

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

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

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

¹⁴ **Abstract**

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

41 Introduction

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

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

66 The objective of the present study is to analyse the process of food web assembly comparing network proper-
67 ties with models across different spatial scales. For this we considered: the Antarctic metaweb, representing
68 an area of 34.8 million Km², and build from a dietary database (Raymond et al. 2011); the Weddell Sea
69 food web that represents 3.5 million Km² (Jacob et al. 2011); and the Potter Cove network that represents
70 6.8 Km², (Marina et al. 2018a).

71 There are several approaches to characterize the structure of ecological networks: emergent or global prop-

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

83 Since the early studies of May (1972) stating that larger and more connected ecosystems will be unstable,
84 there has been a search for factors that would stabilize food webs (???, Neutel et al. 2007, García-Callejas
85 et al. 2018); one of the potential properties is trophic coherence (Johnson et al. 2014). Trophic coherence
86 is based on the distances between the trophic positions of species and measures how well species fall into
87 discrete trophic levels. Then, more coherence implies a more hierarchical food-web structure , which is
88 directly correlated with local asymptotic stability (Johnson et al. 2014). The advantage of coherence as an
89 index of stability is that it does not make any assumptions about interaction strengths. A property related
90 to coherence is the mean trophic level, which historically has been used as an ecosystem health indicator
91 (Pauly et al. 1998), predicting that food webs with higher trophic levels are less stable (Borrelli and Ginzburg
92 2014).

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

102 Species may participate in different ways with respect to modularity, depending on how many trophic links
103 they have within their own module and/or between modules (Guimerà and Nunes Amaral 2005, Kortsch et

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

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

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

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

132 **Methods**

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

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

164 **Models**

165 To unravel the mechanisms of network assembly we considered two models, a random network model that
166 implies that there is no ecological mechanism and a colonization extinction model constrained by the network
167 structure, but with no consideration of population dynamics and interaction strengths. Then we compared
168 the properties of empirical networks with models using a null model approach: if we observe a deviation
169 from the property obtained with the null model then mechanisms that are excluded from the model may be
170 acting (???).

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

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

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

194 **Global network properties**

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

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

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

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

206 and

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

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

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

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

213 called ql, qh :

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

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

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

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

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

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

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

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

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

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

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

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

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

250 Sub-structural properties (motifs)

251 We considered four of the thirteen possible three-species sub-networks: apparent competition, exploitative
252 competition, tri-trophic chain, and omnivory (Figure 1). These are the only motifs present in all networks
253 analysed here. We compared the frequency of these motifs to 1000 null model networks using the 99%
254 confidence interval and the z-score as previously described. To determine if the proportions of motifs change
255 across networks we use the Pearson's Chi-squared test with simulated p-value based on 10000 Monte Carlo
256 replicates.

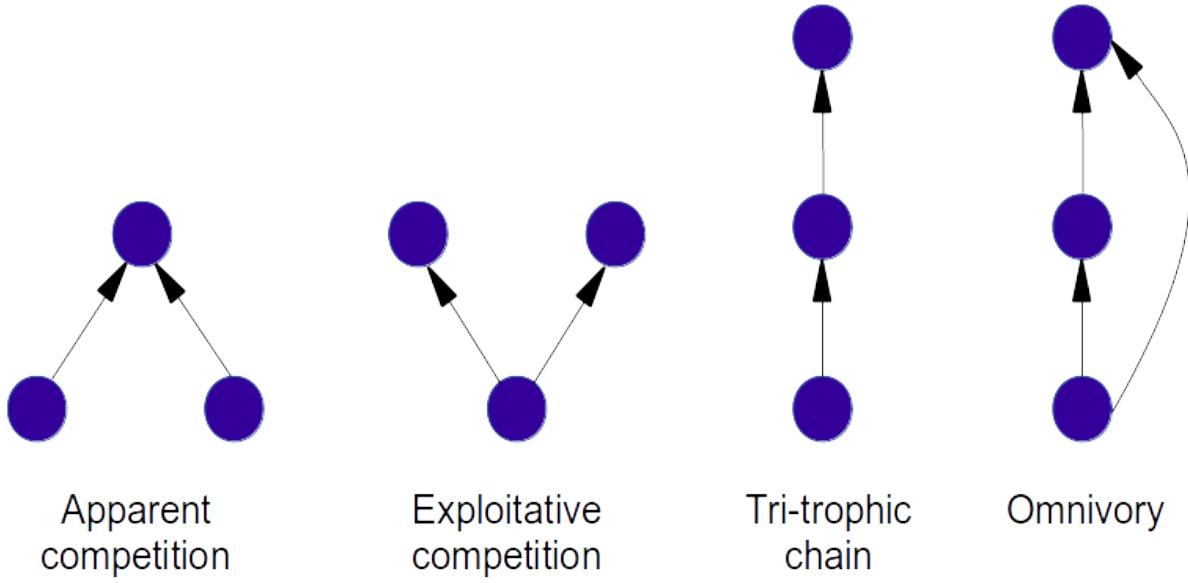


Figure 1: The four three-species sub-networks analysed: apparent competition, exploitative competition, tri-trophic chain, and omnivory. These four sub-networks have been explored both theoretically and empirically in ecological networks and are the most common sub-networks found in food webs

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

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

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

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

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

266 where k_i is the degree of species i (i.e. the number of links), k_{is} is the number of links of species i to

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

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

284 With the aim of giving an integrated visualization of the global and local properties of the food webs, we
285 combined in a single plot information about compartments and the topological roles with the trophic level
286 for each species (Figure 4).

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

291 Results

292 Global network properties

293 Based on the random null model, all networks presented the small-world topology as their small-world-ness
294 index was larger than the 99% confidence interval (Table 1 & S1). However, we did not find differences
295 between the local food webs and the assembly model (Table 1 & S2). Regarding trophic coherence, all

networks presented negative random z-scores and significantly smaller q values (Table 1 & S1), thus they are
 more locally stable as they are more coherent. Using the metaweb assembly model, the Weddell Sea food web
 showed negative z-scores lower than 2, and Potter Cove food web exhibited no significant differences (Table
 1 & S2). Mean trophic level results were similar among networks and significantly lower than the random
 null model (Table 1 & S1), though were not significantly different to the metaweb model. Modularity values
 for the empirical food webs were greater than the random model, but not significantly higher in the Potter
 Cove web. There was no differences in modularity when compared to the metaweb assembly model (Table
 1). Overall, networks differed from the 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, the *Weddell Sea* and *Potter Cove* are the local food webs. Z-scores were calculated against 1000 null model networks (random or metaweb assembly models). Quantities marked with '*' are significant at 1% level. A negative z-score means that the quantity is smaller than the expectation from null model simulations; a positive z-score means that is greater.

Network	Potter Cove	Weddell Sea	Metaweb
Size	91	437	859
Links	309	1908	9003
Area (Km ²)	6.8	3.5e6	34.8e6
Connectance	0.037	0.010	0.012
PathLength	1.81	2.20	2.57
Clustering	0.10	0.048	0.22
Small-World-ness random	*2.75	*4.69	*10.87
Small-World-ness Assembly	0.42	0.21	
Coherence	0.53	0.45	0.70
Coherence random z-score	*-0.54	*-2.08	*-3.54
Coherence assembly z-score	-0.20	*-3.41	
Mean Trophic level	2.13	1.98	1.91
Trophic level random z-score	*-0.27	*-0.86	*-1.60
Trophic level assembly	1.29	1.09	
z-score			
Modularity	0.37	0.48	0.45
Modularity random z-score	0.89	*18.97	*85.75
Modularity assembly z-score	-0.38	0.41	

305 Sub-structural properties (motifs)

The representation of three-species sub-networks with respect to the random model showed similar patterns
 in all networks (Figure 2A). While exploitative competition, apparent competition, and omnivory were over-
 represented, tri-trophic chains were under-represented; all these patterns were significant (Table S3). We

309 found that motifs proportions for the three examined spatial scales were different ($\text{Chi-squared} = 12612$, p-
 310 value < 9.9e-05). this means that local networks are not a random sample of the metaweb. With respect to
 311 the metaweb assembly model only some of them were significant (Table S4): tri-trophic chains and omnivory
 312 were under-represented for Weddell Sea, and apparent competition was over-represented for Potter Cove
 313 (Figure 2B). Contrary to our expectations Potter Cove was more similar to the metaweb than Weddell Sea
 314 food web.

315 *Network motifs z-scores across scales. Motifs are three-node sub-networks counted on each of the networks.:*
 316 *the Metaweb represents the marine predator-prey relationships of Antarctica; the Weddell Sea and Potter*
 317 *Cove are local food webs. A. Z-scores estimated with the random null model. B. Z-scores estimated with the*
 318 *metaweb assembly model. Z-scores were normalized by the square root of the sum of the squared z-scores for*
 319 *that food web, bars marked with '*' are significant at 1% level.*

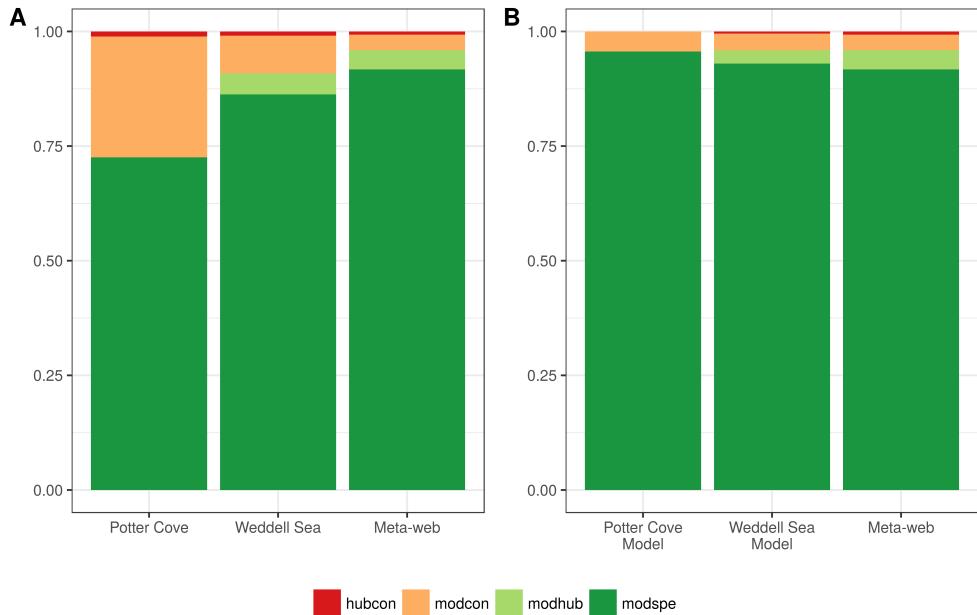


Figure 2: Proportion of topological roles across scales., the *Metaweb* represents the marine predator-prey relationships of Antarctica; the *Weddell Sea* and *Potter Cove* are local food webs. The topological roles are: *Hub connectors*, high number of between-module links; *Module connectors*, low 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-value = 9.9e-05). B. Proportions for local networks obtained from the metaweb assembly model; no differences were found ($\text{Chi-squared} = 5.95$, p-value = 0.41)

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

321 The proportion of species displaying the four topological roles was different among food webs (Chi-squared
322 = 79.31, p-value = 9.9e-05). A higher presence of module connectors (few links, mostly between modules)
323 was observed in Weddell Sea, while a lack of module hubs (high number of links inside its module) was found
324 in Potter Cove (Figure 3 A), which can be related to its low modularity value (Table 1). The proportions
325 obtained with the metaweb assembly model were not different from the food webs (Chi-squared = 5.95,
326 p-value = 0.41)(Figura 3 B).

327 The plot of topological roles combined with trophic levels and modularity revealed important details of the
328 food webs (Figure 4): the metaweb has densely connected compartments but some of them have few low-
329 connected species (module connectors or module specialists). Additionally, we observed in the Weddell Sea
330 food web hub connectors with a basal trophic level (Table S5). These are aggregated nodes that represent
331 generic prey, e.g. fish or zooplankton, they only have incoming links or predators and they cannot have
332 outgoing links or prey because they comprise several species. Different fish species are present in the Weddell
333 Sea food web with detailed information about prey and predators, but for some predators there is insufficient
334 knowledge of its prey and aggregated nodes must be added. Thus the existence of these basal hub connectors
335 is a spurious result of aggregating prey species. The other non-aggregated hub connectors are highly mobile
336 species with an intermediate trophic level like krill (Table S5). The variation of maximum trophic levels is
337 evidenced in Figure 4, where both Potter Cove and Metaweb networks had similar values and Weddell Sea
338 food web exhibited a lower maximum trophic level.

339 **Discussion**

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

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

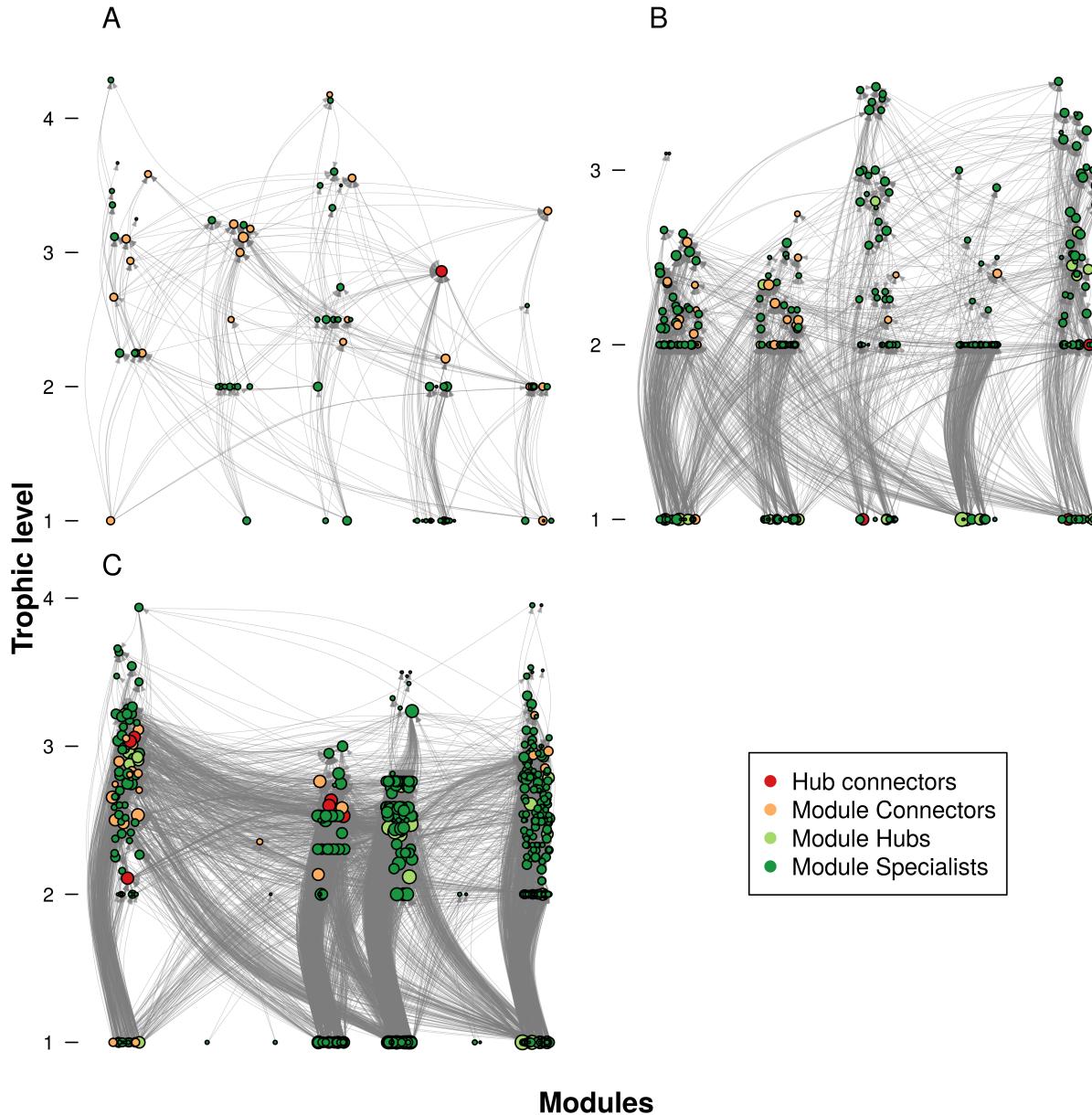


Figure 3: Plot of topological roles combined with trophic levels and modularity for each food web (A) Potter Cove, (B) Weddell Sea (C) the Metaweb. The topological roles are: *Hub connectors* have a high number of between module links, *Module connectors* have a low number of links mostly between modules, *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.

350 web was the only property that is similar to the random model. The existence of a modular structure
351 could be related to different habitats (Krause et al. 2003, Rezende et al. 2009) —in marine environments
352 could be benthic and pelagic. The small extent of Potter Cove (6.8 Km^2) could be the reason of its lack
353 of modularity. Studies suggest that modularity enhances local stability and this effect is stronger the more
354 complex the network is (Stouffer and Bascompte 2011), even though the effect on stability strongly depends
355 on the interaction strength configuration (Grilli et al. 2016) and on the existence of external perturbations
356 (Gilarranz et al. 2017). We found modularity is not different from the assembly model and we observed
357 that the modular structure is present in the metaweb, this suggests that modularity is not produced by
358 maximization of local stability.

359 Dynamical stability represented in the coherence parameter is expected to be maximized at the local level
360 but we only found that Weddell Sea food web exhibited a greater trophic coherence than the assembly model.
361 Thus, although this evidence is not conclusive with regard to the importance of dynamical processes in the
362 assembly of food webs, the structure of the local food webs examined here seem to be a consequence of the
363 metaweb structure.

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

371 Motifs also have the same representation patterns against the random model. If some kind of dynamical
372 non-adaptative selection would be working, local food webs should have motif representations that increase
373 its stability. The expected pattern, based on dynamical models, is an over-representation of omnivory
374 and tri-trophic chains and an under-representation of apparent and exploitative competition (Stouffer and
375 Bascompte 2010). Other studies showed that tri-trophic chains, exploitative and apparent competition should
376 be displayed more frequently (Borrelli 2015), but this was based on the stability of isolated three-species sub-
377 networks and the assumption that during the assembly process these 3 species sub-networks were selected
378 because of their intrinsic stability (Borrelli et al. 2015). The fact that tri-trophic (or n-trophic) interactions
379 cannot account fully for the properties of the food webs (Cohen et al. 2009) make the results based on isolated
380 modules less convincing. Our results showed an over-representation of omnivory, exploitative competition
381 and apparent competition, this configuration is not the most stable one based on either criterion. A first

382 hypothetical explanation is that the structure observed in the metaweb is maintained in local food webs.
383 Despite the fact that almost all motifs were not different from the assembly model, neither tri-trophic chains
384 and omnivory (lower in Weddell Sea) nor apparent competition (higher in Potter Cove) followed the pattern
385 expected from theoretical studies. Thus, the assembly process is not random, there are differences in the
386 frequencies of motifs as the scale change, but the selection of motifs due to its dynamical stability is not the
387 main driver. This implies that other processes that influence the presence or absence of species like habitat
388 filtering or dispersal limitation are acting and probably modifying motif frequencies in empirical food webs.
389 This kind of motif patterns that are a sub-product of network buildin rules, or in general processes that
390 happen at a different level, have been called spandrels of assembly (Solé and Valverde 2006). Our results
391 suggest that motif patterns in our metaweb food-webs system are spandrels of assembly.

392 As expected all the networks have a short mean trophic level (Williams et al. 2002, Borrelli and Ginzburg
393 2014) compared with the random model. Different hypotheses were posed to explain this pattern: the low
394 efficiency of energy transfer between trophic levels, predator size, predator behaviour, and consumer diversity
395 (Young et al. 2013). These have contradictory support, reviewed by Ward and McCann (2017). Recently, it
396 has been proposed that maximum trophic level could be related to productivity and ecosystem size depending
397 on the context but related to energy fluxes that promote omnivory (Ward and McCann 2017). A different
398 mechanism based on dynamic stability of the whole web was proposed: food webs with shorter trophic levels
399 (between 2 and 4) that have more omnivore chains are more likely to be stable, which increase the probability
400 of being observed in nature (Borrelli and Ginzburg 2014). We found that mean trophic level of the local food
401 webs was not different from the assembly model, and omnivory was under-represented. This combination
402 suggests that the trophic level could also be a spandrel of assembly, inherited from the metaweb structure.

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

414 Our results are limited to the Antarctic marine food-webs so this needs to be expanded to different regions
415 and other kinds of habitats (e.g. terrestrial, freshwater, etc.) and confirm if this is a general pattern or not.

416 The spatial scales involved in our study do not represent a continuity; the metaweb and the Weddell sea
417 web have a 10 to 1 ratio but the local web is 10^6 smaller, besides that most of the global network properties
418 and the motif structure showed no changes relative to the null model. Thus, we found evidence that local
419 processes that limit species from the metaweb to local scales are influencing the assembly process but the
420 structure of the food web originated through an emergent process from evolutionary or co-evolutionary forces
421 seems to be more important. This suggest that future studies about food webs should give more attention
422 to evolutionary and assembly process, and less emphasis to local dynamics.

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