

<sup>1</sup> Ecological Network assembly: how the regional metaweb influences  
<sup>2</sup> 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>13</sup> **Running title:** The metaweb influence on local food webs.

14    **Abstract**

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

## 42 Introduction

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

57 Metacommunity theory provides a framework for assessing the roles of local- and regional-scale processes on  
58 network structure (Baiser, Buckley, Gotelli, & Ellison, 2013; Leibold et al., 2004). This approach has been  
59 applied historically to competitive interactions, whereas trophic interactions have received less attention  
60 (Baiser, Elhesha, & Kahveci, 2016). Recently, there has been an increase in food web assembly studies, inte-  
61 grating them with island biogeography (Galiana et al., 2018; Gravel, Massol, Canard, Mouillot, & Mouquet,  
62 2011), metacommunity dynamics (Liao, Chen, Ying, Hiebeler, & Nijs, 2016; Pillai, Gonzalez, & Loreau,  
63 2011) and the effects of habitat fragmentation (Mougi & Kondoh, 2016).

64 Very few studies have analysed the process of food web assembly using experimental or empirical data:  
65 Piechnik, Lawler, & Martinez (2008) found that trophic generalists colonize first and then trophic specialist  
66 supporting the hypothesis that biotic interactions are important in the assembly process (Holt, Lawton, Polis,  
67 & Martinez, 1999); Baiser et al. (2013) showed that habitat characteristics and dispersal capabilities were  
68 the main drivers of the assembly and Fahimipour & Hein (2014) found that colonization rates were also an  
69 important factor. None of them focuses on structural network properties related to resilience and stability.  
70 One of these properties is small-worldness, associated with rapid responses to disturbances and resistance  
71 to secondary extinctions (Montoya & Solé, 2002). The small-world pattern is related to the average of  
72 the shortest distance between all species, called characteristic path length, and the clustering coefficient,

73 the probability that two species linked to the same species are linked. This pattern comes from the general  
74 network theory, beyond ecological networks, and has been recently applied to marine food webs (Bornatowski,  
75 Barreto, Navia, & de Amorim, 2017; Gray et al., 2016; Tomás Ignacio Marina et al., 2018; Navia, Cruz-  
76 Escalona, Giraldo, & Barausse, 2016).

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

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

98 Species may participate in different ways with respect to modularity, depending on how many trophic links  
99 are conducted within their own module and/or between modules (Guimerà & Nunes Amaral, 2005; Kortsch,  
100 Primicerio, Fossheim, Dolgov, & Aschan, 2015). This participation with respect to modularity is called a  
101 species' topological role. Theoretical and empirical results suggest these roles are related to species traits,  
102 such as wide niche breadth, environmental tolerance, apex position in local communities and high motility  
103 (Borthagaray, Arim, & Marquet, 2014; Dupont & Olesen, 2009; Guimerà et al., 2010; Kortsch et al., 2015;  
104 Rezende, Albert, Fortuna, & Bascompte, 2009).

105 If we consider a subset of linked species inside the food web this forms a sub-network. When the abundance  
106 of one of these sub-networks deviates significantly from a null model network, this is called a motif (Milo  
107 et al., 2002). Besides this definition, in the ecological literature motif has been used as a synonym of sub-  
108 network. We analyse here the three-species sub-networks that have been most studied theoretically and  
109 empirically in food webs (Baiser et al., 2016; Prill, Iglesias, & Levchenko, 2005; Stouffer, Camacho, Jiang,  
110 & Nunes Amaral, 2007). Specifically, we focused on four of the thirteen possible three-species sub-networks:  
111 apparent competition, exploitative competition, tri-trophic chain, and omnivory (Figure S5). During the  
112 assembly process those motif structures that are less dynamically stable tend to disappear from the food  
113 web, which represents a system-level selective force where the ecological interactions are shaped by dynamical  
114 constraints rather than Darwinian processes (Borrelli, 2015), this has been called non-adaptative systemic  
115 selection (Borrelli et al., 2015).

116 In this study we analysed the assembly process by means of a probabilistic model that simulates colonization  
117 from a metaweb with the restriction that predators must have a prey to persist locally (Figure 1), this model  
118 lacks any restriction related to dynamical stability and local habitats. Additionally as some properties  
119 (Small-netwok, motifs, topological roles) were defined in relation to a random network, we also use the  
120 random network to compare the properties of a metaweb and two local empirical networks.

121 The two empirical local webs are: the Weddell Sea food web, which represents 3.5 million km<sup>2</sup> (Jacob et al.,  
122 2011); and the Potter Cove food web, which represents 6.8 km<sup>2</sup> (Tomás I Marina et al., 2018). To simulate  
123 the assembly process we used the Antarctic metaweb, built from a dietary database (Raymond et al., 2011),  
124 representing an area of 34.8 million km<sup>2</sup>.

125 If local food web structure reflects dynamical stability constraints, then we should expect to see the structural  
126 properties change from the metaweb to the local food webs. In particular, we expect properties related to  
127 resilience and stability (i.e. small-worldness, trophic coherence and modularity) to be close to the random  
128 model at the metaweb scale, and different from the assembly model for local food webs.

129 Also a greater frequency of stable motifs should be expected in the local food webs and we expect a change  
130 in the frequency of topological roles since habitat filtering or dispersal limitation may modify them at the  
131 local food web scale. These changes should be also reflected as differences from the metaweb assembly model.  
132 On the other hand, if the assembly model also produces webs with stability-enhancing structural attributes,  
133 then that indicates that these structures may be spandrels of the metaweb (Valverde et al., 2018) rather  
134 than a consequence of some dynamical constraint acting on the local food webs.

135 **Methods**

136 The three datasets used in this study encompass a wide range of spatial scales and were collected inde-  
137 pendently. The Southern Ocean database compiled by Raymond et al. (2011) was used to construct the  
138 Antarctic metaweb selecting only species located at latitudes higher than 60°S. Raymond et al. (2011)  
139 compiled information from direct sampling methods of dietary assessment, including gut, scat, and bolus  
140 content analysis, stomach flushing, and observed feeding. We considered that the metaweb is the regional  
141 pool of species defined by the biogeographic Antarctic region. Next we analysed two local food webs: the  
142 Weddell Sea food web dataset includes species situated between 74°S and 78°S with a West-East extension of  
143 approximately 450 km, and comprises all information about trophic interactions available for the zone since  
144 1983 (Jacob et al., 2011). The Potter Cove dataset comes from a 4 km long and 2.5 km wide Antarctic fjord  
145 located at 62°14'S, 58°40'W, South Shetland Islands (Tomás I Marina et al., 2018). These food web datasets  
146 comprise benthic and pelagic habitats of the Antarctic ecosystem, few aggregated low-trophic level groups  
147 (e.g. detritus, diatoms, phytoplankton, zooplankton) and a high resolution of the macroalgae community  
148 (i.e. 24 biological species of red, brown and green macroalgae). The macroalgae community is responsible for  
149 the majority of the primary production and supports a large fraction of secondary production in Antarctic  
150 fjords (Quartino & Boraso de Zaixso, 2008; Valdivia, Díaz, Garrido, & Gómez, 2015). Higher trophic lev-  
151 els comprise: invertebrate (e.g. ascidians, sponges, isopods, amphipods, bivalves, gastropods, cephalopods,  
152 echinoderms) and vertebrate predator groups (e.g. demersal and pelagic fishes, penguins, seals and whales).  
153 For more information about these datasets refer to the original publications. To make datasets compatible,  
154 we first checked taxonomic names for synonyms, and second, we added species (either prey or predator)  
155 with their interactions to the metaweb when the local food webs contain a greater taxonomic resolution.  
156 This resulted in the addition of 258 species to the metaweb, which represent 33% of the total. We removed  
157 cannibalistic (self-links) and double arrows (i.d. A eats B and B eats A).  
  
158 To describe food webs as networks each species is represented as a node or vertex and the trophic interactions  
159 are represented as edges or links between nodes. These links are directed, from the prey to the predator, as  
160 the flow of energy and matter. Two nodes are neighbours if they are connected by an edge and the degree  
161  $k_i$  of node  $i$  is the number of neighbours it has. The food web can be represented by an adjacency matrix  
162  $A = (a_{ij})$  where  $a_{ij} = 1$  if species  $j$  predaates on species  $i$ , else is 0. Then  $k_i^{in} = \sum_j a_{ji}$  is the number of preys  
163 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  
164 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 (de Bello, 2012).

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

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

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

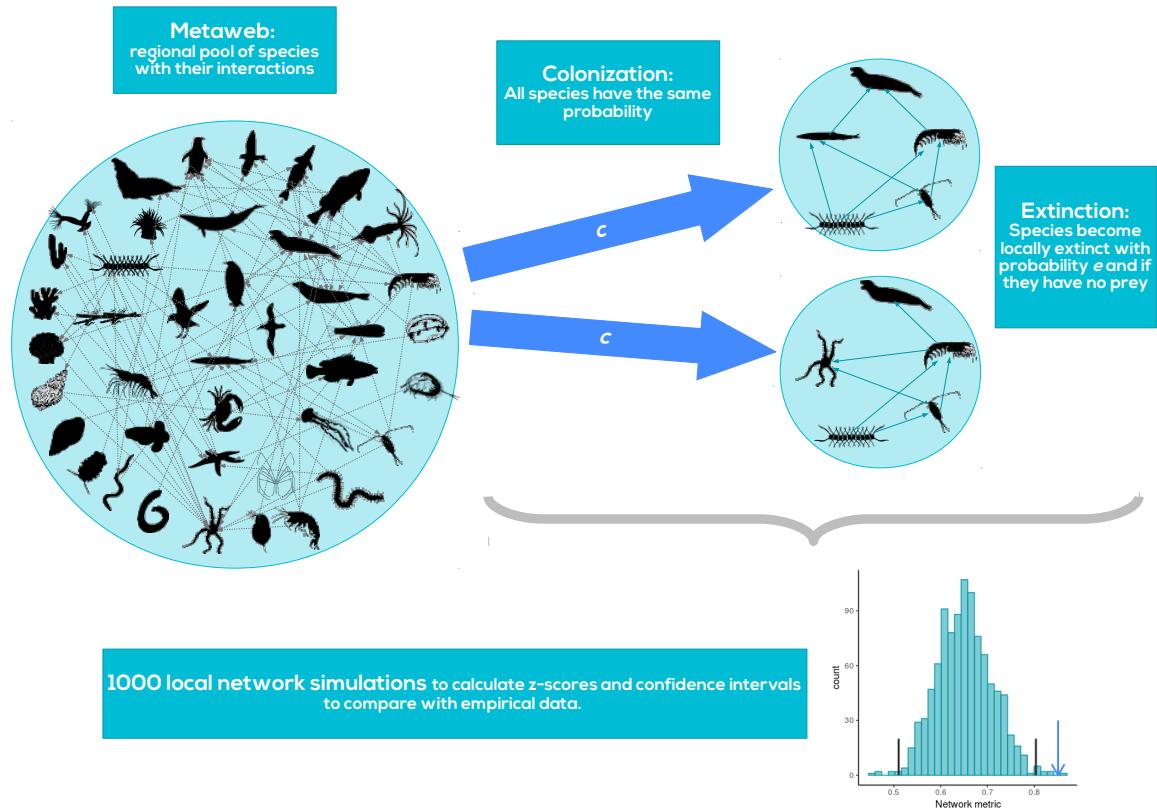


Figure 1: Schematic diagram of the metaweb assembly model: species migrate from the metaweb with a probability  $c$  to a local network carrying their potential links to preys; here they have a probability of extinction  $e$ . Additionally, predators become extinct if their preys are locally extinct.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

195 **Structural network properties**

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

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

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

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

207 and

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

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

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

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

214 called  $ql, qh$ :

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

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

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

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

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

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

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

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

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

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

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

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

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

## 251 Motifs

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

258 **Topological roles**

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

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

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

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

267 where  $k_i$  is the degree of species  $i$  (i.e. the number of links),  $k_{is}$  is the number of links of species  $i$  to species  
268 in module  $s$ . Due to the stochastic nature of the module detection algorithm we made repeated runs of the  
269 algorithm until there were no statistical differences between the distributions of  $PC_i$  and  $dz_i$  in successive  
270 repetitions; to test such statistical difference we used the k-sample Anderson-Darling test (Scholz & Stephens,  
271 1987). Then we calculated the mean and 95% confidence interval of  $dz$  and  $PC$ .

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

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

285 All analyses and simulations were made in R version 3.4.3 (R Core Team, 2017), using the igraph pack-  
286 age version 1.1.2 (Csardi & Nepusz, 2006) for motifs and topological role estimations, and NetIndices  
287 (Kones, Soetaert, van Oevelen, & Owino, 2009) for trophic level calculations. Source code and data  
288 is available at figshare [https://figshare.com/ADD\\_URL\\_HERE](https://figshare.com/ADD_URL_HERE) and github <https://github.com/lsaravia/MetawebsAssembly/>.

## 290 Results

### 291 Structural network properties

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

Table 1: Network structural 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*

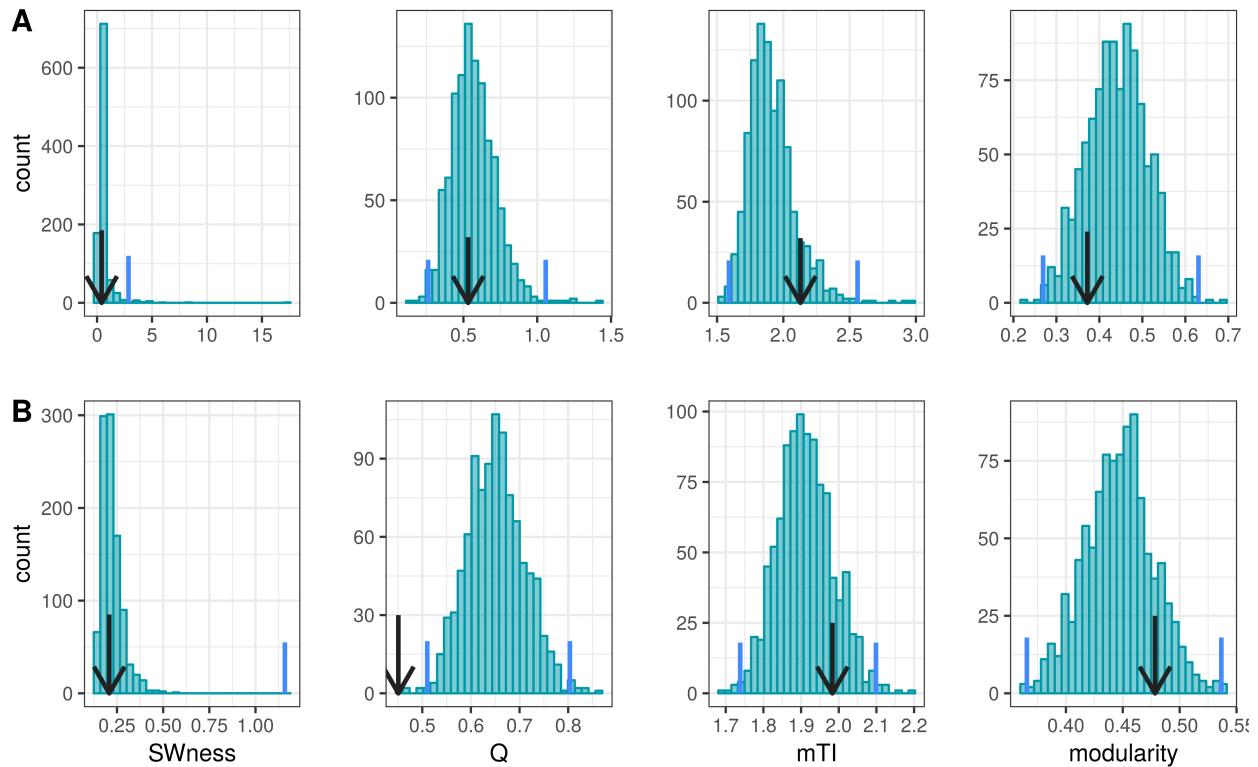


Figure 2: Network structural properties compared with the metaweb assembly model for A) Potter Cove and B) Weddell Sea food webs. The properties were: Small-world-ness (SWness), coherence (Q), mean trophic level (mTl) and modularity. We ran 1000 simulations of local networks fitted to Potter Cove and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

### 304 Motifs

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

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

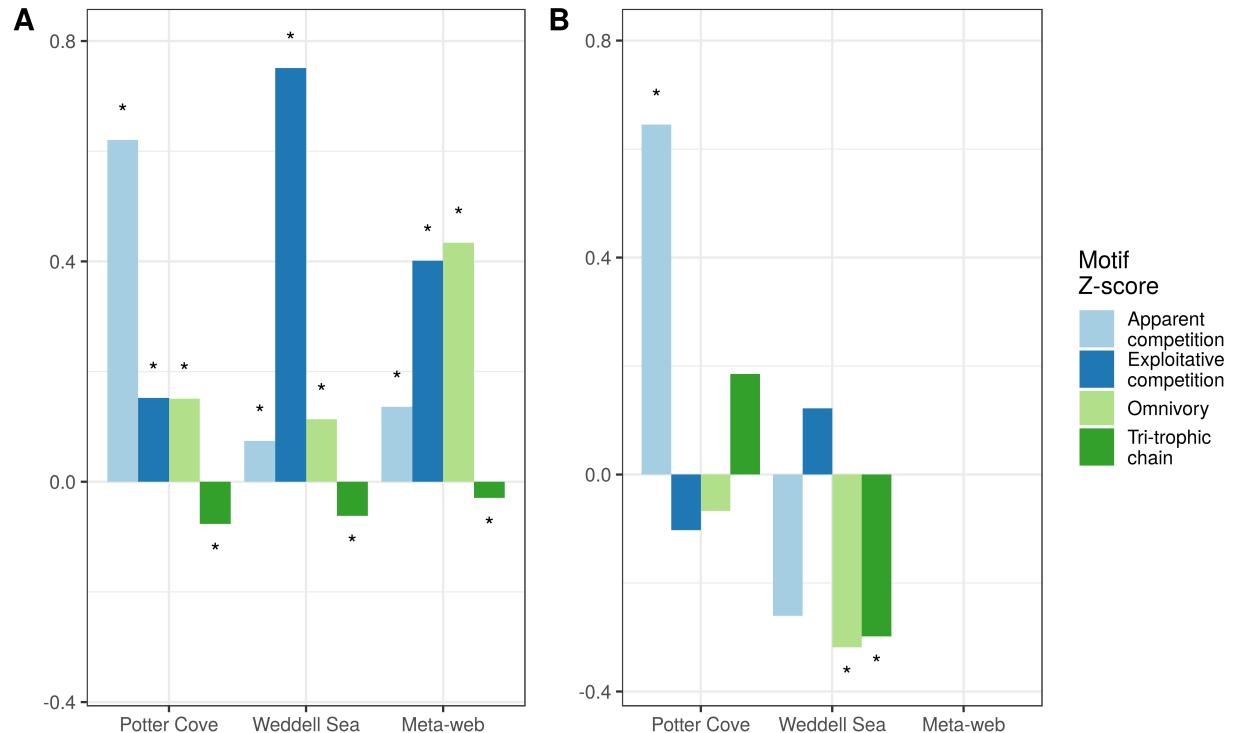


Figure 3: Network motifs z-scores across scales. Motifs are three-node sub-networks counted on each of the networks.: the *Metaweb* represents the marine predator-prey relationships of Antarctica; the *Weddell Sea* and *Potter Cove* are local food webs. A. Z-scores estimated with the random null model.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

### 315 Topological roles

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

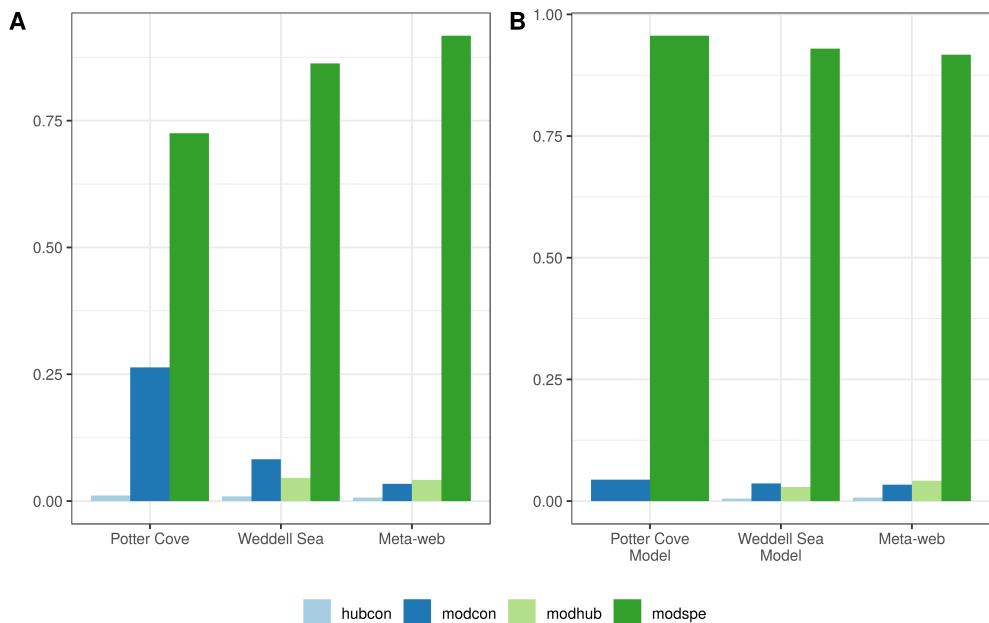


Figure 4: Proportion of topological roles across scales., the *Metaweb* represents the marine predator-prey relationships of Antarctica; the *Weddell Sea* and *Potter Cove* are local food webs. The topological roles are: *Hub connectors*, high number of between-module links; *Module connectors*, low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

321 = 5.95, p-value = 0.41)(Figura 3 B).

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

## 334 Discussion

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

343 Structural network properties showed a similar pattern across scales; most of them were significantly different  
344 from the random null model but not from the assembly model. All networks have a significant value of small-  
345 world-ness compared with the random model and both local food webs are not different from the assembly  
346 model. In general, food webs do not show the small-world topology (Dunne, Williams, & Martinez, 2002;  
347 Tomás Ignacio Marina et al., 2018), which suggests that the small-world property is inherited from the  
348 metaweb and is less influenced by the greater percentage of realized interactions in local food webs. This  
349 result confirms the hypothesis of Tomás Ignacio Marina et al. (2018), If small-world-ness was determinant  
350 for an increased resilience and robustness to secondary extinctions (Bornatowski et al., 2017), local food

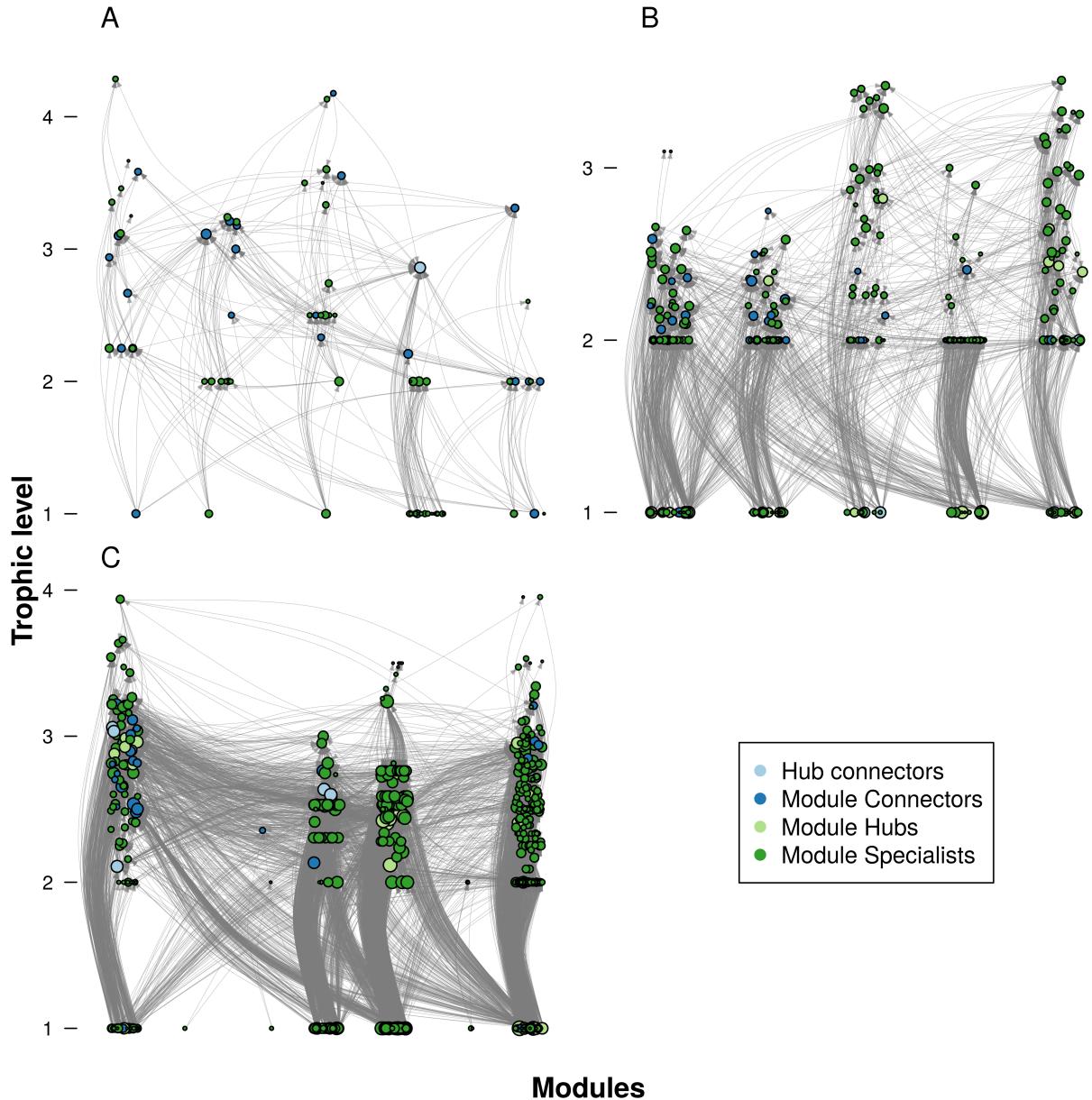


Figure 5: Plot of topological roles combined with trophic levels and modularity for each food web (A) Potter Cove, (B) Weddell Sea (C) the Metaweb. The topological roles are: *Hub connectors* have a high number of between module links, *Module connectors* have a low number of links mostly between modules,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

351 webs should reflect significantly higher values than those obtained from the metaweb assembly model.

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

364 Biotic interactions are expected to be more important at the finest scales (Araújo & Rozenfeld, 2014), thus  
365 dynamical stability represented in trophic coherence is expected to be maximized at Potter Cove, but we  
366 only found that Weddell Sea exhibited a greater trophic coherence than the assembly model. Thus, although  
367 this evidence is not conclusive with regard to the importance of dynamical stability in the assembly of food  
368 webs, the structure of the local food webs examined here seem to be a consequence of the metaweb structure.  
369 Another possibility that would require further investigation is that these properties were not sensitive enough  
370 to detect changes between the simulated and empirical food webs, furthermore Grilli et al. (2016) states  
371 that a particular network structure could be stabilizing or destabilizing depending on specific conditions and  
372 this could render the detection of structures related to stability constraints nearly impossible.

373 As expected, all the networks have a short mean trophic level (Borrelli & Ginzburg, 2014; Williams, Berlow,  
374 Dunne, Barabási, & Martínez, 2002) compared with the random model. Different hypotheses have been  
375 posed to explain this pattern: the low efficiency of energy transfer between trophic levels, predator size,  
376 predator behaviour, and consumer diversity (Young et al., 2013). Recently, it has been proposed that  
377 maximum trophic level could be related to productivity and ecosystem size depending on the context but  
378 related to energy fluxes that promote omnivory (Ward & McCann, 2017). We found that mean trophic level  
379 of the local food webs was not different from the assembly model, and omnivory was under-represented. This  
380 combination suggests that the trophic level could also be a spandrel of assembly, inherited from the metaweb  
381 structure.

382 Motifs have the same representation patterns across networks against the random model. If food web  
383 structure is influenced by dynamical constraints, then we would expect empirical food webs to have a higher  
384 frequency of stability-enhancing motifs than assembled model webs. If we take into account the stability  
385 of three species motifs, the expected pattern is an over-representation tri-trophic chains, exploitative and  
386 apparent competition (Borrelli, 2015), and the omnivory motif could enhance or diminish stability (Monteiro  
387 & Faria, 2016). As food webs are more than the sum of its three species modules (Cohen, Schittler, Raffaelli,  
388 & Reuman, 2009), if the persistence of the whole food web is considered, tri-trophic and omnivory should  
389 be over-represented, exploitative and apparent competition under-represented (Stouffer & Bascompte, 2010).  
390 Instead, our empirical food webs had an under-representation of tri-trophic chains while the other motifs  
391 were over-represented. More importantly, the motif structure observed in the metaweb is not maintained in  
392 local food webs: apparent competition is over-represented in Potter Cove, which would enhance stability and  
393 diminish persistence, and both omnivory and tri-trophic chains are under-represented in Weddell Sea this  
394 combination would have opposite effects on both stability and persistence. Thus, the assembly process is  
395 not random, there are differences in the frequencies of motifs as the scale change, but the selection of motifs  
396 due to its dynamical stability does not seem to be the main driver. This implies that other processes that  
397 influence the presence or absence of species like habitat filtering or dispersal limitation would be acting and  
398 probably modifying motif frequencies in empirical food webs.

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

410 The spatial scales involved in our study do not represent a continuity; the metaweb and the Weddell sea  
411 web have a 10 to 1 ratio but the local web is  $10^6$  smaller, besides that most of the global network properties  
412 and the motif structure showed no changes relative to the null model. We did not find evidence that the  
413 structure of the food web was strongly influenced by dynamical stability constraints. Instead, we found that

414 other local processes, that limit which species from the metaweb can colonise the local web, are influencing  
415 the assembly process.

416 In this work we assume that the metaweb influence the structure of local webs by means of the assembly  
417 process, but local webs are a part of the metaweb and in fact there is also an influence going in the other  
418 direction. Thus, this means that the structure of the metaweb could be already shaped by stability constraints  
419 of the local food webs. This is suggested by the fact that the metaweb have the same structural parameters  
420 and the same motifs representation than the local food webs when we compare against the random model  
421 and this would be the reason why we are not detecting differences.

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

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## 431 References

- 432 Allesina, S., Grilli, J., Barabás, G., Tang, S., Aljadeff, J., & Maritan, A. (2015). Predicting the stability of  
433 large structured food webs. *Nature Communications*, 6, 7842. doi: 10.1038/ncomms8842
- 434 Araújo, M. B., & Rozenfeld, A. (2014). The geographic scaling of biotic interactions. *Ecography*, 37(5),  
435 406–415. doi: 10.1111/j.1600-0587.2013.00643.x
- 436 Baiser, B., Buckley, H. L., Gotelli, N. J., & Ellison, A. M. (2013). Predicting food-web structure with  
437 metacommunity models. *Oikos*, 122(4), 492–506. doi: 10.1111/j.1600-0706.2012.00005.x
- 438 Baiser, B., Elhesha, R., & Kahveci, T. (2016). Motifs in the assembly of food web networks. *Oikos*, 125(4),  
439 480–491. doi: 10.1111/oik.02532

- 440 Bornatowski, H., Barreto, R., Navia, A. F., & de Amorim, A. F. (2017). Topological redundancy and “small-  
441 world” patterns in a food web in a subtropical ecosystem of Brazil. *Marine Ecology*, 38(2), e12407. doi:  
442 10.1111/maec.12407
- 443 Borrelli, J. J. (2015). Selection against instability: Stable subgraphs are most frequent in empirical food  
444 webs. *Oikos*, 124(12), 1583–1588. doi: 10.1111/oik.02176
- 445 Borrelli, J. J., Allesina, S., Amarasekare, P., Arditi, R., Chase, I., Damuth, J., ... Ginzburg, L. R. (2015).  
446 Selection on stability across ecological scales. *Trends in Ecology & Evolution*, 30(7), 417–425. doi:  
447 10.1016/j.tree.2015.05.001
- 448 Borrelli, J. J., & Ginzburg, L. R. (2014). Why there are so few trophic levels: Selection against instability  
449 explains the pattern. *Food Webs*, 1(1), 10–17. doi: <https://doi.org/10.1016/j.fooweb.2014.11.002>
- 450 Borthagaray, A. I., Arim, M., & Marquet, P. A. (2014). Inferring species roles in metacommunity structure  
451 from species co-occurrence networks. *Proceedings of the Royal Society B: Biological Sciences*, 281(1792).  
452 Retrieved from <http://rspb.royalsocietypublishing.org/content/281/1792/20141425.abstract>
- 453 Carstensen, D. W., Lessard, J.-P., Holt, B. G., Krabbe Borregaard, M., & Rahbek, C. (2013). Introducing  
454 the biogeographic species pool. *Ecography*, 36(12), 1310–1318. doi: 10.1111/j.1600-0587.2013.00329.x
- 455 Cohen, J. E., & Newman, C. M. (1985). When will a large complex system be stable? *Journal of Theoretical  
456 Biology*, 113(1), 153–156. doi: [http://dx.doi.org/10.1016/S0022-5193\(85\)80081-3](http://dx.doi.org/10.1016/S0022-5193(85)80081-3)
- 457 Cohen, J. E., Schittler, D. N., Raffaelli, D. G., & Reuman, D. C. (2009). Food webs are more than the  
458 sum of their tritrophic parts. *Proceedings of the National Academy of Sciences*, 106(52), 22335 LP–22340.  
459 Retrieved from <https://doi.org/10.1073/pnas.0910582106>
- 460 Crowley, P. H. (1992). Resampling methods for computation-intensive data analysis in ecology and evolution.  
461 *Annual Review of Ecology and Systematics*, 23, 405–447.
- 462 Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal,  
463 Complex Sy*, 1695. Retrieved from <http://igraph.org>
- 464 de Bello, F. (2012). The quest for trait convergence and divergence in community assembly: Are null-models  
465 the magic wand? *Global Ecology and Biogeography*, 21(3), 312–317. doi: 10.1111/j.1466-8238.2011.00682.x
- 466 Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Food-web structure and network theory: The  
467 role of connectance and size. *Proceedings of the National Academy of Sciences*, 99(20), 12917–12922. doi:  
468 10.1073/pnas.192407699

- 469 Dupont, Y. L., & Olesen, J. M. (2009). Ecological modules and roles of species in heathland plant–insect  
470 flower visitor networks. *Journal of Animal Ecology*, 78(2), 346–353. doi: 10.1111/j.1365-2656.2008.01501.x
- 471 Erdős, P., & Rényi, A. (1959). On random graphs. *Publicationes Mathematicae Debrecen*, 6, 290–297.
- 472 Fahimipour, A. K., & Hein, A. M. (2014). The dynamics of assembling food webs. *Ecology Letters*, 17(5),  
473 606–613. doi: 10.1111/ele.12264
- 474 Fortuna, M. A., Stouffer, D. B., Olesen, J. M., Jordano, P., Mouillot, D., Krasnov, B. R., ... Bascompte, J.  
475 (2010). Nestedness versus modularity in ecological networks: Two sides of the same coin? *Journal of Animal  
476 Ecology*, 79(4), 811–817. doi: 10.1111/j.1365-2656.2010.01688.x
- 477 Galiana, N., Lurgi, M., Claramunt-López, B., Fortin, M.-J., Leroux, S., Cazelles, K., ... Montoya, J. M.  
478 (2018). The spatial scaling of species interaction networks. *Nature Ecology & Evolution*, 2(5), 782–790. doi:  
479 10.1038/s41559-018-0517-3
- 480 Gilarranz, L. J., Rayfield, B., Liñán-Cembrano, G., Bascompte, J., & Gonzalez, A. (2017). Effects of network  
481 modularity on the spread of perturbation impact in experimental metapopulations. *Science*, 357(6347), 199  
482 LP–201. Retrieved from <http://science.sciencemag.org/content/357/6347/199.abstract>
- 483 Gravel, D., Massol, F., Canard, E., Mouillot, D., & Mouquet, N. (2011). Trophic theory of island biogeog-  
484 raphy. *Ecology Letters*, 14(10), 1010–1016. doi: 10.1111/j.1461-0248.2011.01667.x
- 485 Gray, C., Hildrew, A. G., Lu, X., Ma, A., McElroy, D., Monteith, D., ... Woodward, G. (2016). Chapter Ten  
486 - Recovery and Nonrecovery of Freshwater Food Webs from the Effects of Acidification. In A. J. Dumbrell,  
487 R. L. Kordas, & G. B. T. A. in E. R. Woodward (Eds.), *Large-Scale Ecology: Model Systems to Global  
488 Perspectives* (Vol. 55, pp. 475–534). doi: <https://doi.org/10.1016/bs.aecr.2016.08.009>
- 489 Grilli, J., Adorisio, M., Suweis, S., Barabás, G., Banavar, J. R., Allesina, S., & Maritan, A. (2017).  
490 Feasibility and coexistence of large ecological communities. *Nature Communications*, 8, 14389. doi:  
491 10.1038/ncomms14389
- 492 Grilli, J., Rogers, T., & Allesina, S. (2016). Modularity and stability in ecological communities. *Nature  
493 Communications*, 7, 12031. Retrieved from <http://dx.doi.org/10.1038/ncomms12031>
- 494 Guimerà, R., & Nunes Amaral, L. A. (2005). Functional cartography of complex metabolic networks. *Nature*,  
495 433, 895–900. Retrieved from <http://dx.doi.org/10.1038/nature03288>
- 496 Guimerà, R., Stouffer, D. B., Sales-Pardo, M., Leicht, E. A., Newman, M. E. J., & Amaral, L. A. N. (2010).  
497 Origin of compartmentalization in food webs. *Ecology*, 91(10), 2941–2951. doi: 10.1890/09-1175.1

- 498 Hanski, I. (1999). *Metapopulation Ecology*. Retrieved from [https://books.google.com.ar/books?id=jsk4Nt\\_](https://books.google.com.ar/books?id=jsk4Nt_)
- 499 8X8sC
- 500 HilleRisLambers, J., Adler, P. B., Harpole, W. S., Levine, J. M., & Mayfield, M. M. (2012). Rethinking  
501 Community Assembly through the Lens of Coexistence Theory. *Annual Review of Ecology, Evolution, and*  
502 *Systematics*, 43(1), 227–248. doi: 10.1146/annurev-ecolsys-110411-160411
- 503 Holt, R. D., Lawton, J. H., Polis, G. A., & Martinez, N. D. (1999). Trophic rank and the species-area  
504 relationship. *Ecology*, 80(5), 1495–1504.
- 505 Humphries, M. D., & Gurney, K. (2008). Network “Small-World-Ness”: A Quantitative Method for Deter-  
506 mining Canonical Network Equivalence. *PLOS ONE*, 3(4), e0002051. Retrieved from <https://doi.org/10.1371/journal.pone.0002051>
- 508 Jacob, U., Thierry, A., Brose, U., Arntz, W. E., Berg, S., Brey, T., ... Mollmann, C. (2011). The role of  
509 body size in complex food webs: A cold case. In A. B. B. T. A. in E. Research (Ed.), *Advances In Ecological*  
510 *Research* (Vol. 45, pp. 181–223). doi: <http://dx.doi.org/10.1016/B978-0-12-386475-8.00005-8>
- 511 Johnson, S., Domínguez-García, V., Donetti, L., & Muñoz, M. A. (2014). Trophic coherence deter-  
512 mines food-web stability. *Proceedings of the National Academy of Sciences*, 111(50), 17923–17928. doi:  
513 [10.1073/pnas.1409077111](https://doi.org/10.1073/pnas.1409077111)
- 514 Johnson, S., & Jones, N. S. (2017). Looplessness in networks is linked to trophic coherence. *Proceedings of*  
515 *the National Academy of Sciences*, 114(22), 5618–5623. doi: [10.1073/pnas.1613786114](https://doi.org/10.1073/pnas.1613786114)
- 516 Kones, J. K., Soetaert, K., van Oevelen, D., & Owino, J. (2009). Are network indices robust indi-  
517 cators of food web functioning? A Monte Carlo approach. *Ecological Modelling*, 220, 370–382. doi:  
518 <http://dx.doi.org/10.1016/j.ecolmodel.2008.10.012>
- 519 Kortsch, S., Primicerio, R., Aschan, M., Lind, S., Dolgov, A. V., & Planque, B. (2018). Food-web  
520 structure varies along environmental gradients in a high-latitude marine ecosystem. *Ecography*. doi:  
521 [10.1111/ecog.03443](https://doi.org/10.1111/ecog.03443)
- 522 Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V., & Aschan, M. (2015). Climate change alters the  
523 structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proceedings of the Royal*  
524 *Society B: Biological Sciences*, 282(1814). Retrieved from <http://rspb.royalsocietypublishing.org/content/282/1814/20151546.abstract>
- 526 Krause, A. E., Frank, K. A., Mason, D. M., Ulanowicz, R. E., & Taylor, W. W. (2003). Compartments  
527 revealed in food-web structure. *Nature*, 426, 282. Retrieved from <http://dx.doi.org/10.1038/nature02115>

- 528 Landi, P., Minoarivelو, H. O., Bränström, Å., Hui, C., & Dieckmann, U. (2018). Complexity and stability  
529 of ecological networks: A review of the theory. *Population Ecology*, *60*(4), 319–345. doi: 10.1007/s10144-  
530 018-0628-3
- 531 Leibold, M. A., Chase, J. M., & Ernest, S. K. M. (2017). Community assembly and the functioning of  
532 ecosystems: How metacommunity processes alter ecosystems attributes. *Ecology*, *98*(4), 909–919. doi:  
533 10.1002/ecy.1697
- 534 Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., ... Gonzalez,  
535 A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*,  
536 *7*(7), 601–613. doi: 10.1111/j.1461-0248.2004.00608.x
- 537 Liao, J., Chen, J., Ying, Z., Hiebeler, D. E., & Nijs, I. (2016). An extended patch-dynamic framework for  
538 food chains in fragmented landscapes. *Scientific Reports*, *6*, 33100. Retrieved from <http://dx.doi.org/10.1038/srep33100>
- 540 MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton (New Jersey), USA.:  
541 Princeton University Press.
- 542 Marina, T. I., Salinas, V., Cordone, G., Campana, G., Moreira, E., Deregbus, D., ... Momo, F. R. (2018).  
543 The Food Web of Potter Cove (Antarctica): Complexity, structure and function. *Estuarine, Coastal and  
544 Shelf Science*, *200*, 141–151. doi: 10.1016/j.ecss.2017.10.015
- 545 Marina, T. I., Saravia, L. A., Cordone, G., Salinas, V., Doyle, S. R., & Momo, F. R. (2018). Architec-  
546 ture of marine food webs: To be or not be a “small-world”. *PLoS ONE*, *13*(5), 1–13. doi: 10.1371/jour-  
547 nal.pone.0198217
- 548 May, R. M. (1972). Will a Large Complex System be Stable? *Nature*, *238*(5364), 413–414. doi:  
549 10.1038/238413a0
- 550 McCann, K. S. (2000). The diversity–stability debate. *Nature*, *405*(6783), 228–233. doi: 10.1038/35012234
- 551 Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., & Alon, U. (2002). Network Motifs:  
552 Simple Building Blocks of Complex Networks. *Science*, *298*(5594), 824 LP–827. Retrieved from <http://science.sciencemag.org/content/298/5594/824.abstract>
- 554 Monteiro, A. B., & Faria, L. D. B. (2016). The interplay between population stability and food-web topology  
555 predicts the occurrence of motifs in complex food-webs. *Journal of Theoretical Biology*, *409*, 165–171. doi:  
556 <https://doi.org/10.1016/j.jtbi.2016.09.006>

- 557 Montoya, J. M., & Solé, R. V. (2002). Small world patterns in food webs. *Journal of Theoretical Biology*,  
558 214(3), 405–412. doi: 10.1006/jtbi.2001.2460
- 559 Mougi, A., & Kondoh, M. (2016). Food-web complexity, meta-community complexity and community sta-  
560 bility. *Scientific Reports*, 6, 24478. doi: 10.1038/srep24478
- 561 Navia, A. F., Cruz-Escalona, V. H., Giraldo, A., & Barausse, A. (2016). The structure of a marine tropical  
562 food web, and its implications for ecosystem-based fisheries management. *Ecological Modelling*, 328, 23–33.  
563 doi: <https://doi.org/10.1016/j.ecolmodel.2016.02.009>
- 564 Neutel, A.-M., Heesterbeek, J. A. P., van de Koppel, J., Hoenderboom, G., Vos, A., Kaldeway, C., ... de  
565 Ruiter, P. C. (2007). Reconciling complexity with stability in naturally assembling food webs. *Nature*, 449,  
566 599. Retrieved from <https://doi.org/10.1038/nature06154>
- 567 Newman, M. E. J., & Girvan, M. (2004). Finding and evaluating community structure in networks. *Phys.*  
568 *Rev. E*, 69(2), 26113. doi: 10.1103/PhysRevE.69.026113
- 569 Paine, R. T. (1966). Food Web Complexity and Species Diversity. *The American Naturalist*, 100(910), 65–75.  
570 doi: 10.1086/282400
- 571 Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., & Torres, F. (1998). Fishing Down Marine Food  
572 Webs. *Science*, 279(5352), 860 LP–863. Retrieved from <http://science.sciencemag.org/content/279/5352/>  
573 860.abstract
- 574 Piechnik, D. A., Lawler, S. P., & Martinez, N. D. (2008). Food-web assembly during a classic bioge-  
575 graphic study: Species’“Trophic breadth” corresponds to colonization order. *Oikos*, 117(5), 665–674. doi:  
576 10.1111/j.0030-1299.2008.15915.x
- 577 Pillai, P., Gonzalez, A., & Loreau, M. (2011). Metacommunity theory explains the emergence of  
578 food web complexity. *Proceedings of the National Academy of Sciences*, 108(48), 19293–19298. doi:  
579 10.1073/pnas.1106235108
- 580 Prill, R. J., Iglesias, P. A., & Levchenko, A. (2005). Dynamic Properties of Network Motifs Contribute  
581 to Biological Network Organization. *PLOS Biology*, 3(11), e343. Retrieved from <https://doi.org/10.1371/journal.pbio.0030343>
- 583 Quartino, M. L., & Boraso de Zaixso, A. L. (2008). Summer macroalgal biomass in Potter Cove, South  
584 Shetland Islands, Antarctica: Its production and flux to the ecosystem. *Polar Biology*, 31(3), 281–294. doi:  
585 10.1007/s00300-007-0356-1

- 586 Raymond, B., Marshall, M., Nevitt, G., Gillies, C. L., van den Hoff, J., Stark, J. S., ... Constable, A. J.  
587 (2011). A Southern Ocean dietary database. *Ecology*, 92(5), 1188. doi: 10.1890/10-1907.1
- 588 R Core Team. (2017). *R: A Language and Environment for Statistical Computing*. Retrieved from <http://www.r-project.org/>
- 589
- 590 Reichardt, J., & Bornholdt, S. (2006). Statistical mechanics of community detection. *Phys. Rev. E*, 74(1),  
591 16110. doi: 10.1103/PhysRevE.74.016110
- 592 Rezende, E. L., Albert, E. M., Fortuna, M. A., & Bascompte, J. (2009). Compartments in a marine food  
593 web associated with phylogeny, body mass, and habitat structure. *Ecology Letters*, 12(8), 779–788. doi:  
594 10.1111/j.1461-0248.2009.01327.x
- 595 Rohr, R. P., Saavedra, S., & Bascompte, J. (2014). On the structural stability of mutualistic systems.  
596 *Science*, 345(6195), 1253497. doi: 10.1126/science.1253497
- 597 Scholz, F. W., & Stephens, M. A. (1987). K-Sample Anderson–Darling Tests. *Journal of the American  
598 Statistical Association*, 82(399), 918–924. doi: 10.1080/01621459.1987.10478517
- 599 Solé, R. V., & Montoya, M. (2001). Complexity and fragility in ecological networks. *Proceedings of the  
600 Royal Society of London. Series B: Biological Sciences*, 268(1480), 2039 LP–2045. Retrieved from <http://rspb.royalsocietypublishing.org/content/268/1480/2039.abstract>
- 601
- 602 Stouffer, D. B., & Bascompte, J. (2010). Understanding food-web persistence from local to global scales.  
603 *Ecology Letters*, 13(2), 154–161. doi: 10.1111/j.1461-0248.2009.01407.x
- 604 Stouffer, D. B., & Bascompte, J. (2011). Compartmentalization increases food-web persistence. *Pro-  
605 ceedings of the National Academy of Sciences of the United States of America*, 108(9), 3648–3652. doi:  
606 10.1073/pnas.1014353108
- 607 Stouffer, D. B., Camacho, J., Jiang, W., & Nunes Amaral, L. A. (2007). Evidence for the existence of a robust  
608 pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences*, 274(1621),  
609 1931 LP–1940. Retrieved from <http://rspb.royalsocietypublishing.org/content/274/1621/1931.abstract>
- 610 Thebault, E., & Fontaine, C. (2010). Stability of Ecological Communities and the Architecture of Mutualistic  
611 and Trophic Networks. *Science*, 329(5993), 853–856. doi: 10.1126/science.1188321
- 612 Valdivia, N., Díaz, M. J., Garrido, I., & Gómez, I. (2015). Consistent richness-biomass relationship across  
613 environmental gradients in a marine macroalgal-dominated subtidal community on the western antarctic  
614 peninsula. *PLoS ONE*, 10(9), 1–20. doi: 10.1371/journal.pone.0138582

- 615 Valverde, S., Piñero, J., Corominas-Murtra, B., Montoya, J., Joppa, L., & Solé, R. (2018). The architecture  
616 of mutualistic networks as an evolutionary spandrel. *Nature Ecology & Evolution*, 2(1), 94–99. doi:  
617 10.1038/s41559-017-0383-4
- 618 Ward, C. L., & McCann, K. S. (2017). A mechanistic theory for aquatic food chain length. *Nature Communications*, 8(1), 2028. doi: 10.1038/s41467-017-02157-0
- 620 Watts, D. J., & Strogatz, S. H. (1998). Collective dynamics of 'small-world' networks. *Nature*, 393, 440–442.
- 621 Williams, R. J., Berlow, E. L., Dunne, J. A., Barabási, A.-L., & Martinez, N. D. (2002). Two degrees of  
622 separation in complex food webs. *Proceedings of the National Academy of Sciences*, 99(20), 12913–12916.  
623 doi: 10.1073/pnas.192448799
- 624 Wölfel, A.-C., Lim, C. H., Hass, H. C., Lindhorst, S., Tosonotto, G., Lettmann, K. A., ... Abele, D. (2014).  
625 Distribution and characteristics of marine habitats in a subpolar bay based on hydroacoustics and bed shear  
626 stress estimates—Potter Cove, King George Island, Antarctica. *Geo-Marine Letters*, 34(5), 435–446. doi:  
627 10.1007/s00367-014-0375-1
- 628 Young, H. S., McCauley, D. J., Dunbar, R. B., Hutson, M. S., Ter-Kuile, A. M., & Dirzo, R. (2013). The  
629 roles of productivity and ecosystem size in determining food chain length in tropical terrestrial ecosystems.  
630 *Ecology*, 94(3), 692–701. doi: 10.1890/12-0729.1