

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

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¹⁶ **Running title:** The metaweb influence on local food webs.

17 **Abstract**

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

46 Introduction

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

61 Metacommunity theory provides a framework for assessing the roles of local- and regional-scale processes
62 on network structure (Baiser, Buckley, Gotelli, & Ellison, 2013; M A Leibold et al., 2004). This approach
63 has been applied historically to competitive interactions, whereas trophic interactions have received less
64 attention (Baiser, Elhesha, & Kahveci, 2016). Recently, there has been an increase in food web assembly
65 studies, integrating them with island biogeography (Galiana et al., 2018; Gravel, Massol, Canard, Mouillot,
66 & Mouquet, 2011), metacommunity dynamics (Liao, Chen, Ying, Hiebeler, & Nijs, 2016; Pillai, Gonzalez,
67 & Loreau, 2011) and the effects of habitat fragmentation (Mougi & Kondoh, 2016). Previous attempts to
68 study the food web assembly process have used motifs as building blocks of local communities (Baiser et al.,
69 2016). Motifs are network sub-structures composed of species and links whose frequency deviates from the
70 random expectation (Milo et al., 2002). By comparing motif representation at different spatial scales—from
71 local to regional—the process of assembly of interactions may be revealed (Baiser et al., 2016), e.g. if the
72 same processes structure the food web across scales, motif representation should be the same.

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

77 networks to global threats like climate change and biological invasions. One of these properties is small-
78 worldness, associated with rapid responses to disturbances and resistance to secondary extinctions (J. M.
79 Montoya & Solé, 2002). The small-world pattern is related to two global properties: the average of the
80 shortest distance between all species, called characteristic path length, and the clustering coefficient, the
81 probability that two species linked to the same species are linked. Then, the small-world pattern implies a
82 short average path length and a high level of clustering compared to random networks (Watts & Strogatz,
83 1998). This pattern comes from the general network theory, beyond ecological networks, and has been
84 recently applied to marine food webs (Bornatowski, Barreto, Navia, & de Amorim, 2017; Gray et al., 2016;
85 Tomás Ignacio Marina et al., 2018; A. F. Navia, Cruz-Escalona, Giraldo, & Barausse, 2016).

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

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

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

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

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

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

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

¹⁴¹ food webs. In addition, we expect a change in the frequency of topological roles since habitat filtering or
¹⁴² dispersal limitation may modify them at the local food web scale. These changes should be also reflected as
¹⁴³ differences from the metaweb assembly model. On the other hand, if the assembly model also produces webs
¹⁴⁴ with stability-enhancing structural attributes, then that indicates that these structures may be spandrels of
¹⁴⁵ the metaweb rather than a consequence of some dynamical constraint acting on the local web.

¹⁴⁶ Methods

¹⁴⁷ The three datasets used in this study encompass a wide range of spatial scales and were collected inde-
¹⁴⁸ pendently. The Southern Ocean database compiled by Raymond et al. (2011) was used to construct the
¹⁴⁹ Antarctic metaweb selecting only species located at latitudes higher than 60°S. Raymond et al. (2011)
¹⁵⁰ compiled information from direct sampling methods of dietary assessment, including gut, scat, and bolus
¹⁵¹ content analysis, stomach flushing, and observed feeding. We considered that the metaweb is the regional
¹⁵² pool of species defined by the biogeographic Antarctic region. Next we analysed two local food webs: the
¹⁵³ Weddell Sea food web dataset includes species situated between 74°S and 78°S with a West-East extension of
¹⁵⁴ approximately 450 km, and comprises all information about trophic interactions available for the zone since
¹⁵⁵ 1983 (Jacob et al., 2011). The Potter Cove dataset comes from a 4 km long and 2.5 km wide Antarctic fjord
¹⁵⁶ located at 62°14'S, 58°40'W, South Shetland Islands (Tomás I Marina et al., 2018). These food web datasets
¹⁵⁷ comprise benthic and pelagic habitats of the Antarctic ecosystem, few aggregated low-trophic level groups
¹⁵⁸ (e.g. detritus, diatoms, phytoplankton, zooplankton) and a high resolution of the macroalgae community
¹⁵⁹ (i.e. 24 biological species of red, brown and green macroalgae). The macroalgae community is responsible for
¹⁶⁰ the majority of the primary production and supports a large fraction of secondary production in Antarctic
¹⁶¹ fjords (M. L. Quartino & Boraso de Zaixso, 2008, Valdivia, Díaz, Garrido, & Gómez (2015)). Higher trophic
¹⁶² levels comprise: invertebrate (e.g. ascidians, sponges, isopods, amphipods, bivalves, gastropods, cephalopods,
¹⁶³ echinoderms) and vertebrate predator groups (e.g. demersal and pelagic fishes, penguins, seals and whales).
¹⁶⁴ For more information about these datasets refer to the original publications. To make datasets compatible,
¹⁶⁵ we first checked taxonomic names for synonyms, and second, we added species (either prey or predator)
¹⁶⁶ with their interactions to the metaweb when the local food webs contain a greater taxonomic resolution.
¹⁶⁷ This resulted in the addition of 258 species to the metaweb, which represent 33% of the total. We removed
¹⁶⁸ cannibalistic (self-links) and double arrows (i.d. A eats B and B eats A).

¹⁶⁹ We analysed the structure of the networks using properties that focus on different levels: emergent or global
¹⁷⁰ properties that take into account the whole network, sub-structural properties that consider several nodes,

171 and properties related to one node. To describe food webs as networks each species is represented as a
172 node or vertex and the trophic interactions are represented as edges or links between nodes. These links are
173 directed, from the prey to the predator, as the flow of energy and matter. Two nodes are neighbours if they
174 are connected by an edge and the degree k_i of node i is the number of neighbours it has. The food web can
175 be represented by an adjacency matrix $A = (a_{ij})$ where $a_{ij} = 1$ if species j predaes on species i , else is 0.
176 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
177 predators of i or its out-degree. The total number of edges is $E = \sum_{ij} a_{ij}$.

178 **Models**

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

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

192 To consider network assembly mechanisms we used a metaweb assembly model (Figure 1), called the trophic
193 theory of island biogeography (Gravel et al., 2011). In this model species migrate from the metaweb to a local
194 web with a uniform probability c , and become extinct from the local web with probability e ; a reminiscence of
195 the theory of island biogeography (MacArthur & Wilson, 1967), but with the addition of network structure.
196 Species migrate with their potential network links from the metaweb, then in the local web species can only
197 survive if at least one of its preys is present, or if it is a basal species. When a species goes extinct locally it
198 may produce secondary extinctions; we check that the local predators maintain at least one prey if not they
199 become extinct independent of the probability e . We simulated this model in time and it eventually reaches
200 an equilibrium that depends on the migration and extinction probabilities but also on the structure of the

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

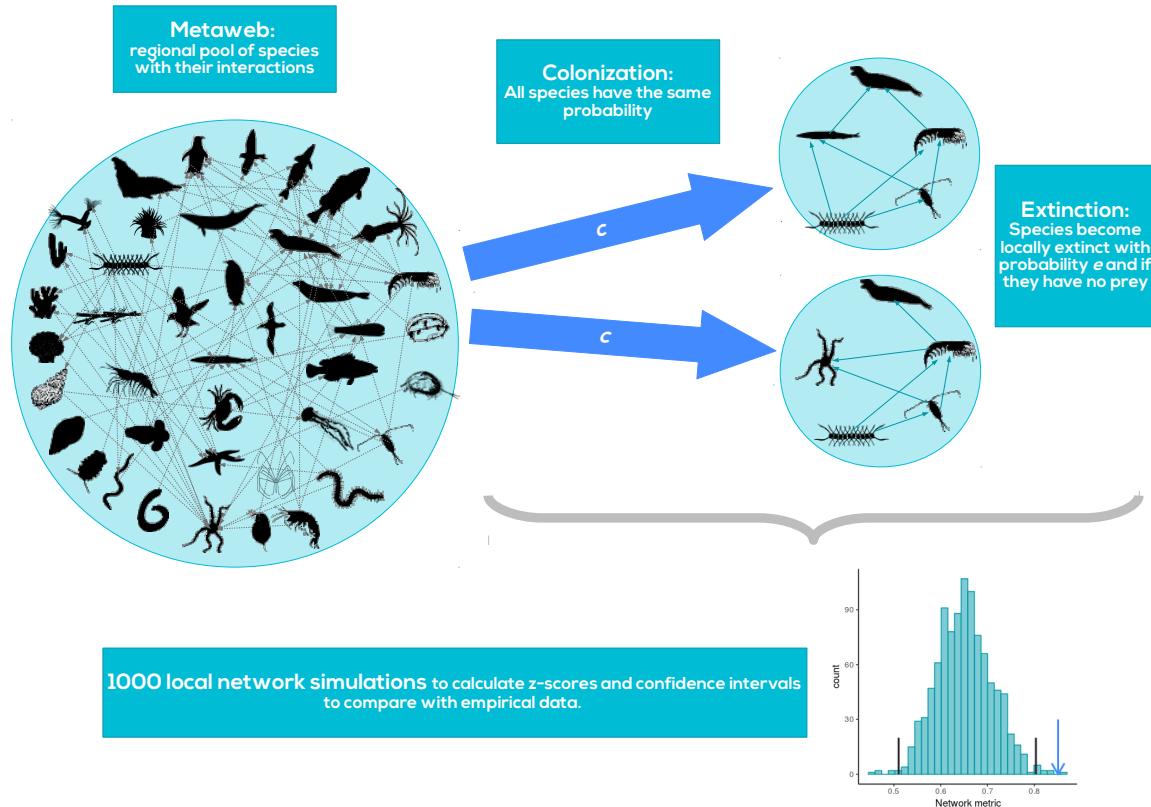


Figure 1: Schematic diagram of the metaweb assembly model: species migrate from the metaweb with a probability c to a local network carrying their potential links to preys; here they have a probability of extinction e . Additionally, predators become extinct if their preys are locally extinct. We simulate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

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

208 **Global network properties**

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

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

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

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

220 and

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

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

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

224 and to determine if S is statistically significant Monte Carlo methods were used (Crowley, 1992). We built
 225 1000 null model networks with the same number of nodes n and edges m than the empirical network; then
 226 we calculated S for each random network and the lower and higher 99% quantiles of the S distribution are

227 called ql, qh :

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

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

231 The second global property was trophic coherence (Johnson et al., 2014), that is related to stability in the
232 sense that small perturbations could get amplified or vanished, which is called local linear stability (May,
233 1972; Rohr et al., 2014). We first needed to estimate the trophic level of a node i , defined as the average
234 trophic level of its preys plus 1. That is:

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

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

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

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

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

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

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

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

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

260 where s is the number of modules or compartments, I_s is the number of links between species in the module
261 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
262 assess the significance of our networks we calculate the 99% confidence intervals and z-scores based on 1000
263 null model networks as previously described.

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

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

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

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

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

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

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

280 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
281 in module s . Due to the stochastic nature of the module detection algorithm we made repeated runs of the
282 algorithm until there were no statistical differences between the distributions of PC_i and dz_i in successive
283 repetitions; to test such statistical difference we used the k-sample Anderson-Darling test (Scholz & Stephens,
284 1987). Then we calculated the mean and 95% confidence interval of dz and PC .

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

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

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

303 Results

304 Global network properties

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

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

Network	Potter Cove	Weddell Sea	Metaweb
Size	91	437	859
Links	309	1908	9003
Area (Km ²)	6.8	3.5e6	34.8e6
Connectance	0.037	0.010	0.012
PathLength	1.81	2.20	2.57
Clustering	0.10	0.048	0.22

Network	Potter Cove	Weddell Sea	Metaweb
Small-World-ness random	2.75*	4.69*	10.87*
Trophic coherence	0.53	0.45	0.70
Trophic coherence random	-0.54*	-2.08*	-3.54*
z-score			
Mean Trophic level	2.13	1.98	1.91
Trophic level random z-score	-0.27*	-0.86*	-1.60*
Modularity	0.37	0.48	0.45
Modularity random z-score	0.89	18.97*	85.75*

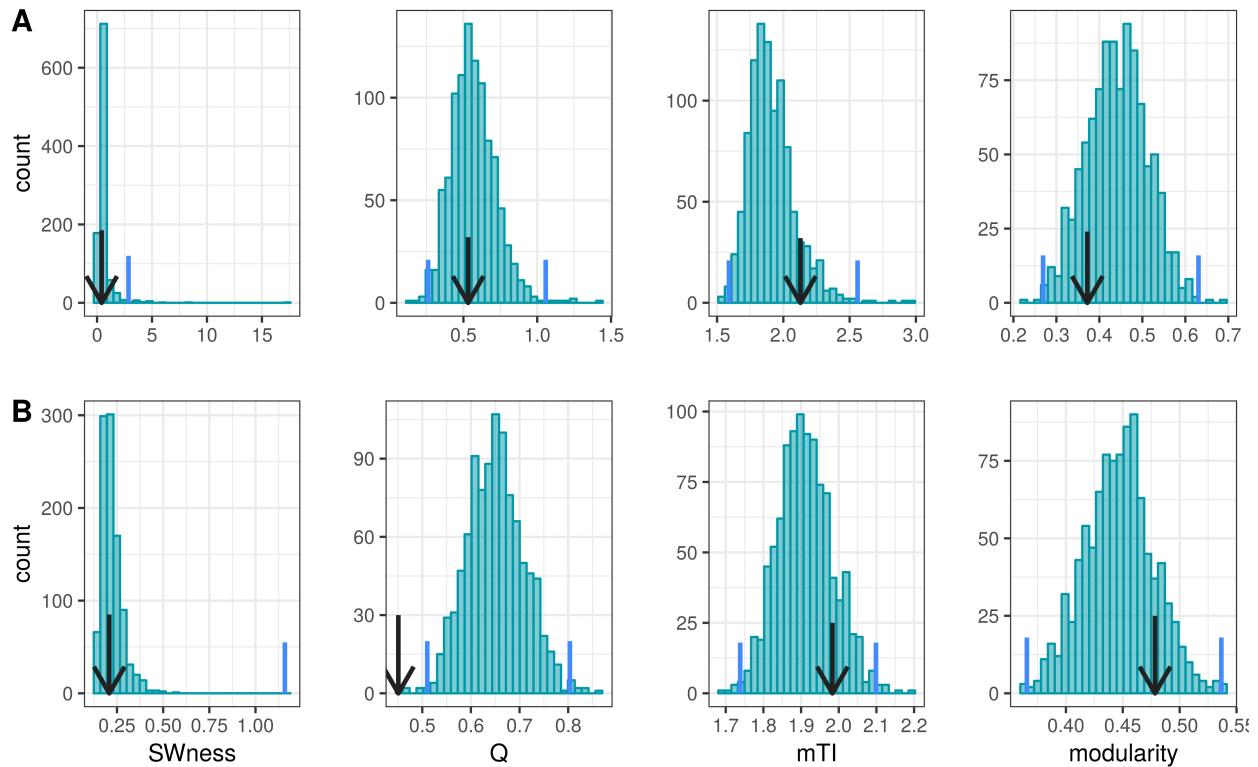


Figure 2: Network global properties compared with the metaweb assembly model for A) Potter Cove and B) Weddell Sea food webs. The properties were: Small-world-ness (SWness), coherence (Q), mean trophic level (mTl) and modularity. We ran 1000 simulations of local networks fitted to Potter Cove and Weddell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

317 Sub-structural properties (motifs)

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

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

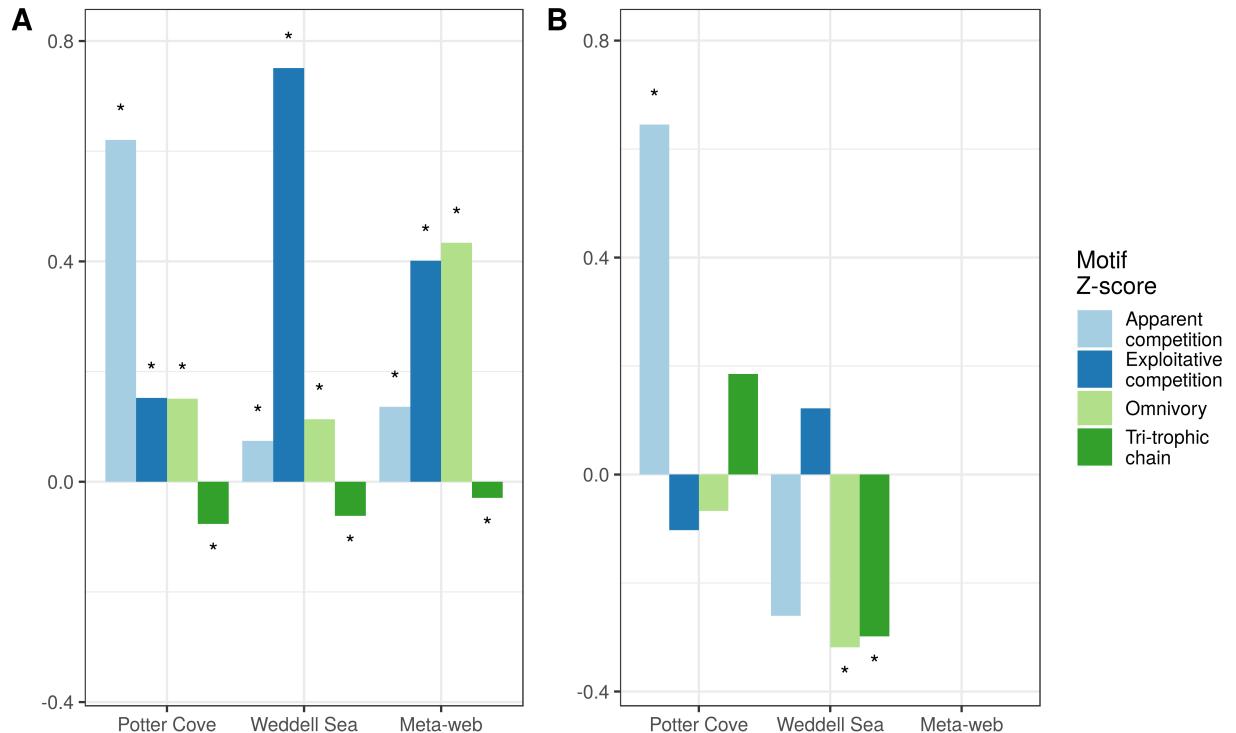


Figure 3: Network motifs z-scores across scales. Motifs are three-node sub-networks counted on each of the networks.: the *Metaweb* represents the marine predator-prey relationships of Antarctica; the *Weddell Sea* and *Potter Cove* are local food webs. A. Z-scores estimated with the random null model.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

328 Node-level properties (Topological roles)

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

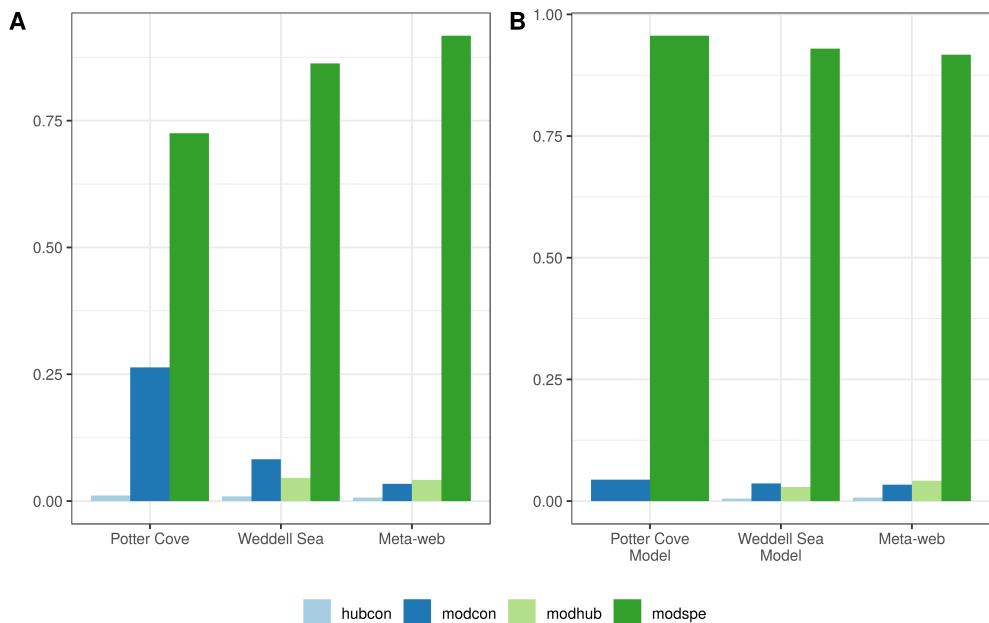


Figure 4: Proportion of topological roles across scales., the *Metaweb* represents the marine predator-prey relationships of Antarctica; the *Weddell Sea* and *Potter Cove* are local food webs. The topological roles are: *Hub connectors*, high number of between-module links; *Module connectors*, low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

³³⁴ = 5.95, p-value = 0.41)(Figura 3 B).

³³⁵ The plot of topological roles combined with trophic levels and modularity revealed important details of
³³⁶ the food webs (Figure 5): the metaweb presents densely connected compartments but some of them have
³³⁷ few low-connected species (module connectors or module specialists). Additionally, we observed in the
³³⁸ Weddell Sea food web hub connectors with a basal trophic level (Table S5). These are aggregated nodes that
³³⁹ represent generic prey, e.g. fish or zooplankton, they only have incoming links or predators and they cannot
³⁴⁰ have outgoing links or prey because they comprise several species. Different fish species are present in the
³⁴¹ Weddell Sea food web with detailed information about prey and predators, but for some predators there is
³⁴² insufficient knowledge of its prey and aggregated nodes must be added. Thus the existence of these basal
³⁴³ hub connectors is a spurious result of aggregating prey species. The other non-aggregated hub connectors
³⁴⁴ are highly mobile species with an intermediate trophic level like krill (Table S5). The variation of maximum
³⁴⁵ trophic levels is evidenced in Figure 5, where both Potter Cove and Metaweb networks have similar values
³⁴⁶ and Weddell Sea food web exhibit a lower maximum trophic level.

³⁴⁷ Discussion

³⁴⁸ By definition, the metaweb structure should reflect the evolutionary constraints of the species interactions,
³⁴⁹ and the local networks should be influenced and determined by the assembly processes and the local en-
³⁵⁰ vironment. Our results showed that the structure of the metaweb does not differ from local food webs in
³⁵¹ many properties as the spatial scale changes. We did not find a clear pattern in the properties expected to
³⁵² be maximized by dynamical assembly and local stability (modularity, coherence, motifs), though we found
³⁵³ clear differences in the properties influenced by habitat filtering and dispersal limitation (motif, topological
³⁵⁴ roles). These suggest that food webs would be mainly shaped by evolutionary forces and local environment
³⁵⁵ drivers and less constrained by dynamical and assembly processes.

³⁵⁶ Global level network properties showed a similar pattern across scales; most of them were significantly
³⁵⁷ different from the random null model but not from the assembly model. Modularity for Potter Cove food
³⁵⁸ web was the only property that is similar to the random model. The existence of a modular structure could
³⁵⁹ be related to different habitats (Krause et al., 2003; Rezende et al., 2009) —in marine environments, these
³⁶⁰ could be benthic with different depths and pelagic with different extensions. Even though Potter Cove has
³⁶¹ a small extent (6.8 Km²) studies suggest there exist different habitats (Wölfel et al., 2014), then the lack of
³⁶² significant modularity compared to random and to the assembly model could be a sampling effect. Recent
³⁶³ studies suggest that modularity enhances local stability and this effect is stronger the more complex the

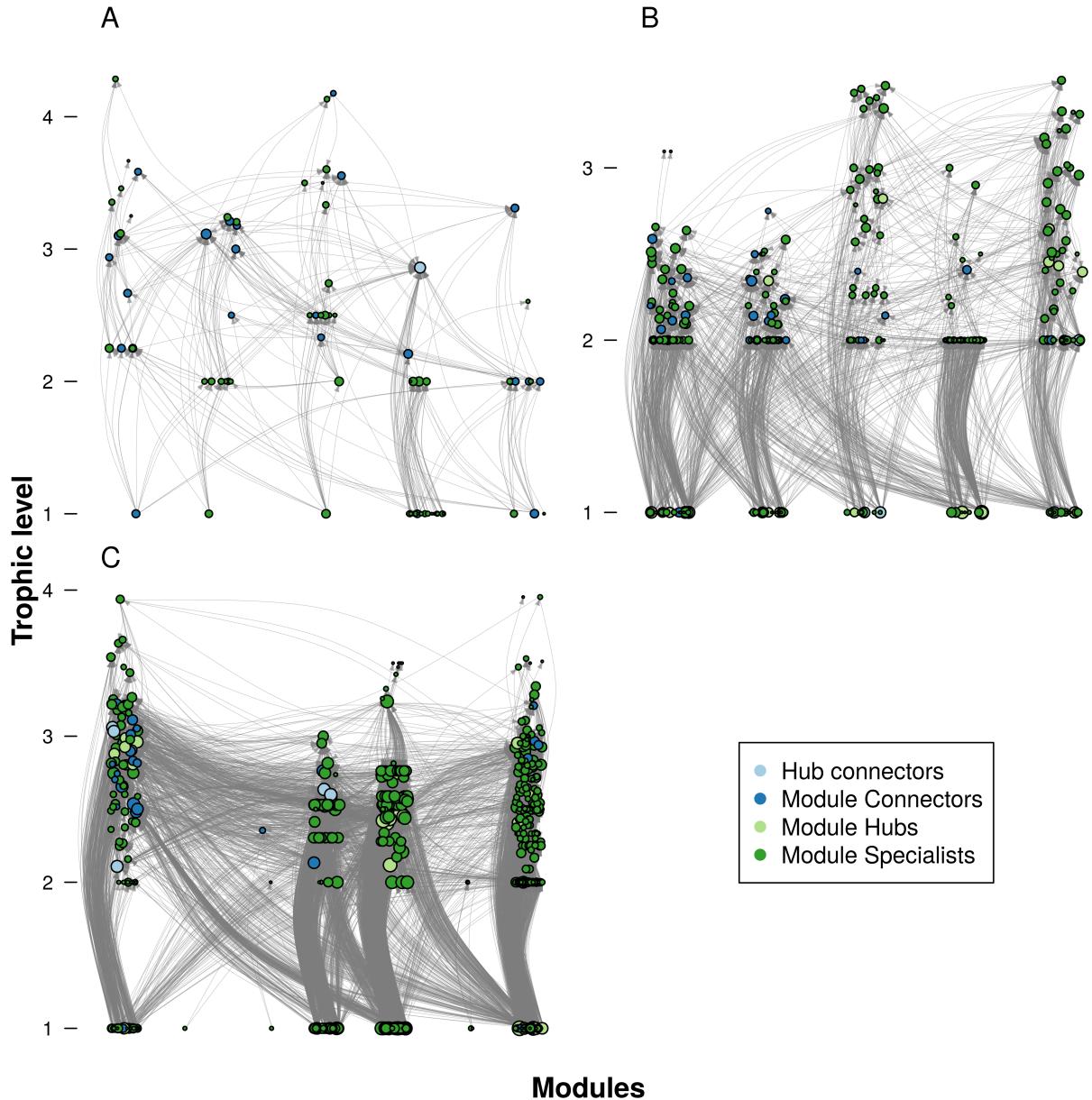


Figure 5: Plot of topological roles combined with trophic levels and modularity for each food web (A) Potter Cove, (B) Weddell Sea (C) the Metaweb. The topological roles are: *Hub connectors* have a high number of between module links, *Module connectors* have a low number of links mostly between modules,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

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

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

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

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

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

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

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

420 The spatial scales involved in our study do not represent a continuity; the metaweb and the Weddell sea
421 web have a 10 to 1 ratio but the local web is 10^6 smaller, besides that most of the global network properties
422 and the motif structure showed no changes relative to the null model. We did not find evidence that the
423 structure of the food web was strongly influenced by dynamical constraints. Instead, we hypothesise that
424 other local processes, that limit which species from the metaweb can colonise the local web, are influencing
425 the assembly process. Although our results are limited to Antarctic marine food webs, our findings suggest
426 that future studies about food webs should give more attention to evolutionary and assembly processes, and
427 less emphasis to local dynamics. This kind of analysis needs to be expanded to different regions and other

428 kinds of habitats (e.g. terrestrial, freshwater, etc.) to confirm if this is a general pattern or not.

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433 References

- 434 Allesina, S., Grilli, J., Barabás, G., Tang, S., Aljadeff, J., & Maritan, A. (2015). Predicting the stability of
435 large structured food webs. *Nature Communications*, 6, 7842. doi: 10.1038/ncomms8842
- 436 Araújo, M. B., & Rozenfeld, A. (2014). The geographic scaling of biotic interactions. *Ecography*, 37(5),
437 406–415. doi: 10.1111/j.1600-0587.2013.00643.x
- 438 Baiser, B., Buckley, H. L., Gotelli, N. J., & Ellison, A. M. (2013). Predicting food-web structure with
439 metacommunity models. *Oikos*, 122(4), 492–506. doi: 10.1111/j.1600-0706.2012.00005.x
- 440 Baiser, B., Elhesha, R., & Kahveci, T. (2016). Motifs in the assembly of food web networks. *Oikos*, 125(4),
441 480–491. doi: 10.1111/oik.02532
- 442 Bornatowski, H., Barreto, R., Navia, A. F., & de Amorim, A. F. (2017). Topological redundancy and “small-
443 world” patterns in a food web in a subtropical ecosystem of Brazil. *Marine Ecology*, 38(2), e12407. doi:
444 10.1111/maec.12407
- 445 Borrelli, J. J. (2015). Selection against instability: Stable subgraphs are most frequent in empirical food
446 webs. *Oikos*, 124(12), 1583–1588. doi: 10.1111/oik.02176
- 447 Borrelli, J. J., & Ginzburg, L. R. (2014). Why there are so few trophic levels: Selection against instability
448 explains the pattern. *Food Webs*, 1(1), 10–17. doi: <https://doi.org/10.1016/j.fooweb.2014.11.002>
- 449 Borrelli, J. J., Allesina, S., Amarasekare, P., Arditi, R., Chase, I., Damuth, J., ... Ginzburg, L. R. (2015).
450 Selection on stability across ecological scales. *Trends in Ecology & Evolution*, 30(7), 417–425. doi:
451 10.1016/j.tree.2015.05.001
- 452 Borthagaray, A. I., Arim, M., & Marquet, P. A. (2014). Inferring species roles in metacommunity structure
453 from species co-occurrence networks. *Proceedings of the Royal Society B: Biological Sciences*, 281(1792).

- 454 Retrieved from <http://rspb.royalsocietypublishing.org/content/281/1792/20141425.abstract>
- 455 Carstensen, D. W., Lessard, J.-P., Holt, B. G., Krabbe Borregaard, M., & Rahbek, C. (2013). Introducing
456 the biogeographic species pool. *Ecography*, 36(12), 1310–1318. doi: 10.1111/j.1600-0587.2013.00329.x
- 457 Cohen, J. E., & Newman, C. M. (1985). When will a large complex system be stable? *Journal of Theoretical
458 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)
- 459 Cohen, J. E., Schittler, D. N., Raffaelli, D. G., & Reuman, D. C. (2009). Food webs are more than the
460 sum of their tritrophic parts. *Proceedings of the National Academy of Sciences*, 106(52), 22335 LP–22340.
- 461 Retrieved from <https://doi.org/10.1073/pnas.0910582106>
- 462 Crowley, P. H. (1992). Resampling methods for computation-intensive data analysis in ecology and evolution.
463 *Annual Review of Ecology and Systematics*, 23, 405–447.
- 464 Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal,
465 Complex Sy*, 1695. Retrieved from <http://igraph.org>
- 466 de Bello, F. (2012). The quest for trait convergence and divergence in community assembly: Are null-models
467 the magic wand? *Global Ecology and Biogeography*, 21(3), 312–317. doi: 10.1111/j.1466-8238.2011.00682.x
- 468 Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Food-web structure and network theory: The
469 role of connectance and size. *Proceedings of the National Academy of Sciences*, 99(20), 12917–12922. doi:
470 [10.1073/pnas.192407699](https://doi.org/10.1073/pnas.192407699)
- 471 Erdős, P., & Rényi, A. (1959). On random graphs. *Publicationes Mathematicae Debrecen*, 6, 290–297.
- 472 Fortuna, M. A., Stouffer, D. B., Olesen, J. M., Jordano, P., Mouillot, D., Krasnov, B. R., ... Bascompte, J.
473 (2010). Nestedness versus modularity in ecological networks: Two sides of the same coin? *Journal of Animal
474 Ecology*, 79(4), 811–817. doi: 10.1111/j.1365-2656.2010.01688.x
- 475 Galiana, N., Lurgi, M., Claramunt-López, B., Fortin, M.-J., Leroux, S., Cazelles, K., ... Montoya, J. M.
476 (2018). The spatial scaling of species interaction networks. *Nature Ecology & Evolution*, 2(5), 782–790. doi:
477 [10.1038/s41559-018-0517-3](https://doi.org/10.1038/s41559-018-0517-3)
- 478 Gilarranz, L. J., Rayfield, B., Liñán-Cembrano, G., Bascompte, J., & Gonzalez, A. (2017). Effects of network
479 modularity on the spread of perturbation impact in experimental metapopulations. *Science*, 357(6347), 199
480 LP–201. Retrieved from <http://science.sciencemag.org/content/357/6347/199.abstract>
- 481 Gravel, D., Massol, F., Canard, E., Mouillot, D., & Mouquet, N. (2011). Trophic theory of island biogeog-

- raphy. *Ecology Letters*, 14(10), 1010–1016. doi: 10.1111/j.1461-0248.2011.01667.x
- Gray, C., Hildrew, A. G., Lu, X., Ma, A., McElroy, D., Monteith, D., ... Woodward, G. (2016). Chapter Ten – Recovery and Nonrecovery of Freshwater Food Webs from the Effects of Acidification. In A. J. Dumbrell, R. L. Kordas, & G. B. T. A. in E. R. Woodward (Eds.), *Large-Scale Ecology: Model Systems to Global Perspectives* (Vol. 55, pp. 475–534). doi: <https://doi.org/10.1016/bs.aecr.2016.08.009>
- Grilli, J., Adorisio, M., Suweis, S., Barabás, G., Banavar, J. R., Allesina, S., & Maritan, A. (2017). Feasibility and coexistence of large ecological communities. *Nature Communications*, 8, 14389. doi: 10.1038/ncomms14389
- Grilli, J., Rogers, T., & Allesina, S. (2016). Modularity and stability in ecological communities. *Nature Communications*, 7, 12031. Retrieved from <http://dx.doi.org/10.1038/ncomms12031>
- Guimerà, R., & Nunes Amaral, L. A. (2005). Functional cartography of complex metabolic networks. *Nature*, 433, 895–900. Retrieved from <http://dx.doi.org/10.1038/nature03288>
- Guimerà, R., Stouffer, D. B., Sales-Pardo, M., Leicht, E. A., Newman, M. E. J., & Amaral, L. A. N. (2010). Origin of compartmentalization in food webs. *Ecology*, 91(10), 2941–2951. doi: 10.1890/09-1175.1
- Hanski, I. (1999). *Metapopulation Ecology*. Retrieved from https://books.google.com.ar/books?id=jsk4Nt_8X8sC
- HilleRisLambers, J., Adler, P. B., Harpole, W. S., Levine, J. M., & Mayfield, M. M. (2012). Rethinking Community Assembly through the Lens of Coexistence Theory. *Annual Review of Ecology, Evolution, and Systematics*, 43(1), 227–248. doi: 10.1146/annurev-ecolsys-110411-160411
- Humphries, M. D., & Gurney, K. (2008). Network “Small-World-Ness”: A Quantitative Method for Determining Canonical Network Equivalence. *PLOS ONE*, 3(4), e0002051. Retrieved from <https://doi.org/10.1371/journal.pone.0002051>
- Jacob, U., Thierry, A., Brose, U., Arntz, W. E., Berg, S., Brey, T., ... Mollmann, C. (2011). The role of body size in complex food webs: A cold case. In A. B. B. T. A. in E. Research (Ed.), *Advances In Ecological Research* (Vol. 45, pp. 181–223). doi: <http://dx.doi.org/10.1016/B978-0-12-386475-8.00005-8>
- Johnson, S., & Jones, N. S. (2017). Looplessness in networks is linked to trophic coherence. *Proceedings of the National Academy of Sciences*, 114(22), 5618–5623. doi: 10.1073/pnas.1613786114
- Johnson, S., Domínguez-García, V., Donetti, L., & Muñoz, M. A. (2014). Trophic coherence determines food-web stability. *Proceedings of the National Academy of Sciences*, 111(50), 17923–17928. doi:

- 511 10.1073/pnas.1409077111
- 512 Kones, J. K., Soetaert, K., van Oevelen, D., & Owino, J. (2009). Are network indices robust indi-
513 cators of food web functioning? A Monte Carlo approach. *Ecological Modelling*, 220, 370–382. doi:
514 <http://dx.doi.org/10.1016/j.ecolmodel.2008.10.012>
- 515 Kortsch, S., Primicerio, R., Aschan, M., Lind, S., Dolgov, A. V., & Planque, B. (2018). Food-web
516 structure varies along environmental gradients in a high-latitude marine ecosystem. *Ecography*. doi:
517 10.1111/ecog.03443
- 518 Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V., & Aschan, M. (2015). Climate change alters the
519 structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proceedings of the Royal
520 Society B: Biological Sciences*, 282(1814). Retrieved from <http://rspb.royalsocietypublishing.org/content/282/1814/20151546.abstract>
- 522 Krause, A. E., Frank, K. A., Mason, D. M., Ulanowicz, R. E., & Taylor, W. W. (2003). Compartments
523 revealed in food-web structure. *Nature*, 426, 282. Retrieved from <http://dx.doi.org/10.1038/nature02115>
- 524 Landi, P., Minoarivelo, H. O., Brännström, Å., Hui, C., & Dieckmann, U. (2018). Complexity and stability
525 of ecological networks: A review of the theory. *Population Ecology*, 60(4), 319–345. doi: 10.1007/s10144-
526 018-0628-3
- 527 Leibold, M. A., Chase, J. M., & Ernest, S. K. M. (2017). Community assembly and the functioning of
528 ecosystems: How metacommunity processes alter ecosystems attributes. *Ecology*, 98(4), 909–919. doi:
529 10.1002/ecy.1697
- 530 Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., ... Gonzalez,
531 A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*,
532 7(7), 601–613. doi: 10.1111/j.1461-0248.2004.00608.x
- 533 Liao, J., Chen, J., Ying, Z., Hiebeler, D. E., & Nijs, I. (2016). An extended patch-dynamic framework for
534 food chains in fragmented landscapes. *Scientific Reports*, 6, 33100. Retrieved from <http://dx.doi.org/10.1038/srep33100>
- 536 MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton (New Jersey), USA.:
537 Princeton University Press.
- 538 Marina, T. I., Salinas, V., Cordone, G., Campana, G., Moreira, E., Deregbibus, D., ... Momo, F. R. (2018).
539 The Food Web of Potter Cove (Antarctica): Complexity, structure and function. *Estuarine, Coastal and*

- 540 *Shelf Science*, 200, 141–151. doi: 10.1016/j.ecss.2017.10.015
- 541 Marina, T. I., Saravia, L. A., Cordone, G., Salinas, V., Doyle, S. R., & Momo, F. R. (2018). Architecture of marine food webs: To be or not be a “small-world”. *PLoS ONE*, 13(5), 1–13. doi: 10.1371/journal.pone.0198217
- 544 May, R. M. (1972). Will a Large Complex System be Stable? *Nature*, 238(5364), 413–414. doi:
545 10.1038/238413a0
- 546 McCann, K. S. (2000). The diversity–Stability debate. *Nature*, 405(6783), 228–233. doi: 10.1038/35012234
- 547 Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., & Alon, U. (2002). Network Motifs:
548 Simple Building Blocks of Complex Networks. *Science*, 298(5594), 824 LP–827. Retrieved from <http://science.sciencemag.org/content/298/5594/824.abstract>
- 550 Monteiro, A. B., & Faria, L. D. B. (2016). The interplay between population stability and food-web topology
551 predicts the occurrence of motifs in complex food-webs. *Journal of Theoretical Biology*, 409, 165–171. doi:
552 <https://doi.org/10.1016/j.jtbi.2016.09.006>
- 553 Montoya, J. M., & Solé, R. V. (2002). Small world patterns in food webs. *Journal of Theoretical Biology*,
554 214(3), 405–412. doi: 10.1006/jtbi.2001.2460
- 555 Mougi, A., & Kondoh, M. (2016). Food-web complexity, meta-community complexity and community sta-
556 bility. *Scientific Reports*, 6, 24478. doi: 10.1038/srep24478
- 557 Navia, A. F., Cruz-Escalona, V. H., Giraldo, A., & Barausse, A. (2016). The structure of a marine tropical
558 food web, and its implications for ecosystem-based fisheries management. *Ecological Modelling*, 328, 23–33.
559 doi: <https://doi.org/10.1016/j.ecolmodel.2016.02.009>
- 560 Neutel, A.-M., Heesterbeek, J. A. P., van de Koppel, J., Hoenderboom, G., Vos, A., Kaldeway, C., ... de
561 Ruiter, P. C. (2007). Reconciling complexity with stability in naturally assembling food webs. *Nature*, 449,
562 599. Retrieved from <https://doi.org/10.1038/nature06154>
- 563 Newman, M. E. J., & Girvan, M. (2004). Finding and evaluating community structure in networks. *Phys.*
564 *Rev. E*, 69(2), 26113. doi: 10.1103/PhysRevE.69.026113
- 565 Paine, R. T. (1966). Food Web Complexity and Species Diversity. *The American Naturalist*, 100(910), 65–75.
566 doi: 10.1086/282400
- 567 Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., & Torres, F. (1998). Fishing Down Marine Food
568 Webs. *Science*, 279(5352), 860 LP–863. Retrieved from <http://science.sciencemag.org/content/279/5352/>

569 860.abstract

- 570 Pillai, P., Gonzalez, A., & Loreau, M. (2011). Metacommunity theory explains the emergence of
571 food web complexity. *Proceedings of the National Academy of Sciences*, 108(48), 19293–19298. doi:
572 10.1073/pnas.1106235108
- 573 Prill, R. J., Iglesias, P. A., & Levchenko, A. (2005). Dynamic Properties of Network Motifs Contribute
574 to Biological Network Organization. *PLOS Biology*, 3(11), e343. Retrieved from <https://doi.org/10.1371/journal.pbio.0030343>
- 576 Quartino, M. L., & Boraso de Zaixso, A. L. (2008). Summer macroalgal biomass in Potter Cove, South
577 Shetland Islands, Antarctica: Its production and flux to the ecosystem. *Polar Biology*, 31(3), 281–294. doi:
578 10.1007/s00300-007-0356-1
- 579 R Core Team. (2017). *R: A Language and Environment for Statistical Computing*. Retrieved from <http://www.r-project.org/>
- 581 Raymond, B., Marshall, M., Nevitt, G., Gillies, C. L., van den Hoff, J., Stark, J. S., ... Constable, A. J.
582 (2011). A Southern Ocean dietary database. *Ecology*, 92(5), 1188. doi: 10.1890/10-1907.1
- 583 Reichardt, J., & Bornholdt, S. (2006). Statistical mechanics of community detection. *Phys. Rev. E*, 74(1),
584 16110. doi: 10.1103/PhysRevE.74.016110
- 585 Rezende, E. L., Albert, E. M., Fortuna, M. A., & Bascompte, J. (2009). Compartments in a marine food
586 web associated with phylogeny, body mass, and habitat structure. *Ecology Letters*, 12(8), 779–788. doi:
587 10.1111/j.1461-0248.2009.01327.x
- 588 Rohr, R. P., Saavedra, S., & Bascompte, J. (2014). On the structural stability of mutualistic systems.
589 *Science*, 345(6195), 1253497. doi: 10.1126/science.1253497
- 590 Scholz, F. W., & Stephens, M. A. (1987). K-Sample Anderson–Darling Tests. *Journal of the American
591 Statistical Association*, 82(399), 918–924. doi: 10.1080/01621459.1987.10478517
- 592 Solé, R. V., & Montoya, M. (2001). Complexity and fragility in ecological networks. *Proceedings of the
593 Royal Society of London. Series B: Biological Sciences*, 268(1480), 2039 LP–2045. Retrieved from <http://rspb.royalsocietypublishing.org/content/268/1480/2039.abstract>
- 595 Stouffer, D. B., & Bascompte, J. (2010). Understanding food-web persistence from local to global scales.
596 *Ecology Letters*, 13(2), 154–161. doi: 10.1111/j.1461-0248.2009.01407.x
- 597 Stouffer, D. B., & Bascompte, J. (2011). Compartmentalization increases food-web persistence. *Pro-*

- 598 *ceedings of the National Academy of Sciences of the United States of America*, 108(9), 3648–3652. doi:
599 10.1073/pnas.1014353108
- 600 Stouffer, D. B., Camacho, J., Jiang, W., & Nunes Amaral, L. A. (2007). Evidence for the existence of a robust
601 pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences*, 274(1621),
602 1931 LP–1940. Retrieved from <http://rspb.royalsocietypublishing.org/content/274/1621/1931.abstract>
- 603 Thebault, E., & Fontaine, C. (2010). Stability of Ecological Communities and the Architecture of Mutualistic
604 and Trophic Networks. *Science*, 329(5993), 853–856. doi: 10.1126/science.1188321
- 605 Valdivia, N., Díaz, M. J., Garrido, I., & Gómez, I. (2015). Consistent richness-biomass relationship across
606 environmental gradients in a marine macroalgal-dominated subtidal community on the western antarctic
607 peninsula. *PLoS ONE*, 10(9), 1–20. doi: 10.1371/journal.pone.0138582
- 608 Ward, C. L., & McCann, K. S. (2017). A mechanistic theory for aquatic food chain length. *Nature Commu-*
609 *nications*, 8(1), 2028. doi: 10.1038/s41467-017-02157-0
- 610 Watts, D. J., & Strogatz, S. H. (1998). Collective dynamics of 'small-world' networks. *Nature*, 393, 440–442.
- 611 Williams, R. J., Berlow, E. L., Dunne, J. A., Barabási, A.-L., & Martinez, N. D. (2002). Two degrees of
612 separation in complex food webs. *Proceedings of the National Academy of Sciences*, 99(20), 12913–12916.
613 doi: 10.1073/pnas.192448799
- 614 Wölfli, A.-C., Lim, C. H., Hass, H. C., Lindhorst, S., Tosonotto, G., Lettmann, K. A., ... Abele, D. (2014).
615 Distribution and characteristics of marine habitats in a subpolar bay based on hydroacoustics and bed shear
616 stress estimates—Potter Cove, King George Island, Antarctica. *Geo-Marine Letters*, 34(5), 435–446. doi:
617 10.1007/s00367-014-0375-1
- 618 Young, H. S., McCauley, D. J., Dunbar, R. B., Hutson, M. S., Ter-Kuile, A. M., & Dirzo, R. (2013). The
619 roles of productivity and ecosystem size in determining food chain length in tropical terrestrial ecosystems.
620 *Ecology*, 94(3), 692–701. doi: 10.1890/12-0729.1