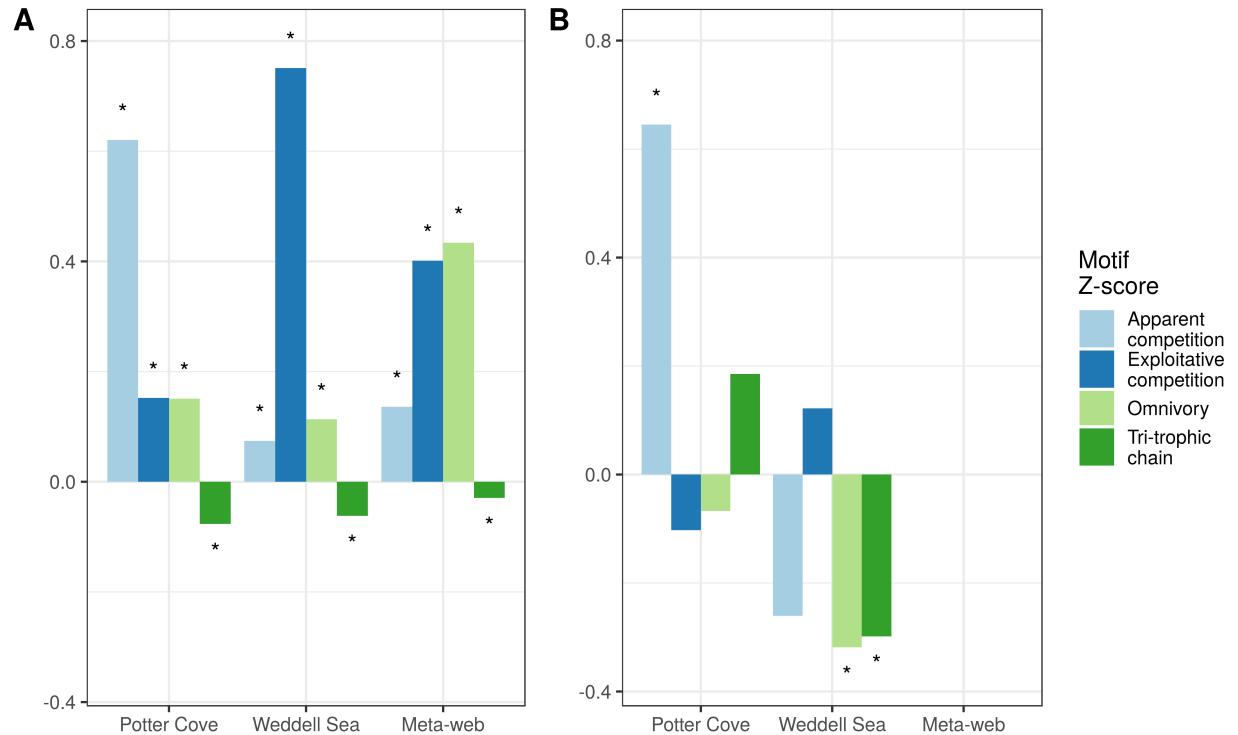


Figure 3: Network motifs z-scores across scales. Motifs are three-node sub-networks counted on each of the networks.: the *Metaweb* represents the marine predator-prey relationships of Antarctica; the *Weddell Sea* and *Potter Cove* are local food webs. A. Z-scores estimated with the random null model. 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.

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

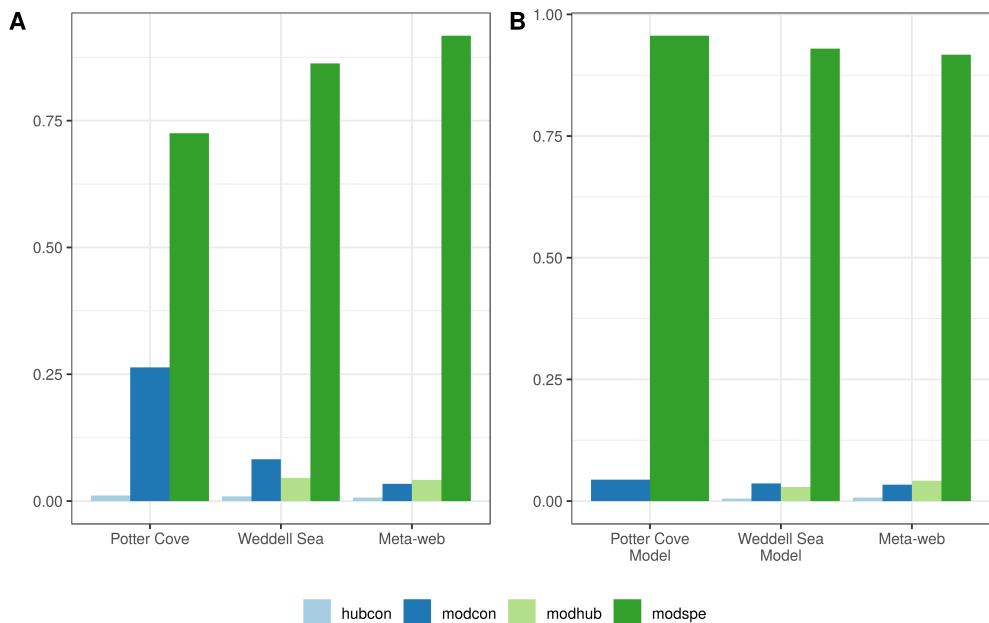


Figure 4: Proportion of topological roles across scales., the *Metaweb* represents the marine predator-prey relationships of Antarctica; the *Weddell Sea* and *Potter Cove* are local food webs. The topological roles are: *Hub connectors*, high number of between-module links; *Module connectors*, low 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 ($\text{Chi-squared} = 5.95$, $p\text{-value} = 0.41$)

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
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 Km²) 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

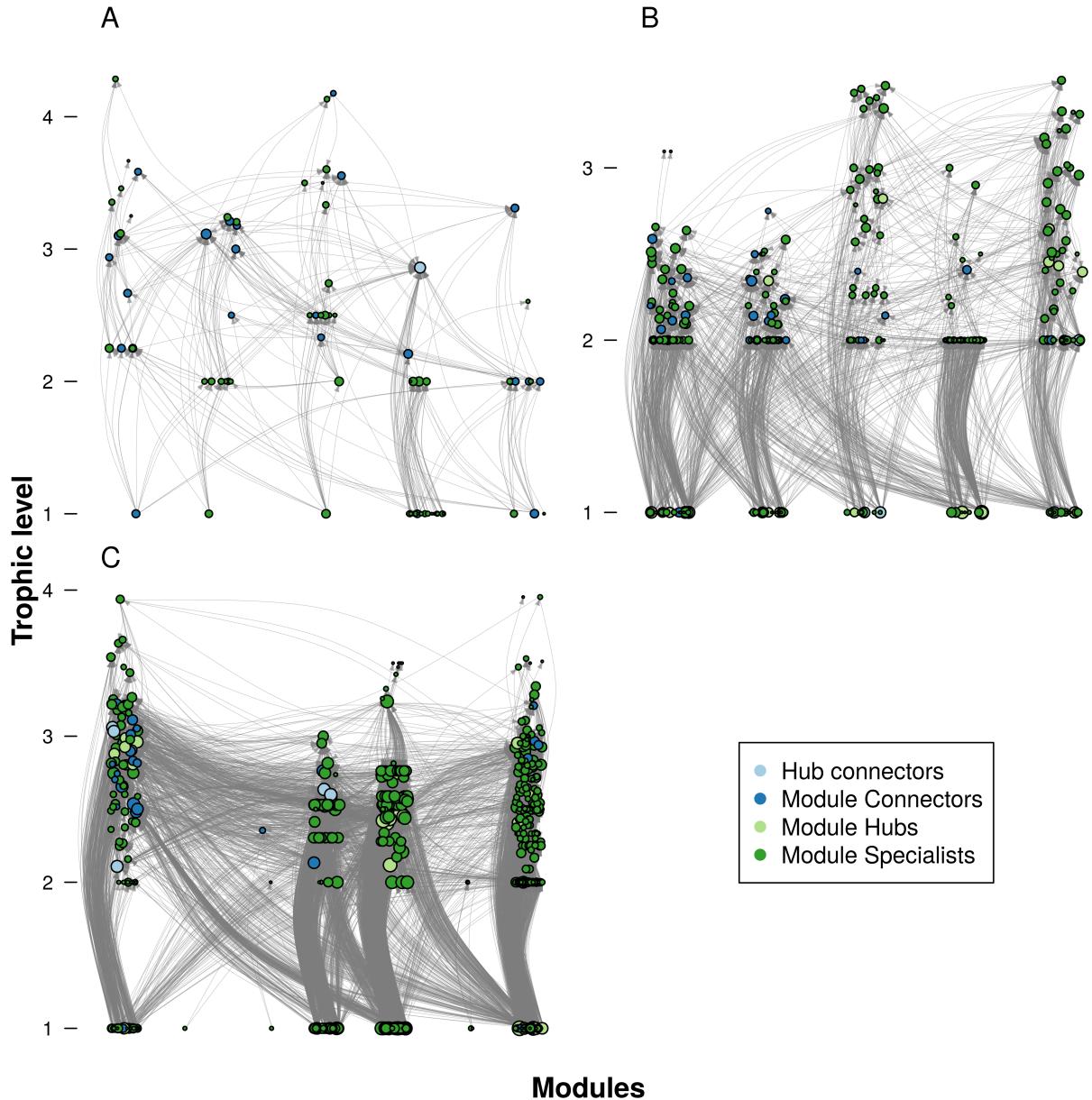


Figure 5: Plot of topological roles combined with trophic levels and modularity for each food web (A) Potter Cove, (B) Weddell Sea (C) the Metaweb. The topological roles are: *Hub connectors* have a high number of between module links, *Module connectors* have a low number of links mostly between modules, *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.

network is (Daniel B Stouffer & Bascompte, 2011), even though the effect on stability strongly depends on the interaction strength configuration (Grilli et al., 2016) and on the existence of external perturbations (Gilarranz, Rayfield, Liñán-Cembrano, Bascompte, & Gonzalez, 2017). We found that modularity is not different from the assembly model and we observed that the modular structure is present in the metaweb. This suggests that modularity is not produced by maximization of local stability and could be a spandrel of assembly.

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

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

Motifs have the same representation patterns across networks against the random model. If food web structure is influenced by dynamical constraints, then we would expect real food webs to have a higher frequency of stability-enhancing motifs than assembled model webs. If we take into account the stability of three species motifs, the expected pattern is an over-representation tri-trophic chains, exploitative and apparent competition (Borrelli, 2015), and the omnivory motif could enhance or diminish stability (Monteiro & Faria, 2016). As food webs are more than the sum of its three species modules (Cohen, Schittler, Raffaelli, & Reuman, 2009), if the persistence of the whole food web is considered, tri-trophic and omnivory should be over-represented, exploitative and apparent competition under-represented (Daniel B. Stouffer & Bascompte, 2010). Instead, our empirical food webs had an under-representation of tri-trophic chains while the other motifs were over-represented. More importantly, the motif structure observed in the metaweb is not maintained in local food webs: apparent competition is over-represented in Potter Cove, which would enhance stability and diminish persistence, and both omnivory and tri-trophic chains are under-represented in Weddell Sea this combination would have opposite effects on both stability and persistence. Thus, the assembly process

392 is not random, there are differences in the frequencies of motifs as the scale change, but the selection of
393 motifs due to its dynamical stability does not seem to be the main driver. This implies that other processes
394 that influence the presence or absence of species like habitat filtering or dispersal limitation would be acting
395 and probably modifying motif frequencies in empirical food webs.

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

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

419 The spatial scales involved in our study do not represent a continuity; the metaweb and the Weddell sea web
420 have a 10 to 1 ratio but the local web is 10^6 smaller, besides that most of the global network properties and
421 the motif structure showed no changes relative to the null model. We did not find evidence that the structure
422 of the food web was influenced by dynamical constraints. Instead, we hypothesise that other local processes,
423 that limit which species from the metaweb can colonise the local web, are influencing the assembly process.

424 Although our results are limited to Antarctic marine food webs, our findings suggest that future studies
425 about food webs should give more attention to evolutionary and assembly processes, and less emphasis to
426 local dynamics. This kind of analysis needs to be expanded to different regions and other kinds of habitats
427 (e.g. terrestrial, freshwater, etc.) to confirm if this is a general pattern or not.

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