

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

³ Leonardo A. Saravia^{1 2 5}, Tomás I. Marina^{1 2 3}, Marleen De Troch⁴, Fernando R. Momo^{1 2}

⁴ 1. Instituto de Ciencias, Universidad Nacional de General Sarmiento, J.M. Gutierrez 1159 (1613), Los
⁵ Polvorines, Buenos Aires, Argentina.

⁶ 2. INEDES, Universidad Nacional de Luján, CC 221, 6700 Luján, Argentina.

⁷ 3. Centro Austral de Investigaciones Científicas (CADIC-CONICET)

⁸ 4. Marine Biology, Ghent University, Krijgslaan 281/S8, B-9000, Ghent, Belgium.

⁹ 5. Corresponding author e-mail lsaravia@campus.ungs.edu.ar, ORCID <https://orcid.org/0000-0002-7911->

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¹² , trophic coherence, motif, topological roles, null models

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

¹⁴ **Abstract**

- 15 1. Ecological communities are assembled in a sequence of colonization events, this has been mostly studied
16 with relation to competitive interactions. Similar processes act in trophic networks: a regional pool
17 of species act as the source from which species colonize local areas, called the metaweb. Local food
18 webs are realizations of metawebs that result from assembly processes influenced by migration, habitat
19 filtering, stochastic factors, and dynamical constraints.
- 20 2. We analyse how the structure of a metaweb influences local food webs using a trophic assembly model
21 with no population dynamics and a random model. We evaluate global properties and network sub-
22 structures—motifs—related to ecological stability, and topological roles that are node-level properties.
23 Our hypothesis is that the local food webs have dynamical stability constraints that modify their
24 structure, thus local food webs will be different from the assembly model.
- 25 3. Three data-sets were used: the marine Antarctic metaweb, built using a dietary database, the Weddell
26 Sea and Potter Cove local food webs. Most network global properties are different from random
27 networks but there are almost no differences with the assembly model. Local food webs showed
28 different motif representations compared to the assembly model but these did not represent an increase
29 in stability. Species' topological roles showed differences between the metaweb and local food webs
30 that were not explained by the assembly model, suggesting that in empirical food webs species are
31 selected by habitat or dispersal limitations.
- 32 4. Our results suggest that there is not a strong dynamical restriction that operates at local scales. Thus
33 a great portion of the structure of the food webs might be inherited from the metaweb implying that
34 evolutionary processes acting on large temporal and spatial scales have an important influence.
- 35 5. Recently, it has been found in competitive and mutualistic networks that structures that are often
36 attributed as causes or consequences of ecological stability are probably a by-product of the assembly
37 processes (i.e. spandrels). We extended these results to trophic networks suggesting that this could
38 be a more general phenomenon.

³⁹ **Introduction**

- 40 The characterization of ecological systems as networks of interacting elements has a long history (Paine 1966,
41 May 1972, Cohen and Newman 1985). Much of this work has been devoted to investigate network structure
42 and its effects on dynamics and stability (Thebault and Fontaine 2010). In recent years a renewed emphasis

43 on structural stability (Rohr et al. 2014, Grilli et al. 2017) and new developments in random matrix theory
44 (Allesina et al. 2015) has greatly expanded our capability to analyse ecological networks. However, the ef-
45 fects of ecological dynamical processes on food web structure are not fully understood. One such dynamical
46 process is community assembly: how species from a regional pool colonize a site and build local interactions
47 (Carstensen et al. 2013). Regional species pools are shaped by evolutionary and biogeographical processes
48 that imply large spatial and temporal scales (Carstensen et al. 2013, Kortsch et al. 2018). More specifi-
49 cally, the assembly of local communities is influenced by dispersal, environmental filters, biotic interactions
50 and stochastic events (HilleRisLambers et al. 2012). These processes have been studied by means of meta-
51 community theory (Leibold et al. 2017), where different spatial assemblages are connected through species
52 dispersal.

53 Metacommunity theory provides a framework for assessing the roles of local- and regional-scale procesess
54 on network structure (Leibold et al. 2004, Baiser et al. 2013). This approach has been applied historically
55 to competitive interactions, whereas trophic interactions have received less attention (Baiser et al. 2016).
56 Recently, there has been an increase in food web assembly studies, integrating them with island biogeography
57 (Gravel et al. 2011, Galiana et al. 2018) and with metacommunity (Pillai et al. 2011, Liao et al. 2016) and
58 the effect of habitat fragmentation (Mougi and Kondoh 2016). Previous attempts to study the food web
59 assembly process have used motifs as building blocks of local communities (Baiser et al. 2016). Motifs are
60 network sub-structures composed of species and links whose frequency deviates from the random expectation
61 (Milo et al. 2002). By comparing motif representation at different spatial scales—from local to regional—the
62 process of assembly of interactions may be revealed (Baiser et al. 2016), e.g. if the same processes structure
63 the food web across scales, motif representation should be the same.

64 The objective of the present study is to analyse the process of food web assembly by comparing network
65 properties with models across different spatial scales. For this we considered the following networks: Antarc-
66 tic metaweb, representing an area of 34.8 million Km² and built from a dietary database (Raymond et al.
67 2011); the Weddell Sea food web that represents 3.5 million Km² (Jacob et al. 2011); and Potter Cove
68 network that represents 6.8 Km² (Marina et al. 2018a).

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 (Montoya

75 and Solé 2002). The small-world pattern is related to two global properties: the average of the shortest
76 distance between all species, called characteristic path length, and the clustering coefficient, the probability
77 that two species linked to the same species are linked. Then, the small-world pattern implies a short average
78 path length and a high level of clustering compared to random networks (Watts and Strogatz 1998). This
79 pattern comes from the general network theory, beyond ecological networks, and has been recently applied
80 to marine food webs (Gray et al. 2016, Navia et al. 2016, Bornatowski et al. 2017, Marina et al. 2018b).

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

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

101 Species may participate in different ways with respect to modularity, depending on how many trophic links are
102 conducted within their own module and/or between modules (Guimerà and Nunes Amaral 2005, Kortsch et
103 al. 2015). This participation with respect to modularity is called a species' topological role. Theoretical and
104 empirical results suggest these roles are related to species traits, such as wide niche breadth, environmental
105 tolerance, apex position in local communities and high motility (Rezende et al. 2009, Guimerà et al. 2010,
106 Borthagaray et al. 2014, Kortsch et al. 2015). This is a local property at an individual species level.

107 If we consider a subset of linked species inside the food web this forms a sub-network. When the abundance
108 of one of these sub-networks deviates significantly from a null model network, this is called a motif (Milo et al.
109 2002). Besides this definition, in the ecological literature motif has been used as a synonym of sub-network.
110 We analyse here the three-species sub-networks that have been most studied theoretically and empirically
111 in food webs (Prill et al. 2005, Stouffer et al. 2007, Baiser et al. 2016). Specifically, we focused on four of
112 the thirteen possible three-species sub-networks: apparent competition, exploitative competition, tri-trophic
113 chain, and omnivory (Figure 1).

114 The frequency of motifs (i.e over-represented, under-represented or random) at different spatial scales may
115 reveal aspects about the process behind the assembly of interactions: if the same motif representation
116 is observed across scales, this suggests that the same process may be structuring the network (Baiser et
117 al. 2016). Ecological interactions occur at the local scale so differences may show the importance of local
118 interactions in the assembly of the food web. During the assembly process those motif structures that are less
119 dynamically stable tend to disappear from the food web (Borrelli 2015), this has been called non-adaptative
120 systemic selection (Borrelli et al. 2015). The process is non-adaptative because the selection process is not
121 adapting the system to local conditions (Borrelli et al. 2015).

122 In this study, we analyze food web assembly from a metaweb to local networks with different spatial scales.
123 First we compared the networks—including the metaweb—against a random network model (i.e. absence of
124 ecological mechanisms), and then a metaweb assembly model (i.e. representing an assembly process). We
125 hypothesize that network properties will change from the metaweb to a local scale at which interactions
126 are realized. We particularly expect global properties related to resilience and stability (i.e. small-worldness,
127 trophic coherence and modularity) to be close to the random null model at the metaweb scale and significantly
128 different at the local scale; a greater frequency of stable motifs in the local food webs; as well as a change in
129 the frequency of topological roles since habitat filtering or dispersal limitation may modify them at the local
130 food web scale. These last two changes should be also reflected as differences from the metaweb assembly
131 model.

132 Methods

133 The three datasets used in this study encompass a wide range of spatial scales and were collected inde-
134 pendently. The Southern Ocean database compiled by Raymond et al. (2011) was used to construct the
135 Antarctic metaweb selecting only species located at latitudes higher than 60°S. Raymond et al. (2011)
136 compiled information from direct sampling methods of dietary assessment, including gut, scat, and bolus

content analysis, stomach flushing, and observed feeding. We considered that the metaweb is the regional pool of species defined by the biogeographic Antarctic region. Next we analysed two local food webs: the Weddell Sea food web dataset includes species situated between 74°S and 78°S with a West-East extension of approximately 450 km, and comprises all information about trophic interactions available for the zone since 1983 (Jacob et al. 2011). The Potter Cove dataset comes from a 4 km long and 2.5 km wide Antarctic fjord located at 62°14'S, 58°40'W, South Shetland Islands (Marina et al. 2018a). These food web datasets comprise benthic and pelagic habitats of the Antarctic ecosystem, few aggregated low-trophic level groups (e.g. detritus, diatoms, phytoplankton, zooplankton) and a high resolution of the macroalgae community (i.e. 24 biological species of red, brown and green macroalgae). The macroalgae community is responsible for the majority of the primary production and supports a large fraction of secondary production in Antarctic fjords (Quartino and Boraso de Zaixso 2008, Valdivia et al. (2015)). Higher trophic levels comprise: invertebrate (e.g. ascidians, sponges, isopods, amphipods, bivalves, gastropods, cephalopods, echinoderms) and vertebrate predator groups (e.g. demersal and pelagic fishes, penguins, seals and whales). For more information about these datasets refer to the original publications. To make datasets compatible, we first checked taxonomic names for synonyms, and second, we added species (either prey or predator) with their interactions to the metaweb when the local food webs contain a greater taxonomic resolution. This resulted in the addition of 258 species to the metaweb, which represent 33% of the total. We removed cannibalistic (self-links) and double arrows (i.d. A eats B and B eats A).

We analysed the structure of the networks using properties that focus on different levels: emergent or global 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 $E = \sum_{ij} a_{ij}$.

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

168 networks with such models using a null model approach: if we observe a deviation from the property obtained
169 with the null model then mechanisms that are excluded from the model may be acting (Bello 2012).

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

178 To consider network assembly mechanisms we used a metaweb assembly model (Figure 1), called the trophic
179 theory of island biogeography (Gravel et al. 2011). In this model species migrate from the metaweb to a local
180 web with a uniform probability c , and become extinct from the local web with probability e ; a reminiscence of
181 the theory of island biogeography (MacArthur and Wilson 1967), but with the addition of network structure.
182 Species migrate with their potential network links from the metaweb, then in the local web species can only
183 survive if at least one of its preys is present, or if it is a basal species. When a species goes extinct locally it
184 may produce secondary extinctions; we check that the local predators maintain at least one prey if not they
185 become extinct independent of the probability e . We simulated this model in time and it eventually reaches
186 an equilibrium that depends on the migration and extinction probabilities but also on the structure of the
187 metaweb. The ratio of immigration vs. extinction $\alpha = c/e$ is hypothesized to be inversely related to the
188 distance to the mainland (MacArthur and Wilson 1967), and as extinction e should be inversely proportional
189 to population size (Hanski 1999), the ratio α is also hypothesized to be related to the local area.

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

194 Global network properties

195 The first global emergent property we analysed was the small-world pattern, which examines the average
196 of the shortest distance between nodes and the clustering coefficient of the network (Watts and Strogatz
197 1998). This property is associated with an increased resilience and resistance to secondary extinctions (Solé

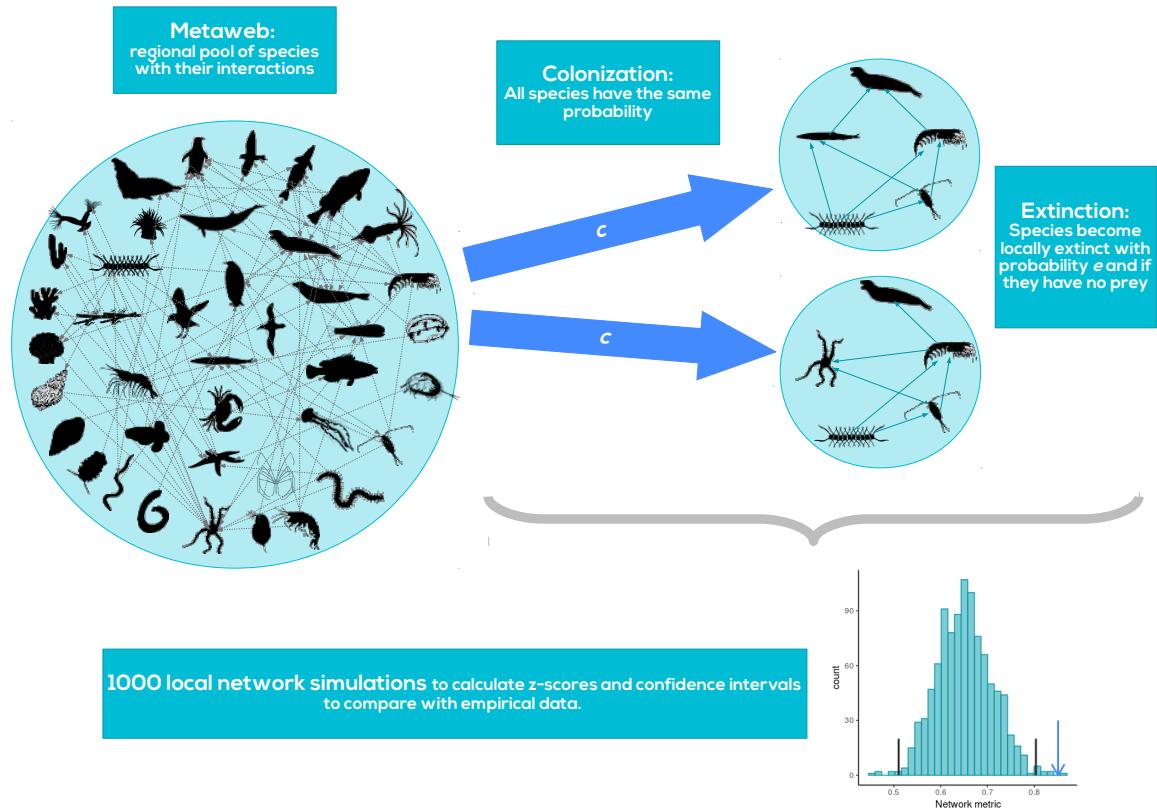


Figure 1: Schematic diagram of the metaweb assembly model: species migrate from the metaweb with a probability c to a local network carrying their potential links to preys; here they have a probability of extinction e . Additionally, predators become extinct if their preys are locally extinct. We simulate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

198 and Montoya 2001, Bornatowski et al. 2017). We first calculated the characteristic path length that is the
 199 shortest path between any two nodes. Then L is the mean value of the shortest path length across all pairs
 200 of nodes. The clustering coefficient of node i was defined as

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

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

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

206 and

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

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

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

210 and to determine if S is statistically significant Monte Carlo methods were used (Crowley 1992). We built
 211 1000 null model networks with the same number of nodes n and edges m than the empirical network; then
 212 we calculated S for each random network and the lower and higher 99% quantiles of the S distribution are
 213 called ql, qh :

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

214 the upper 99% confidence limit is then $CL^{0.01} = 1 + CI$. Thus, if a network has $S > CL^{0.01}$ it is considered

215 a small-world network (Humphries and Gurney 2008). We also calculated the small-world-ness and the CI
 216 using the metaweb assembly model as a null model.

217 The second global property was trophic coherence (Johnson et al. 2014), that is related to stability in the
 218 sense that small perturbations could get amplified or vanished, which is called local linear stability (May
 219 1972, Rohr et al. 2014). We first needed to estimate the trophic level of a node i , defined as the average
 220 trophic level of its preys plus 1. That is:

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

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

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

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

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

232 where q_{obs} is the observed coherence, q_{null} is the mean coherence from the null model networks and $\sigma_{q_{null}}$
 233 is the standard deviation. The same formula is used for tp . The z-score thus measures the significance of
 234 deviations of the real network from the null hypothesis. If the distribution of the quantity (q , tp) under the
 235 null model is normal, a z-score greater than 2 is evidence that the observed quantity is significantly greater
 236 than its random counterpart, and a z-score less than -2 means that the quantity is significantly lower. If the
 237 distribution under the null model is skewed this is not necessarily true and thus we must rely on confidence

238 intervals.

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

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

246 where s is the number of modules or compartments, I_s is the number of links between species in the module
247 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
248 assess the significance of our networks we calculate the 99% confidence intervals and z-scores based on 1000
249 null model networks as previously described.

250 Sub-structural properties (motifs)

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

257 Node-level properties (Topological roles)

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

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

263 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
 264 deviation of k_{is} over all species in s . The participation coefficient PC estimates the distribution of the links
 265 of species i among modules; thus it can be defined as:

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

266 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
 267 species in module s . Due to the stochastic nature of the module detection algorithm we made repeated
 268 runs of the algorithm until there were no statistical differences between the distributions of PC_i and dz_i in
 269 successive repetitions; to test such statistical difference we used the k-sample Anderson-Darling test (Scholz
 270 and Stephens 1987). Then we calculated the mean and 95% confidence interval of dz and PC .

271 To determine each species' role the $dz - PC$ parameter space was divided into four areas, modified from
 272 Guimerà and Nunes Amaral (2005), using the same scheme as Kortsch et al. (2015). Two thresholds were
 273 used to define the species' roles: $PC = 0.625$ and $dz = 2.5$. If a species had at least 60% of links within
 274 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
 275 parameter space defines species with relatively high number of links, the majority within its own module.
 276 If a species had $PC < 0.625$ and $dz < 2.5$, then it was called a peripheral or specialist; this refers to a
 277 species with relatively few links, mostly within its module. Species that had $PC \geq 0.625$ and $dz < 2.5$ were
 278 considered module connectors, since they have relatively few links, mostly between modules. Finally, if a
 279 species had $PC \geq 0.625$ and $dz \geq 2.5$, then it was classified as a super-generalist or hub-connector, because
 280 it has high between- and within-module connectivity. To test if the proportion of species' roles changed
 281 between networks we performed a Pearson's Chi-squared test with simulated p-value based on 10000 Monte
 282 Carlo replicates. Also, we tested if these proportions changed for one realization of the metaweb assembly
 283 model fitted for each local network.

284 All analyses and simulations were made in R version 3.4.3 (R Core Team 2017), using the igraph package
 285 version 1.1.2 (Csardi and Nepusz 2006) for motifs and topological role estimations, and NetIndices (Kones
 286 et al. 2009) for trophic level calculations. Source code and data is available at figshare <https://figshare.com/>
 287 ADD_URL_HERE and github https://github.com//ADD_URL_HERE.

288 **Results**

289 **Global network properties**

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

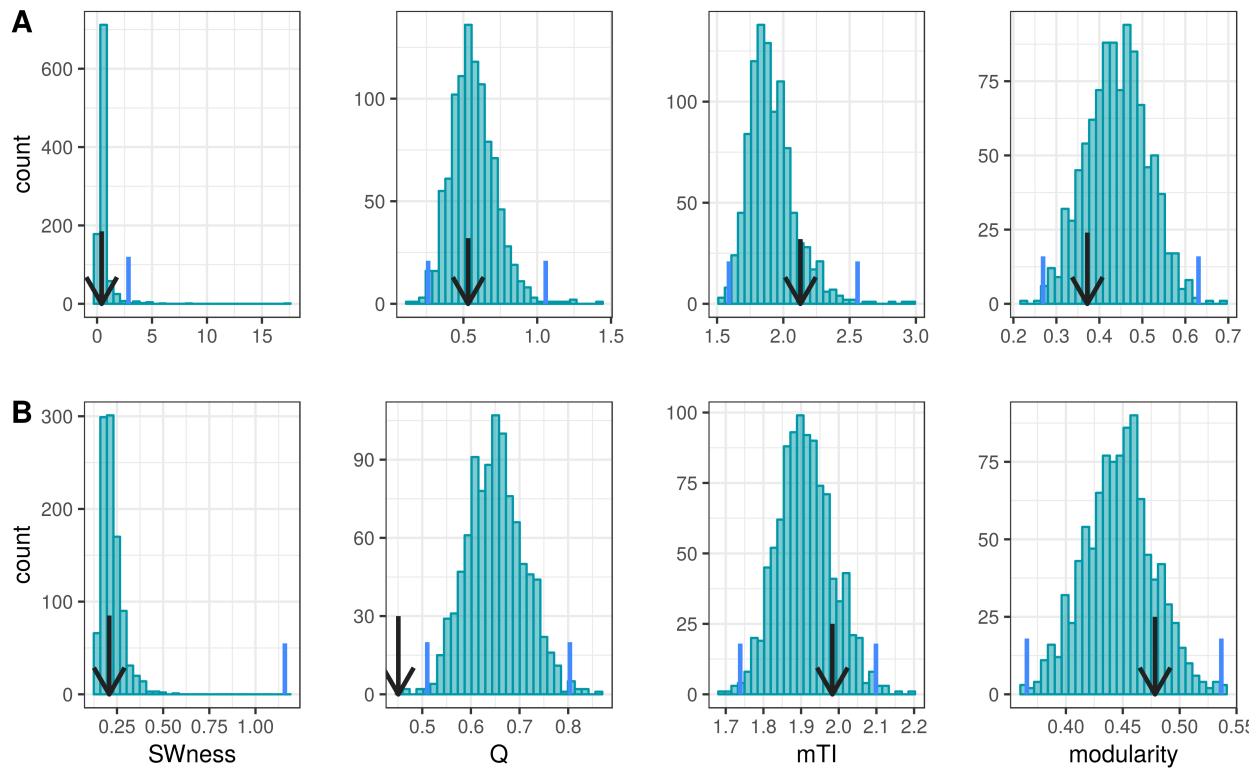


Figure 2: Network global properties compared with the metaweb assembly model for A) Potter Cove and B) Weddell Sea food webs. The properties were: Small-world-ness (SWness), coherence (Q), mean trophic level (mTl) and modularity. We ran 1000 simulations of local networks fitted to Potter Cove and Weddell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

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

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

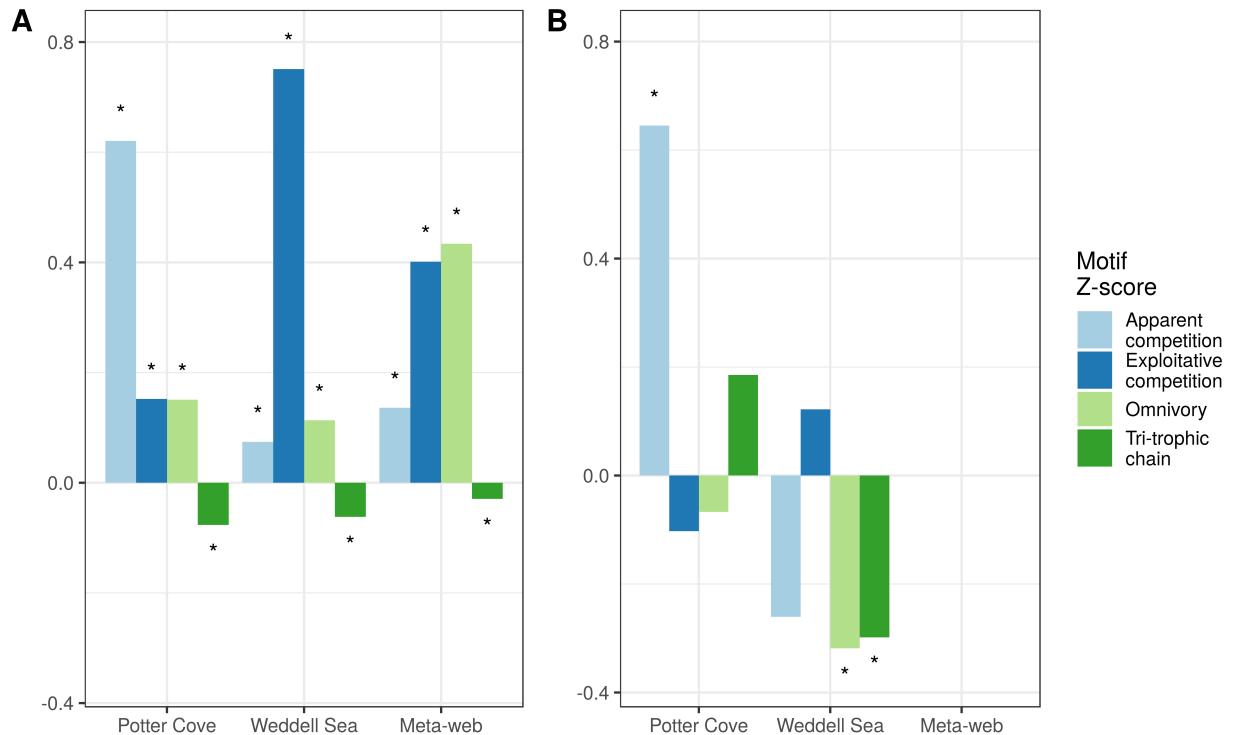


Figure 3: Network motifs z-scores across scales. Motifs are three-node sub-networks counted on each of the networks.: the *Metaweb* represents the marine predator-prey relationships of Antarctica; the *Weddell Sea* and *Potter Cove* are local food webs. A. Z-scores estimated with the random null model.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

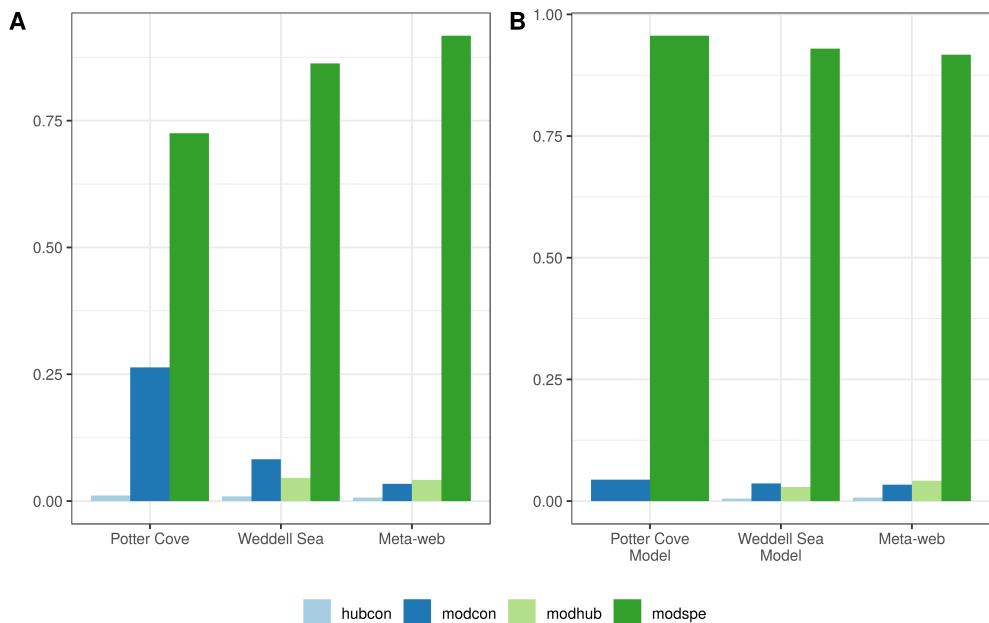


Figure 4: Proportion of topological roles across scales., the *Metaweb* represents the marine predator-prey relationships of Antarctica; the *Weddell Sea* and *Potter Cove* are local food webs. The topological roles are: *Hub connectors*, high number of between-module links; *Module connectors*, low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

³¹⁴ **Node-level properties (Topological roles)**

³¹⁵ The proportion of species displaying the four topological roles was different among networks (Chi-squared =
³¹⁶ 79.31, p-value = 1e-04). A higher presence of module connectors (few links, mostly between modules) was
³¹⁷ observed in Weddell Sea, while a lack of module hubs (high number of links inside its module) was found
³¹⁸ in Potter Cove (Figure 3 A), which can be related to its low modularity value (Table 1). The proportions
³¹⁹ obtained with the metaweb assembly model were not different across the simulated networks (Chi-squared
³²⁰ = 5.95, p-value = 0.41)(Figura 3 B).

³²¹ The plot of topological roles combined with trophic levels and modularity revealed important details of
³²² the food webs (Figure 5): the metaweb presents densely connected compartments but some of them have
³²³ few low-connected species (module connectors or module specialists). Additionally, we observed in the
³²⁴ Weddell Sea food web hub connectors with a basal trophic level (Table S5). These are aggregated nodes that
³²⁵ represent generic prey, e.g. fish or zooplankton, they only have incoming links or predators and they cannot
³²⁶ have outgoing links or prey because they comprise several species. Different fish species are present in the
³²⁷ Weddell Sea food web with detailed information about prey and predators, but for some predators there is
³²⁸ insufficient knowledge of its prey and aggregated nodes must be added. Thus the existence of these basal
³²⁹ hub connectors is a spurious result of aggregating prey species. The other non-aggregated hub connectors
³³⁰ are highly mobile species with an intermediate trophic level like krill (Table S5). The variation of maximum
³³¹ trophic levels is evidenced in Figure 5, where both Potter Cove and Metaweb networks have similar values
³³² and Weddell Sea food web exhibit a lower maximum trophic level.

³³³ **Discussion**

³³⁴ By definition, the metaweb structure should reflect the evolutionary constraints of the species interactions,
³³⁵ and the local networks should be influenced and determined by the assembly processes and the local en-
³³⁶ vironment. Our results showed that the structure of the metaweb does not differ from local food webs in
³³⁷ many properties as the spatial scale changes. We did not find a clear pattern in the properties expected to
³³⁸ be maximized by dynamical assembly and local stability (modularity, coherence, motifs), though we found
³³⁹ clear differences in the properties influenced by habitat filtering and dispersal limitation (motif, topological
³⁴⁰ roles). These suggest that food webs would be mainly shaped by evolutionary forces and local environment
³⁴¹ drivers and less constrained by dynamical and assembly processes.

³⁴² Global level network properties showed a similar pattern across scales; most of them were significantly
³⁴³ different from the random null model but not from the assembly model. Modularity for Potter Cove food

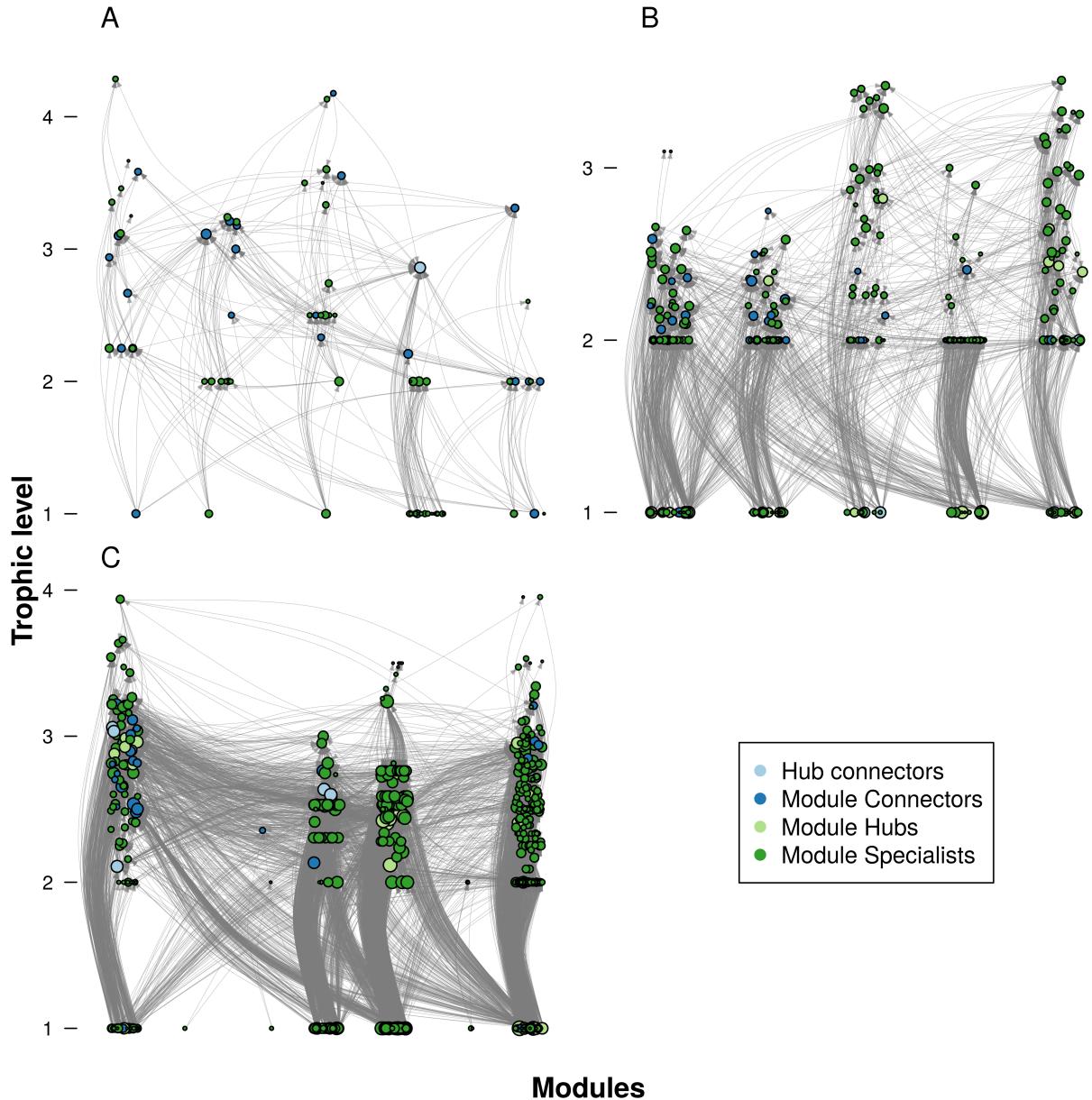


Figure 5: Plot of topological roles combined with trophic levels and modularity for each food web (A) Potter Cove, (B) Weddell Sea (C) the Metaweb. The topological roles are: *Hub connectors* have a high number of between module links, *Module connectors* have a low number of links mostly between modules,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

344 web was the only property that is similar to the random model. The existence of a modular structure could be
345 related to different habitats (Krause et al. 2003, Rezende et al. 2009) —in marine environments, these could
346 be benthic with different depths and pelagic with different extensions. Even though Potter Cove have a small
347 extent (6.8 Km²) studies suggest there exist different habitats (Wölfel et al. 2014), then the lack of significant
348 modularity compared to random and to the assembly model could be a sampling effect. Recent studies
349 suggest that modularity enhances local stability and this effect is stronger the more complex the network
350 is (Stouffer and Bascompte 2011), even though the effect on stability strongly depends on the interaction
351 strength configuration (Grilli et al. 2016) and on the existence of external perturbations (Gilarranz et al.
352 2017). We found that modularity is not different from the assembly model and we observed that the modular
353 structure is present in the metaweb. This suggests that modularity is not produced by maximization of local
354 stability and could be a spandrel of assembly.

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

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

367 Motifs have the same representation patterns across networks against the random model. If some kind of
368 dynamical non-adaptative selection would be working, local food webs should have motif representations that
369 increase its stability. The expected pattern, is an over-representation tri-trophic chains, exploitative and
370 apparent competition (Borrelli 2015), and the omnivory motif could enhance or diminish stability (Monteiro
371 and Faria 2016). Our results showed an over-representation of omnivory, exploitative competition and appar-
372 ent competition; and under-representation of tri-trophic chains, which is not the most stable configuration.
373 The motif structure observed in the metaweb is not maintained in local food webs: apparent competition is
374 over-represented in Potter Cove, which would enhance stability, and both omnivory and tri-trophic chains
375 are under-represented in Weddell Sea which seems to have a neutral effect on stability. Thus, the assembly

376 process is not random, there are differences in the frequencies of motifs as the scale change, but the selection
377 of motifs due to its dynamical stability is not the main driver. This implies that other processes that influ-
378 ence the presence or absence of species like habitat filtering or dispersal limitation are acting and probably
379 modifying motif frequencies in empirical food webs.

380 As expected, all the networks have a short mean trophic level (Williams et al. 2002, Borrelli and Ginzburg
381 2014) compared with the random model. Different hypotheses were posed to explain this pattern: the low
382 efficiency of energy transfer between trophic levels, predator size, predator behaviour, and consumer diversity
383 (Young et al. 2013). These have contradictory support, reviewed by Ward and McCann (2017). Recently, it
384 has been proposed that maximum trophic level could be related to productivity and ecosystem size depending
385 on the context but related to energy fluxes that promote omnivory (Ward and McCann 2017). A different
386 mechanism based on dynamic stability of the whole web was proposed: food webs with shorter trophic levels
387 (between 2 and 4) that have more omnivore chains are more likely to be stable, which increase the probability
388 of being observed in nature (Borrelli and Ginzburg 2014). We found that mean trophic level of the local food
389 webs was not different from the assembly model, and omnivory was under-represented. This combination
390 suggests that the trophic level could also be a spandrel of assembly, inherited from the metaweb structure.

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

402 The spatial scales involved in our study do not represent a continuity; the metaweb and the Weddell sea web
403 have a 10 to 1 ratio but the local web is 10^6 smaller, besides that most of the global network properties and the
404 motif structure showed no changes relative to the null model. Thus, we found evidence that local processes
405 that limit species from the metaweb to local scales are influencing the assembly process but the structure of
406 the food web originated through an emergent process from evolutionary or co-evolutionary forces seems to
407 be more important. Besides our results are limited to Antarctic marine food webs our findings suggest that

408 future studies about food webs should give more attention to evolutionary and assembly processes, and less
409 emphasis to local dynamics. This kind of analysis needs to be expanded to different regions and other kinds
410 of habitats (e.g. terrestrial, freshwater, etc.) to confirm if this is a general pattern or not.

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