

<sup>1</sup> **Ecological Network assembly: how the regional metaweb influences  
2 local food webs**

<sup>3</sup> **Leonardo A. Saravia** <sup>1 2 5</sup>, **Tomás I. Marina** <sup>1 2 3</sup>, **Marleen De Troch** <sup>4</sup>, **Fernando R. Momo** <sup>1 2</sup>

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

<sup>6</sup> 2. INEDES, Universidad Nacional de Luján, CC 221, 6700 Luján, Argentina.

<sup>7</sup> 3. Centro Austral de Investigaciones Científicas (CADIC-CONICET)

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

<sup>9</sup> 5. Corresponding author e-mail lsaravia@campus.ungs.edu.ar, ORCID <https://orcid.org/0000-0002-7911-4398>

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<sup>11</sup> , trophic coherence, motif, topological roles, null models

<sup>12</sup> **Running title:** The metaweb influence on local food webs.

13    **Abstract**

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

## 40 Introduction

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

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

65 The objective of the present study is to analyse the process of food web assembly by comparing network  
66 properties with models across different spatial scales. For this we considered the following networks: Antarc-  
67 tic metaweb, representing an area of 34.8 million Km<sup>2</sup> and built from a dietary database (Raymond et al.  
68 2011); the Weddell Sea food web that represents 3.5 million Km<sup>2</sup> (Jacob et al. 2011); and Potter Cove  
69 network that represents 6.8 Km<sup>2</sup> (Marina et al. 2018a).

70 Insight into food web assembly can be also gained by assessing the structure of ecological networks at different

71 levels: emergent or global properties that focus on averages over the entire network (e.g. modularity or  
72 connectance) and local properties that focus on how one or a group of species are related to the whole.  
73 Global properties related to resilience and stability are fundamental to understand the response of ecological  
74 networks to global threats like climate change and biological invasions. One of these properties is small-  
75 worldness, associated with rapid responses to disturbances and resistance to secondary extinctions (Montoya  
76 and Solé 2002). The small-world pattern is related to two global properties: the average of the shortest  
77 distance between all species, called characteristic path length, and the clustering coefficient, the probability  
78 that two species linked to the same species are linked. Then, the small-world pattern implies a short average  
79 path length and a high level of clustering compared to random networks (Watts and Strogatz 1998). This  
80 pattern comes from the general network theory, beyond ecological networks, and has been recently applied  
81 to marine food webs (Gray et al. 2016, Navia et al. 2016, Bornatowski et al. 2017, Marina et al. 2018b).

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

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

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

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

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

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

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

<sup>133</sup> **Methods**

<sup>134</sup> The three datasets used in this study encompass a wide range of spatial scales and were collected inde-  
<sup>135</sup> pendently. The Southern Ocean database compiled by Raymond et al. (2011) was used to construct the  
<sup>136</sup> Antarctic metaweb selecting only species located at latitudes higher than 60°S. Raymond et al. (2011)  
<sup>137</sup> compiled information from direct sampling methods of dietary assessment, including gut, scat, and bolus  
<sup>138</sup> content analysis, stomach flushing, and observed feeding. We considered that the metaweb is the regional  
<sup>139</sup> pool of species defined by the biogeographic Antarctic region. Next we analysed two local food webs: the  
<sup>140</sup> Weddell Sea food web dataset includes species situated between 74°S and 78°S with a West-East extension  
<sup>141</sup> of approximately 450 km, and comprises all information about trophic interactions available for the zone  
<sup>142</sup> since 1983 (Jacob et al. 2011). The Potter Cove dataset comes from a 4 km long and 2.5 km wide Antarctic  
<sup>143</sup> fjord located at 62°14'S, 58°40'W, South Shetland Islands (Marina et al. 2018a). These food web datasets  
<sup>144</sup> comprise benthic and pelagic habitats of the Antarctic ecosystem, few aggregated low-trophic level groups  
<sup>145</sup> (e.g. detritus, diatoms, phytoplankton, zooplankton) and a high resolution of the macroalgae community  
<sup>146</sup> (i.e. 24 biological species of red, brown and green macroalgae). The macroalgae community is responsible  
<sup>147</sup> for the majority of the primary production and supports a large fraction of secondary production in Antarc-  
<sup>148</sup> tic fjords (Quartino and Boraso de Zaixso 2008, Valdivia et al. (2015)). Higher trophic levels comprise:  
<sup>149</sup> invertebrate (e.g. ascidians, sponges, isopods, amphipods, bivalves, gastropods, cephalopods, echinoderms)  
<sup>150</sup> and vertebrate predator groups (e.g. demersal and pelagic fishes, penguins, seals and whales). For more  
<sup>151</sup> information about these datasets refer to the original publications. To make datasets compatible, we first  
<sup>152</sup> checked taxonomic names for synonyms, and second, we added species (either prey or predator) with their  
<sup>153</sup> interactions to the metaweb when the local food webs contain a greater taxonomic resolution. This resulted  
<sup>154</sup> in the addition of 258 species to the metaweb, which represent 33% of the total. We removed cannibalistic  
<sup>155</sup> (self-links) and double arrows (i.d. A eats B and B eats A).

<sup>156</sup> We analysed the structure of the networks using properties that focus on different levels: emergent or global  
<sup>157</sup> properties that take into account the whole network, sub-structural properties that consider several nodes,  
<sup>158</sup> and properties related to one node. To describe food webs as networks each species is represented as a  
<sup>159</sup> node or vertex and the trophic interactions are represented as edges or links between nodes. These links are  
<sup>160</sup> directed, from the prey to the predator, as the flow of energy and matter. Two nodes are neighbours if they  
<sup>161</sup> are connected by an edge and the degree  $k_i$  of node  $i$  is the number of neighbours it has. The food web can  
<sup>162</sup> be represented by an adjacency matrix  $A = (a_{ij})$  where  $a_{ij} = 1$  if species  $j$  predaes on species  $i$ , else is 0.  
<sup>163</sup> 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  
<sup>164</sup> predators of  $i$  or its out-degree. The total number of edges is  $E = \sum_{ij} a_{ij}$ .

165 **Models**

166 To unravel the mechanisms of network assembly we considered two models: 1) a random network model with-  
167 out any ecological mechanism, and 2) a colonization-extinction model constrained by the network structure,  
168 with no consideration of population dynamics and interaction strength. Then we compared the empirical  
169 networks with such models using a null model approach: if we observe a deviation from the property obtained  
170 with the null model then mechanisms that are excluded from the model may be acting (Bello 2012).

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

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

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

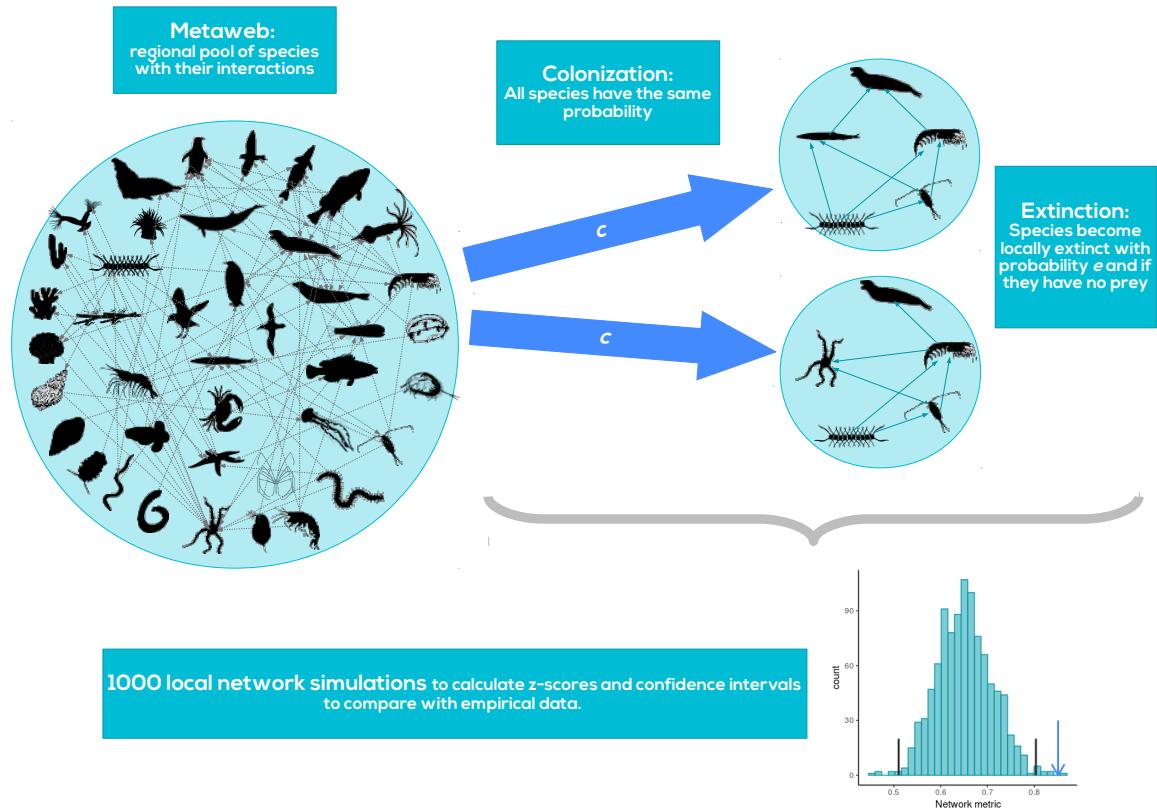


Figure 1: Schematic diagram of the metaweb assembly model: species migrate from the metaweb with a probability  $c$  to a local network carrying their potential links to preys; here they have a probability of extinction  $e$ . Additionally, predators become extinct if their preys are locally extinct. 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

193 **Global network properties**

194 The first global emergent property we analysed was the small-world pattern, which examines the average  
195 of the shortest distance between nodes and the clustering coefficient of the network (Watts and Strogatz  
196 1998). This property is associated with an increased resilience and resistance to secondary extinctions (Solé  
197 and Montoya 2001, Bornatowski et al. 2017). We first calculated the characteristic path length that is the  
198 shortest path between any two nodes. Then  $L$  is the mean value of the shortest path length across all pairs  
199 of nodes. The clustering coefficient of node  $i$  was defined as

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

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

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

205 and

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

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

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

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

212 called  $ql, qh$ :

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

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

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

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

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

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

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

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

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

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

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

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

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

#### 249 Sub-structural properties (motifs)

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

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

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

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

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

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

265 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  
266 species in module  $s$ . Due to the stochastic nature of the module detection algorithm we made repeated  
267 runs of the algorithm until there were no statistical differences between the distributions of  $PC_i$  and  $dz_i$  in  
268 successive repetitions; to test such statistical difference we used the k-sample Anderson-Darling test (Scholz  
269 and Stephens 1987). Then we calculated the mean and 95% confidence interval of  $dz$  and  $PC$ .

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

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

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

## 287 Results

### 288 Global network properties

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

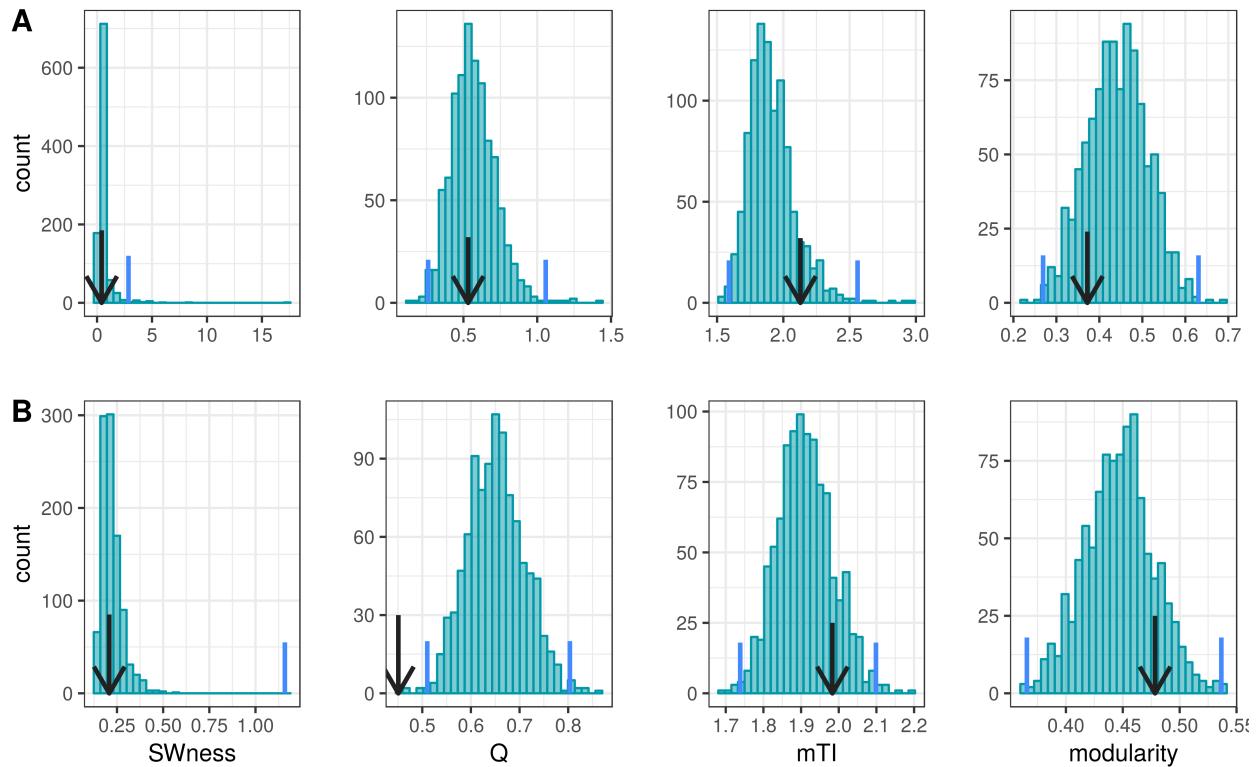


Figure 2: Network global properties compared with the metaweb assembly model for A) Potter Cove and B) Weddell Sea food-webs. The properties were: Small-world-ness (SWness), coherence (Q), mean trophic level (mTl) and modularity. We ran 1000 simulations of local networks fitted to Potter Cove and Weddell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

### 302 Sub-structural properties (motifs)

303 The representation of three-species sub-networks with respect to the random model showed similar patterns  
 304 in all networks (Figure 3A). While exploitative competition, apparent competition, and omnivory were over-  
 305 represented, tri-trophic chains were under-represented; all these patterns were significant (Table S3). We  
 306 found that motifs proportions for the three examined spatial scales were different (Chi-squared = 12612,

307 p-value < 1e-04). this means that local networks are not a random sample of the metaweb. With respect to  
 308 the metaweb assembly model only some of them were significant (Figure 3B, Table S4): tri-trophic chains  
 309 and omnivory were under-represented for Weddell Sea, and apparent competition was over-represented for  
 310 Potter Cove (Figure 3B). Contrary to our expectations Potter Cove was more similar to the metaweb than  
 311 Weddell Sea food web. The under-representation of omnivory is related to the low value of coherence index  
 312 in .

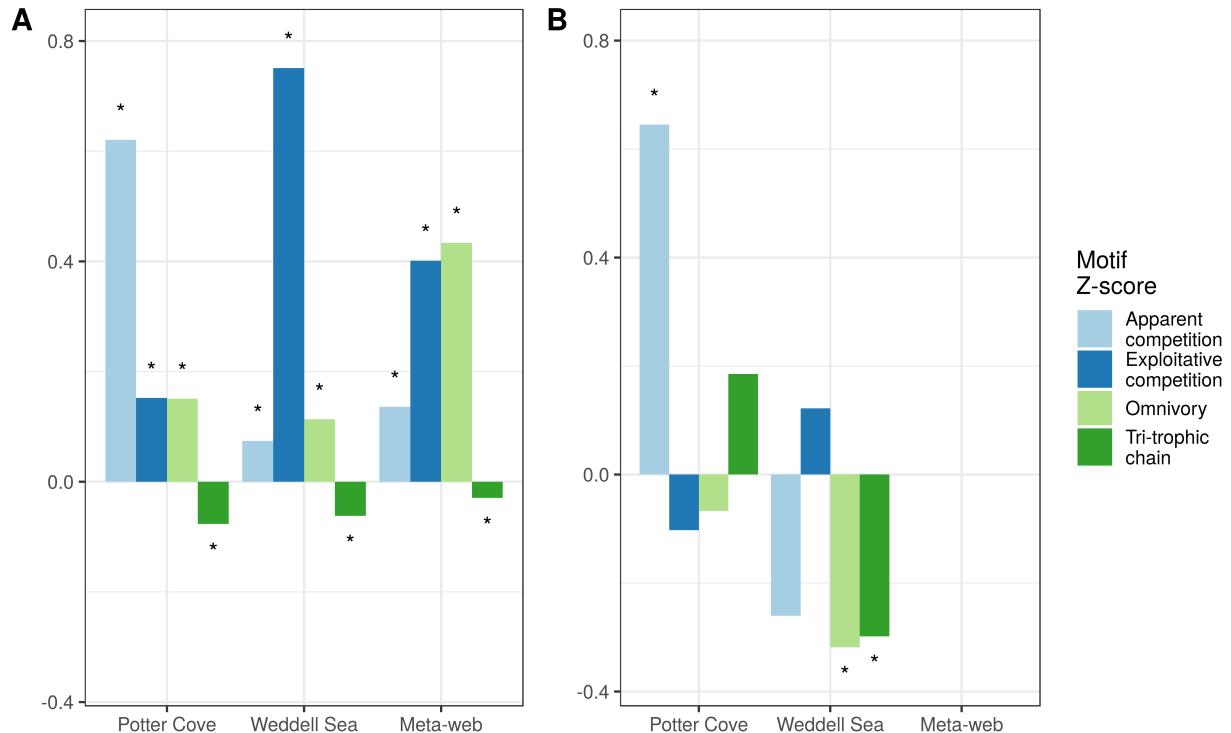


Figure 3: Network motifs z-scores across scales. Motifs are three-node sub-networks counted on each of the networks.: the *Metaweb* represents the marine predator-prey relationships of Antarctica; the *Weddell Sea* and *Potter Cove* are local food webs. A. Z-scores estimated with the random null model.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

### 313 Node-level properties (Topological roles)

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

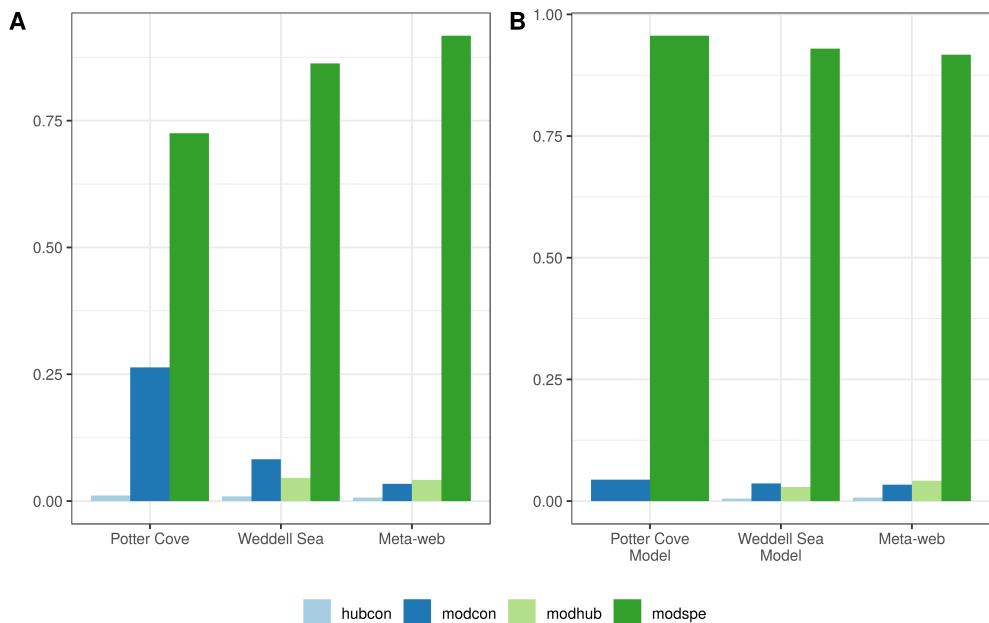


Figure 4: Proportion of topological roles across scales., the *Metaweb* represents the marine predator-prey relationships of Antarctica; the *Weddell Sea* and *Potter Cove* are local food webs. The topological roles are: *Hub connectors*, high number of between-module links; *Module connectors*, low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

319 = 5.95, p-value = 0.41)(Figura 3 B).

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

## 332 Discussion

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

341 Global level network properties showed a similar pattern across scales; most of them were significantly  
342 different from the random null model but not from the assembly model. Modularity for Potter Cove food  
343 web was the only property that is similar to the random model. The existence of a modular structure could  
344 be related to different habitats (Krause et al. 2003, Rezende et al. 2009) —in marine environments, these  
345 could be benthic with different depths and pelagic with different extensions. Even though Potter Cove have  
346 a small extent (6.8 Km<sup>2</sup>) studies suggest there exist different habitats (Wölfli et al. 2014), then the lack of  
347 significant modularity compared to random and to the assembly model could be a sampling effect. Studies  
348 suggest that modularity enhances local stability and this effect is stronger the more complex the network

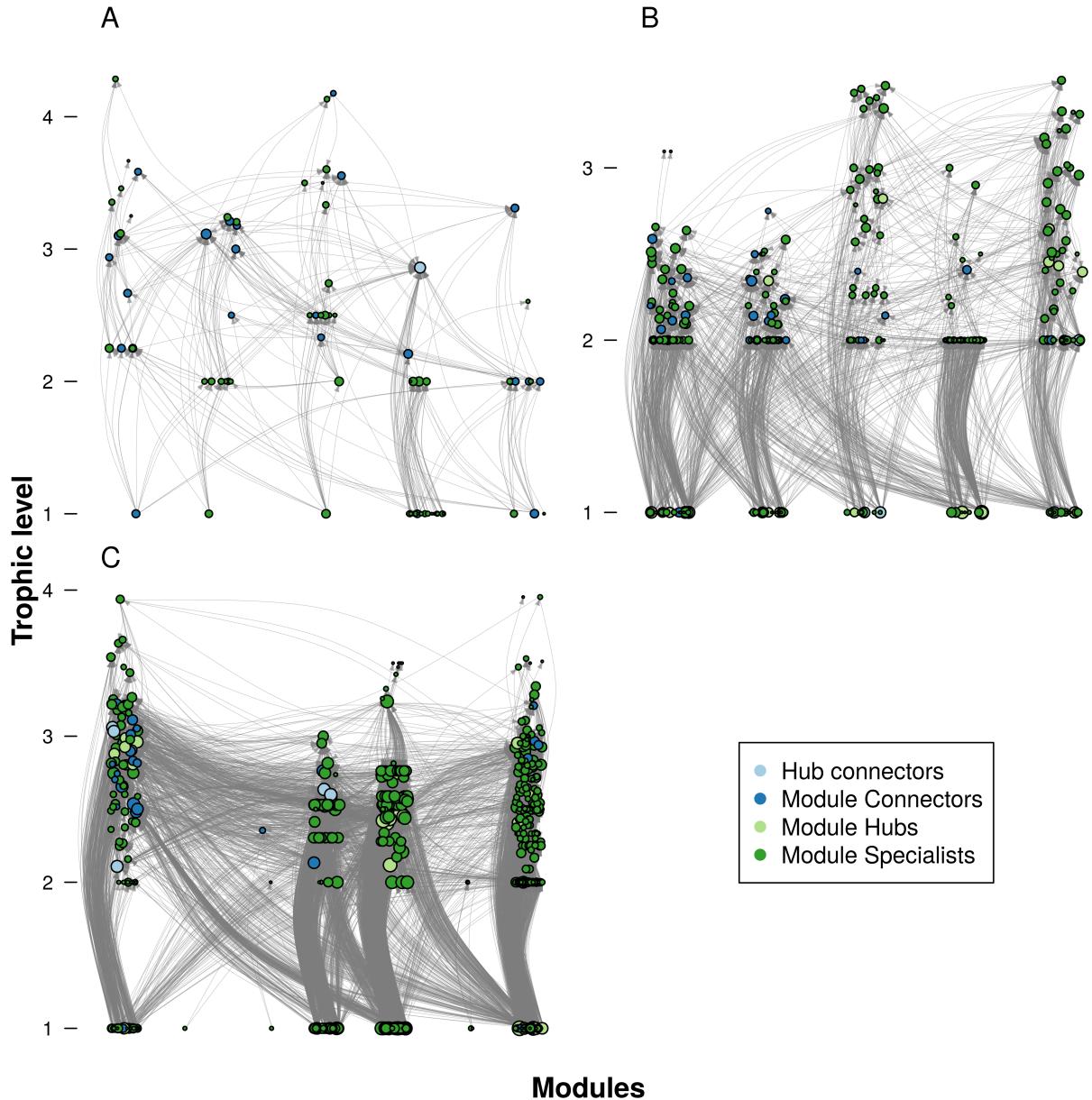


Figure 5: Plot of topological roles combined with trophic levels and modularity for each food web (A) Potter Cove, (B) Weddell Sea (C) the Metaweb. The topological roles are: *Hub connectors* have a high number of between module links, *Module connectors* have a low number of links mostly between modules,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

349 is (Stouffer and Bascompte 2011), even though the effect on stability strongly depends on the interaction  
350 strength configuration (Grilli et al. 2016) and on the existence of external perturbations (Gilaranz et al.  
351 2017). We found that modularity is not different from the assembly model and we observed that the modular  
352 structure is present in the metaweb. This suggests that modularity is not produced by maximization of local  
353 stability.

354 Biotic interactions are expected to be more important at the finest scales (Araújo and Rozenfeld 2014), thus  
355 dynamical stability represented in the coherence parameter is expected to be maximized at Potter Cove but  
356 we only found that Weddell Sea food web exhibited a greater trophic coherence than the assembly model.  
357 Thus, although this evidence is not conclusive with regard to the importance of dynamical processes in the  
358 assembly of food webs, the structure of the local food webs examined here seem to be a consequence of the  
359 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  
368 of dynamical non-adaptative selection would be working, local food webs should have motif representations  
369 that 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  
372 apparent competition; and under-representation of tri-trophic chains, this configuration is not the most stable.  
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 are  
375 under-represented in Weddell Sea which seems to have a neutral effect on stability. Thus, the assembly process  
376 is not random, there are differences in the frequencies of motifs as the scale change, but the selection of motifs  
377 due to its dynamical stability is not the main driver. This implies that other processes that influence the  
378 presence or absence of species like habitat filtering or dispersal limitation are acting and probably modifying  
379 motif frequencies in empirical food webs. This kind of motif patterns that are a sub-product of network  
380 building rules, or in general processes that happen at a different level, have been called spandrels of assembly

381 (Solé and Valverde 2006). Our results suggest that motif patterns in our metaweb food-webs system are  
382 spandrels of assembly.

383 As expected, all the networks have a short mean trophic level (Williams et al. 2002, Borrelli and Ginzburg  
384 2014) compared with the random model . Different hypotheses were posed to explain this pattern: the  
385 low efficiency of energy transfer between trophic levels, predator size, predator behaviour, and consumer  
386 diversity (Young et al. 2013). These have contradictory support, reviewed by Ward and McCann (2017).

387 Recently, it has been proposed that maximum trophic level could be related to productivity and ecosystem  
388 size depending on the context but related to energy fluxes that promote omnivory (Ward and McCann 2017).

389 A different mechanism based on dynamic stability of the whole web was proposed: food webs with shorter  
390 trophic levels (between 2 and 4) that have more omnivore chains are more likely to be stable, which increase  
391 the probability of being observed in nature (Borrelli and Ginzburg 2014). We found that mean trophic level  
392 of the local food webs was not different from the assembly model, and omnivory was under-represented. This  
393 combination suggests that the trophic level could also be a spandrel of assembly, inherited from the metaweb  
394 structure.

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

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

<sup>413</sup> less emphasis to local dynamics. This kind of analysis needs to be expanded to different regions and other  
<sup>414</sup> kinds of habitats (e.g. terrestrial, freshwater, etc. ) to confirm if this is a general pattern or not.

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