

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

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

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

14 **Abstract**

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

42 Introduction

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

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

67 Insight into food web assembly can be also gained by assessing the structure of ecological networks at different
68 levels: emergent or global properties that focus on averages over the entire network (e.g. modularity or
69 connectance) and local properties that focus on how one or a group of species are related to the whole.
70 Global properties related to resilience and stability are fundamental to understand the response of ecological
71 networks to global threats like climate change and biological invasions. One of these properties is small-
72 worldness, associated with rapid responses to disturbances and resistance to secondary extinctions (Montoya

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

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

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

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

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 et al.
107 2002). Besides this definition, in the ecological literature motif has been used as a synonym of sub-network.
108 We analyse here the three-species sub-networks that have been most studied theoretically and empirically
109 in food webs (Prill et al. 2005, Stouffer et al. 2007, Baiser et al. 2016). Specifically, we focused on four of
110 the thirteen possible three-species sub-networks: apparent competition, exploitative competition, tri-trophic
111 chain, and omnivory (Figure 1).

112 The frequency of motifs (i.e over-represented, under-represented or random) at different spatial scales may
113 reveal aspects about the process behind the assembly of interactions: if the same motif representation is
114 observed across scales, this suggests that the same process may be structuring the network (Baiser et al.
115 2016). Ecological interactions occur at the local scale so differences may show the importance of local
116 interactions in the assembly of the food web. During the assembly process those motif structures that
117 are less dynamically stable tend to disappear from the food web, which represents a system-level selective
118 force where the ecological interactions are shaped by dynamical constraints rather than Darwinian processes
119 (Borrelli 2015), this has been called non-adaptative systemic selection (Borrelli et al. 2015).

120 In this study, we measure the network-structural properties (above) in two real local webs: the Weddell
121 Sea food web, which represents 3.5 million km² (Jacob et al. 2011); and the Potter Cove network, which
122 represents 6.8 km² (Marina et al. 2018b). We compare the real webs to the Antarctic metaweb, built
123 from a dietary database (Raymond et al. 2011), representing an area of 34.8 million km². To provide a
124 baseline for comparison, we compare metrics of the real webs to: (1) random networks, representing an
125 absence of ecological mechanisms; and (2) webs obtained from an assembly model, representing an absence
126 of dynamical stability constraints while preserving species' trophic relationships. If real food web structure
127 reflects dynamical stability constraints, then we should expect to see the structural properties change from
128 the metaweb to the local scale. In particular, we expect global properties related to resilience and stability
129 (i.e. small-worldness, trophic coherence and modularity) to be close to the random model at the metaweb
130 scale, and significantly different at the local scale ; and a greater frequency of stable motifs in the local
131 food webs. In addition, we expect a change in the frequency of topological roles since habitat filtering or
132 dispersal limitation may modify them at the local food web scale. These changes should be also reflected as
133 differences from the metaweb assembly model. On the other hand, if the assembly model also produces webs
134 with stability-enhancing structural attributes, then that indicates that these structures may be spandrels of
135 the metaweb rather than a consequence of some dynamical constraint acting on the local web.

¹³⁶ **Methods**

¹³⁷ The three datasets used in this study encompass a wide range of spatial scales and were collected inde-
¹³⁸ pendently. The Southern Ocean database compiled by Raymond et al. (2011) was used to construct the
¹³⁹ Antarctic metaweb selecting only species located at latitudes higher than 60°S. Raymond et al. (2011)
¹⁴⁰ compiled information from direct sampling methods of dietary assessment, including gut, scat, and bolus
¹⁴¹ content analysis, stomach flushing, and observed feeding. We considered that the metaweb is the regional
¹⁴² pool of species defined by the biogeographic Antarctic region. Next we analysed two local food webs: the
¹⁴³ Weddell Sea food web dataset includes species situated between 74°S and 78°S with a West-East extension
¹⁴⁴ of approximately 450 km, and comprises all information about trophic interactions available for the zone
¹⁴⁵ since 1983 (Jacob et al. 2011). The Potter Cove dataset comes from a 4 km long and 2.5 km wide Antarctic
¹⁴⁶ fjord located at 62°14'S, 58°40'W, South Shetland Islands (Marina et al. 2018b). These food web datasets
¹⁴⁷ comprise benthic and pelagic habitats of the Antarctic ecosystem, few aggregated low-trophic level groups
¹⁴⁸ (e.g. detritus, diatoms, phytoplankton, zooplankton) and a high resolution of the macroalgae community
¹⁴⁹ (i.e. 24 biological species of red, brown and green macroalgae). The macroalgae community is responsible
¹⁵⁰ for the majority of the primary production and supports a large fraction of secondary production in Antarc-
¹⁵¹ tic fjords (Quartino and Boraso de Zaixso 2008, Valdivia et al. (2015)). Higher trophic levels comprise:
¹⁵² invertebrate (e.g. ascidians, sponges, isopods, amphipods, bivalves, gastropods, cephalopods, echinoderms)
¹⁵³ and vertebrate predator groups (e.g. demersal and pelagic fishes, penguins, seals and whales). For more
¹⁵⁴ information about these datasets refer to the original publications. To make datasets compatible, we first
¹⁵⁵ checked taxonomic names for synonyms, and second, we added species (either prey or predator) with their
¹⁵⁶ interactions to the metaweb when the local food webs contain a greater taxonomic resolution. This resulted
¹⁵⁷ in the addition of 258 species to the metaweb, which represent 33% of the total. We removed cannibalistic
¹⁵⁸ (self-links) and double arrows (i.d. A eats B and B eats A).

¹⁵⁹ We analysed the structure of the networks using properties that focus on different levels: emergent or global
¹⁶⁰ properties that take into account the whole network, sub-structural properties that consider several nodes,
¹⁶¹ and properties related to one node. To describe food webs as networks each species is represented as a
¹⁶² node or vertex and the trophic interactions are represented as edges or links between nodes. These links are
¹⁶³ directed, from the prey to the predator, as the flow of energy and matter. Two nodes are neighbours if they
¹⁶⁴ are connected by an edge and the degree k_i of node i is the number of neighbours it has. The food web can
¹⁶⁵ be represented by an adjacency matrix $A = (a_{ij})$ where $a_{ij} = 1$ if species j predaes on species i , else is 0.
¹⁶⁶ 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
¹⁶⁷ predators of i or its out-degree. The total number of edges is $E = \sum_{ij} a_{ij}$.

168 **Models**

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

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

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

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

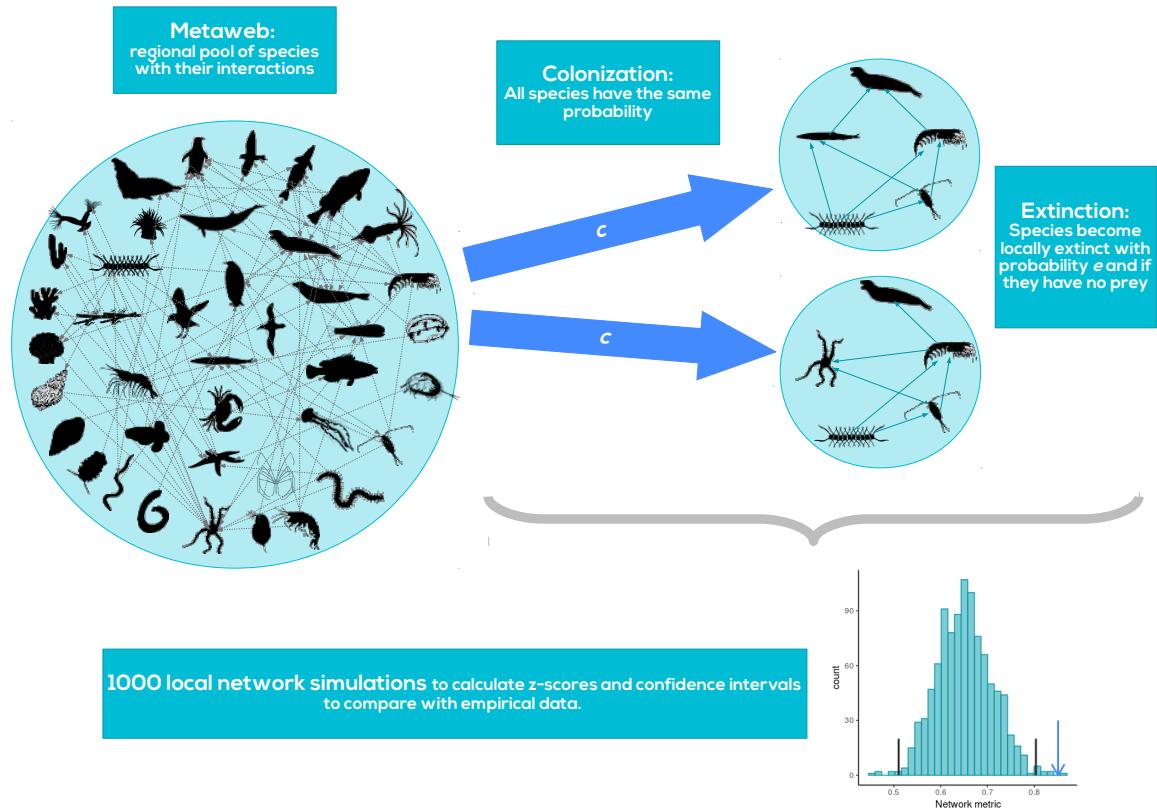


Figure 1: Schematic diagram of the metaweb assembly model: species migrate from the metaweb with a probability c to a local network carrying their potential links to preys; here they have a probability of extinction e . Additionally, predators become extinct if their preys are locally extinct. We simulate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

198 **Global network properties**

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

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

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

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

210 and

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

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

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

214 and to determine if S is statistically significant Monte Carlo methods were used (Crowley 1992). We built
215 1000 null model networks with the same number of nodes n and edges m than the empirical network; then
216 we calculated S for each random network and the lower and higher 99% quantiles of the S distribution are

217 called ql, qh :

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

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

221 The second global property was trophic coherence (Johnson et al. 2014), that is related to stability in the
222 sense that small perturbations could get amplified or vanished, which is called local linear stability (May
223 1972, Rohr et al. 2014). We first needed to estimate the trophic level of a node i , defined as the average
224 trophic level of its preys plus 1. That is:

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

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

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

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

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

236 where q_{obs} is the observed coherence, q_{null} is the mean coherence from the null model networks and σ_{qnull}

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

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

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

250 where s is the number of modules or compartments, I_s is the number of links between species in the module
251 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
252 assess the significance of our networks we calculate the 99% confidence intervals and z-scores based on 1000
253 null model networks as previously described.

254 Sub-structural properties (motifs)

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

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

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

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

267 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
268 deviation of k_{is} over all species in s . The participation coefficient PC estimates the distribution of the links
269 of species i among modules; thus it can be defined as:

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

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

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

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

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

292 Results

293 Global network properties

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

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

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

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*

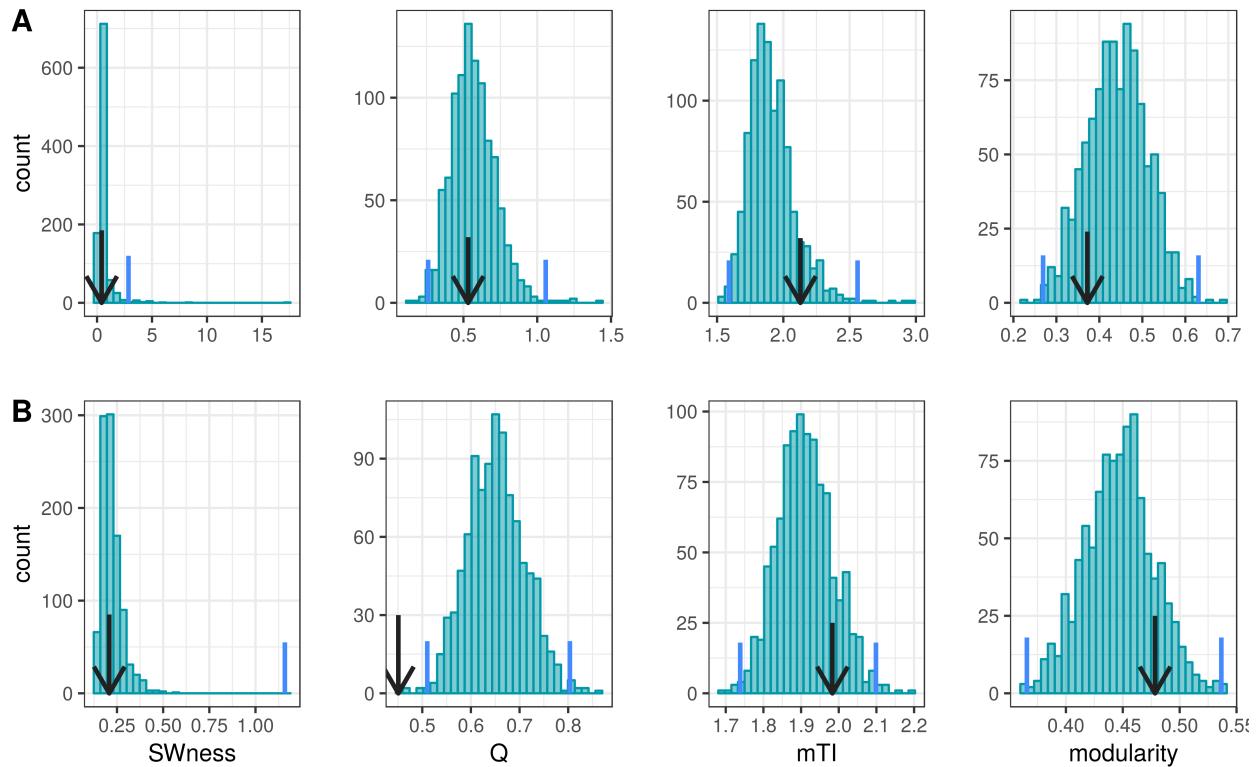


Figure 2: Network global properties compared with the metaweb assembly model for A) Potter Cove and B) Weddell Sea food webs. The properties were: Small-world-ness (SWness), coherence (Q), mean trophic level (mTL) and modularity. We ran 1000 simulations of local networks fitted to Potter Cove and Weddell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

307 Sub-structural properties (motifs)

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

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

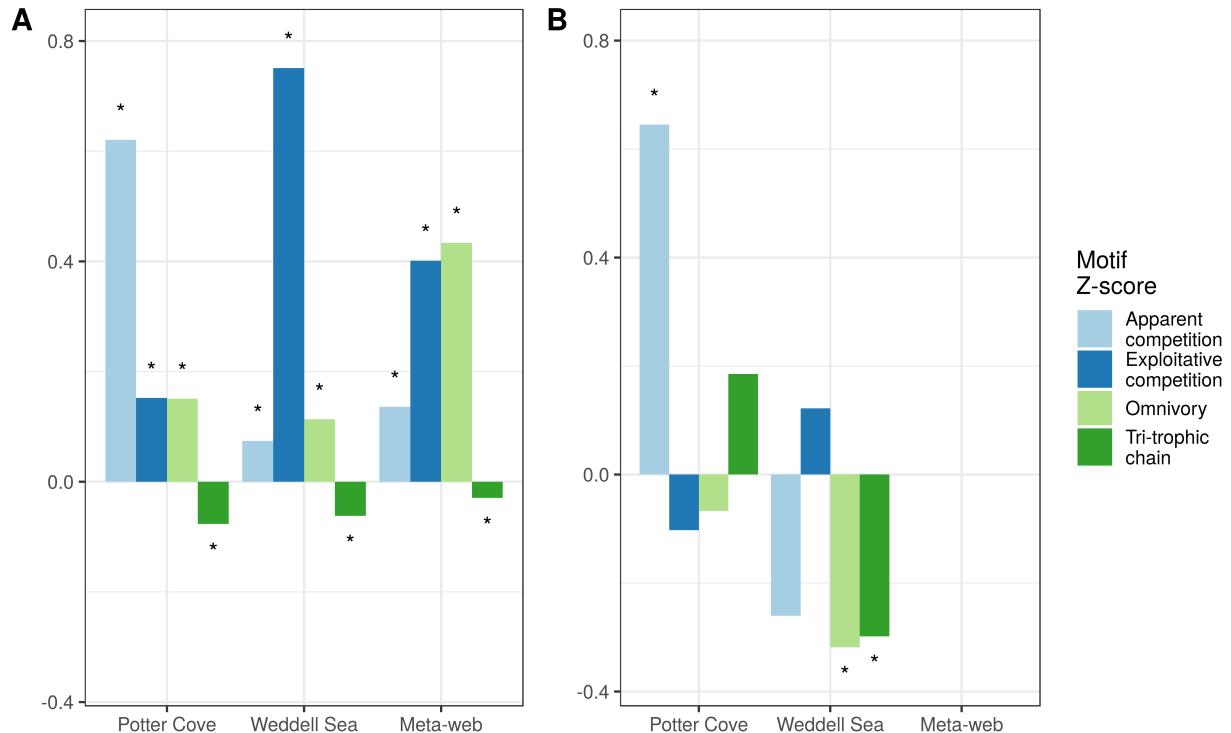


Figure 3: Network motifs z-scores across scales. Motifs are three-node sub-networks counted on each of the networks.: the *Metaweb* represents the marine predator-prey relationships of Antarctica; the *Weddell Sea* and *Potter Cove* are local food webs. A. Z-scores estimated with the random null model.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

318 Node-level properties (Topological roles)

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

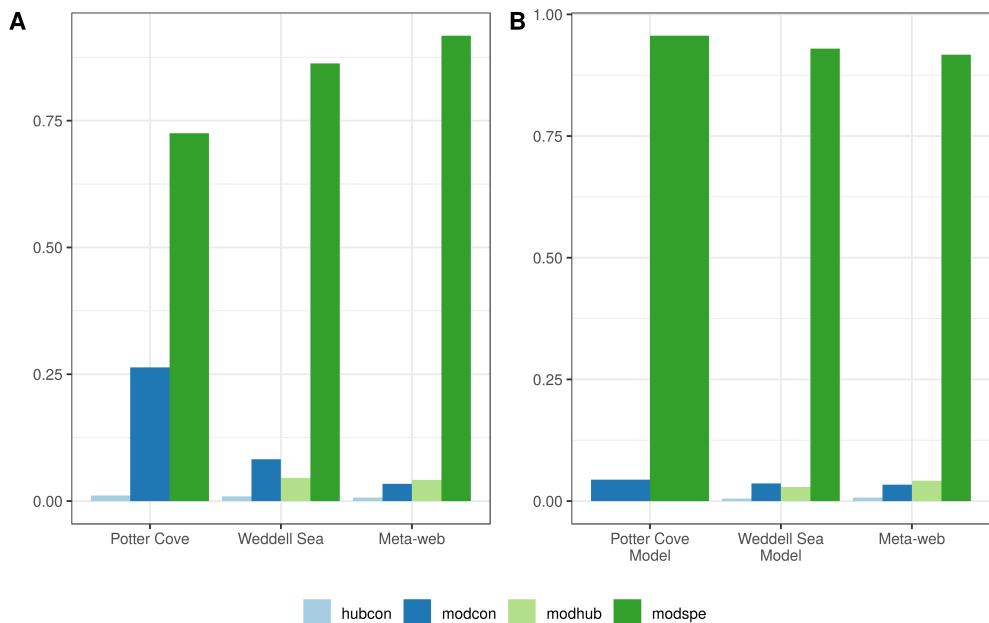


Figure 4: Proportion of topological roles across scales., the *Metaweb* represents the marine predator-prey relationships of Antarctica; the *Weddell Sea* and *Potter Cove* are local food webs. The topological roles are: *Hub connectors*, high number of between-module links; *Module connectors*, low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

324 = 5.95, p-value = 0.41)(Figura 3 B).

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

337 Discussion

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

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

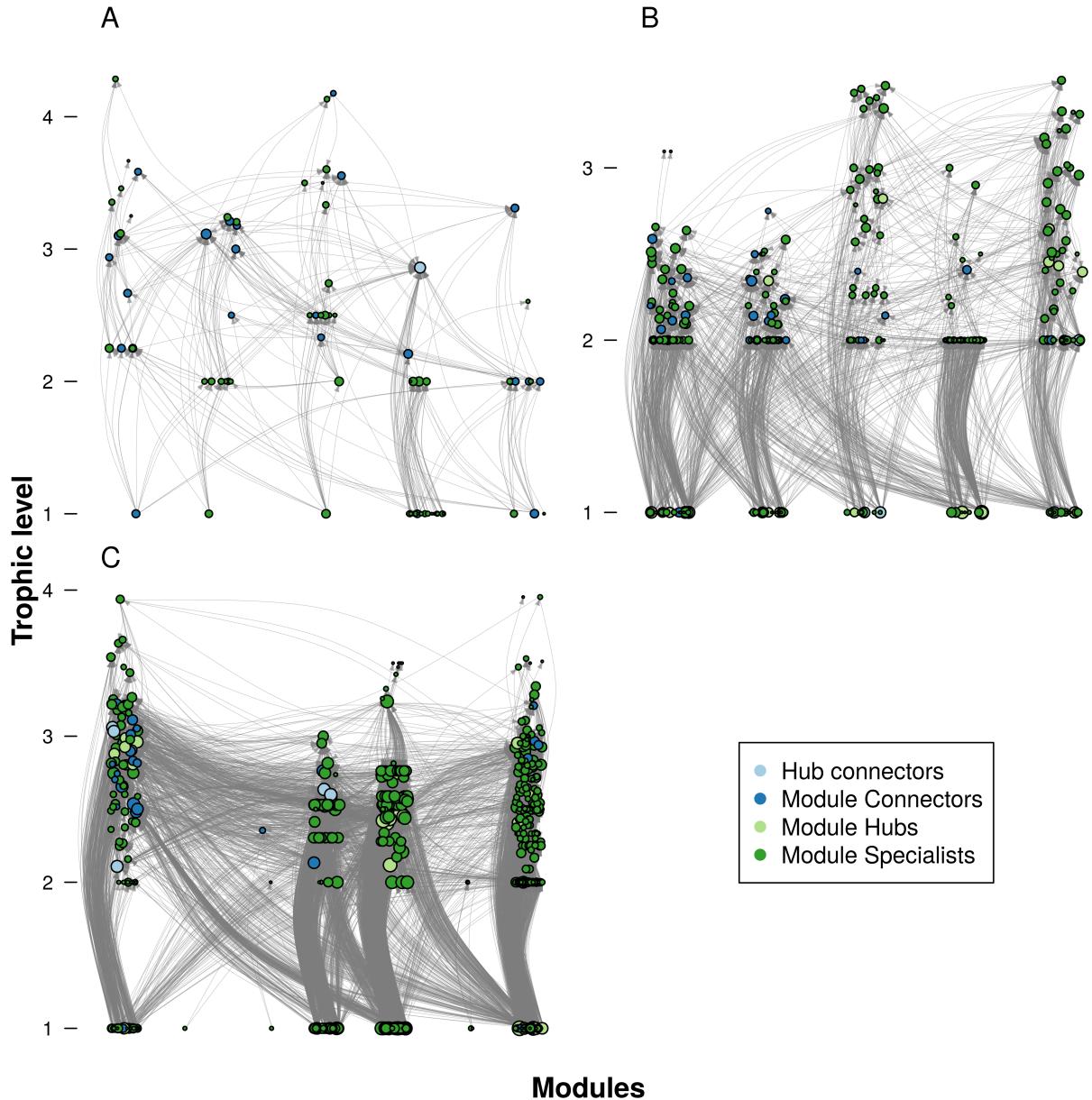


Figure 5: Plot of topological roles combined with trophic levels and modularity for each food web (A) Potter Cove, (B) Weddell Sea (C) the Metaweb. The topological roles are: *Hub connectors* have a high number of between module links, *Module connectors* have a low number of links mostly between modules,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

354 is (Stouffer and Bascompte 2011), even though the effect on stability strongly depends on the interaction
355 strength configuration (Grilli et al. 2016) and on the existence of external perturbations (Gilaranz et al.
356 2017). We found that modularity is not different from the assembly model and we observed that the modular
357 structure is present in the metaweb. This suggests that modularity is not produced by maximization of local
358 stability and could be a spandrel of assembly.

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

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

371 Motifs have the same representation patterns across networks against the random model. If food web struc-
372 ture is influenced by dynamical constraints, then we would expect real food webs to have a higher frequency
373 of stability-enhancing motifs than assembled model webs. The expected pattern is an over-representation
374 tri-trophic chains, exploitative and apparent competition (Borrelli 2015), and the omnivory motif could en-
375 hance or diminish stability (Monteiro and Faria 2016). Instead, our real webs had an under-representation
376 tri-trophic chains while the other motifs matched expectation, and omnivory was over-represented. The
377 motif structure observed in the metaweb is not maintained in local food webs: apparent competition is
378 over-represented in Potter Cove, which would enhance stability, and both omnivory and tri-trophic chains
379 are under-represented in Weddell Sea which seems to have a neutral effect on stability. Thus, the assembly
380 process is not random, there are differences in the frequencies of motifs as the scale change, but the selection
381 of motifs due to its dynamical stability is not the main driver. This implies that other processes that influ-
382 ence the presence or absence of species like habitat filtering or dispersal limitation are acting and probably
383 modifying motif frequencies in empirical food webs.

384 As expected, all the networks have a short mean trophic level (Williams et al. 2002, Borrelli and Ginzburg

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

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

407 The spatial scales involved in our study do not represent a continuity; the metaweb and the Weddell sea web
408 have a 10 to 1 ratio but the local web is 10^6 smaller, besides that most of the global network properties and
409 the motif structure showed no changes relative to the null model. We did not find evidence that the structure
410 of the food web was influenced by dynamical constraints. Instead, we hypothesise that other local processes,
411 that limit which species from the metaweb can colonise the local web, are influencing the assembly process.
412 Although our results are limited to Antarctic marine food webs, our findings suggest that future studies
413 about food webs should give more attention to evolutionary and assembly processes, and less emphasis to
414 local dynamics. This kind of analysis needs to be expanded to different regions and other kinds of habitats
415 (e.g. terrestrial, freshwater, etc.) to confirm if this is a general pattern or not.

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