

# <sup>1</sup> Ecological Network assembly: how the regional meta web influence <sup>2</sup> local food webs

## <sup>3</sup> Abstract

<sup>4</sup> The idea that ecological networks are built in a sequence of colonization events is not new but has been  
<sup>5</sup> applied mostly to competitive interactions. Similar processes act in trophic networks (food webs): a regional  
<sup>6</sup> pool of species is the source from which species colonize local areas, called the meta-web. Local food webs  
<sup>7</sup> are realizations of meta-webs that result from assembly processes influenced by migration, habitat filtering,  
<sup>8</sup> stochastic factors, and dynamical constraints imposed by food web structure. We analyse how the structure  
<sup>9</sup> of a meta-web influence local food-webs with different spatial scales, using an assembly model, a random  
<sup>10</sup> model and properties at three levels: emergent global properties that take into account the whole network  
<sup>11</sup> (like modularity), sub-structural properties that consider several nodes (like motifs), and properties related  
<sup>12</sup> to one node (like topological roles). Three independent data-sets were included: the marine Antarctic  
<sup>13</sup> meta-web (34.8 million Km<sup>2</sup>), the Weddell Sea (3.5 million Km<sup>2</sup>) and Potter Cove (6.8 Km<sup>2</sup>) food-webs.  
<sup>14</sup> Looking at the global properties, the meta-web present a structure very different from the random model  
<sup>15</sup> while the local food-webs follow the same pattern and are very similar to the assembly model. The assembly  
<sup>16</sup> model only takes into account migration, local extinction and secondary extinctions. For sub-structural  
<sup>17</sup> properties meta-web and the local food-webs also showed the same pattern against the random model, but  
<sup>18</sup> we found differences compared to the assembly model that does not increase the local stability of food webs.  
<sup>19</sup> Topological roles also showed differences between the meta-web and local food-webs that are not explained  
<sup>20</sup> by the assembly model. We found that a great portion of the structure of the food webs is determined by  
<sup>21</sup> evolutionary processes that act on large temporal and spatial scales. On the contrary, dynamical processes  
<sup>22</sup> that favour stability have a small influence, but habitat filtering or dispersal limitations seem to be important  
<sup>23</sup> factors that determine food web structure.

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## **30    Introduction**

31    The characterization of ecological systems as networks of interacting elements has a long history (Paine 1966,  
32    May 1972, Cohen and Newman 1985). Much of this work has been devoted to investigate network structure  
33    and its effects on dynamics and stability (Thebault and Fontaine 2010). In recent years a renewed emphasis  
34    on structural stability (Rohr et al. 2014, Grilli et al. 2017) and new developments in random matrix theory  
35    has greatly expanded our capability to analyse ecological networks (Allesina et al. 2015). Besides, the  
36    analyses of the effects of ecological dynamical processes on food web structure are not so well developed.  
37    One such dynamic process is community assembly: how species from a regional pool colonize a site and  
38    build local interactions (Carstensen et al. 2013). Regional species pools are shaped by evolutionary and  
39    biogeographical processes that imply large spatial and temporal scales (Carstensen et al. 2013, Kortsch et al.  
40    2018). More specifically, the assembly of local communities is influenced by dispersal, environmental filters,  
41    biotic interactions and stochastic events (HilleRisLambers et al. 2012). These processes have been studied by  
42    means of metacommunity theory, where different spatial assemblages are connected through species dispersal.  
43    Metacommunity theory provides a framework for assessing which are the roles of local and regional-scale  
44    dynamics (Leibold et al. 2004, Baiser et al. 2013). This approach has been applied mostly to competitive  
45    interactions, while trophic interactions have received less attention (Baiser et al. 2016). Recently, there was  
46    an increase in food web assembly studies, integrating them with island biogeography (Gravel et al. 2011)  
47    and with metacommunity (Pillai et al. 2011, Liao et al. 2016). These were mainly focused on complexity-  
48    stability effects (Mougi and Kondoh 2016). Previous attempts to study the food web assembly process have  
49    used motifs as building blocks of local communities (Baiser et al. 2016). Motifs are sub-networks composed  
50    of species and links whose frequency deviates from the expected in a random network (Milo et al. 2002). By  
51    comparing motif representation at different spatial scales—from local to regional—the process of assembly  
52    of interactions may be revealed (Baiser et al. 2016), e.g. if the same processes structure the food-web across  
53    scales, motif representation should be the same. Besides, as local food-webs should have tighter links and  
54    stronger interaction rates, other structural properties should change as scale changes (Coll et al. 2011).  
55    The objective of the present study is to analyse the process of food web assembly addressing how multilevel  
56    network properties change across different spatial scales. For this we considered: the Antarctic meta-web,  
57    representing an area of 34.8 million Km<sup>2</sup>, and build from a dietary database (Raymond et al. 2011); the  
58    Weddell Sea food web that represents 3.5 million Km<sup>2</sup> (Jacob et al. 2011); and the Potter Cove network  
59    that represents 6.8 Km<sup>2</sup>, (Marina et al. 2018a).  
60    There are several approaches to characterize the structure of ecological networks: emergent or global prop-

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

72 Since the early studies of May (1972) that stated that larger and more connected ecosystems will be unstable,  
73 there is a search for factors that would stabilize food-webs (García-Callejas et al. 2018); one of the potential  
74 properties is trophic coherence (Johnson et al. 2014). Trophic coherence is based on the distances between  
75 the trophic positions of species and measures how well species fall into discrete trophic levels. Then, more  
76 coherence implies a more hierarchical structure of the food-web, which is directly correlated with linear  
77 stability (Johnson et al. 2014). The advantage of coherence as an index of stability is that it does not make  
78 any assumptions about interaction strengths. Related to coherence is the mean trophic level, an approach  
79 historically used as an ecosystem health indicator (Pauly et al. 1998), that predicts that food webs with  
80 higher trophic levels are less stable (Borrelli and Ginzburg 2014).

81 Food webs have highly non-random and structurally complex patterns that contain internal functional units  
82 or sub-modules (Grilli et al. 2016). These are groups of prey and predators that interact more strongly  
83 with each other than with species belonging to other modules. The existence of these modules (also called  
84 compartments) act to buffer the propagation of extinctions throughout the network, increasing its persistence  
85 (Stouffer and Bascompte 2011). It is interesting to mention that small-world patterns and modularity act  
86 in opposite directions. Whereas the small-world structure favours the spread of perturbations through its  
87 rapid dissipation (Gray et al. 2016), the presence of a high degree of modularity prevents the dispersal of  
88 perturbations (Krause et al. 2003, Stouffer and Bascompte 2011). The detection of these modules is an  
89 intermediate approach between the global and local analyses.

90 There are species in ecological networks that have large effects on the whole ecosystem, like keystone species  
91 (Paine 1969), ecosystem engineers (Jones et al. 1994) and network hubs (Borthagaray et al. 2014). In this  
92 sense, species may participate in different ways with respect to modularity, depending on how many trophic

93 links they have within their own module and/or between modules (Guimerà and Nunes Amaral 2005, Kortsch  
94 et al. 2015). This participation has been called the species' topological role; theoretical and empirical results  
95 suggest these roles are related to species traits, such as wide niche breadth, environmental tolerance, apex  
96 position in local communities and high motility (Rezende et al. 2009, Guimerà et al. 2010, Borthagaray et  
97 al. 2014). This is a local property at an individual species level.

98 When we consider several linked species this forms a sub-network, when the abundance of one of these  
99 sub-networks deviates significantly from a null model network, this is called a motif (Milo et al. 2002). We  
100 analyse here the three-species sub-networks that have been most studied theoretically and empirically in  
101 food webs (Prill et al. 2005, Stouffer et al. 2007, Baiser et al. 2016). Specifically, we focused on four of  
102 the thirteen possible three-species sub-networks: apparent competition, exploitative competition, tri-trophic  
103 chain, and omnivory (Figure 1).

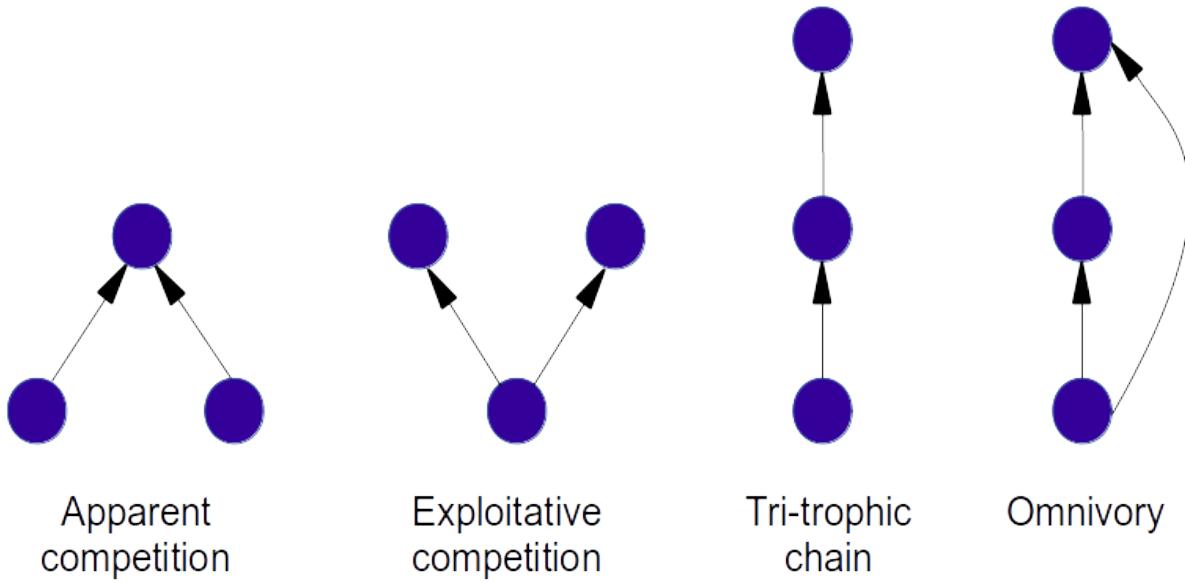


Figure 1: The four three-species sub-networks analysed: apparent competition, exploitative competition, tri-trophic chain, and omnivory. These four sub-networks have been explored both theoretically and empirically in ecological networks and are the most common sub-networks found in food webs

104 These motifs may show the process of assembly of interactions (Baiser et al. 2016) by comparing the frequency  
105 of motifs at each scale (i.e over-represented, under-represented, or random). When the same processes  
106 structure the food-web across scales, motif representation should be the same. Ecological interactions occur  
107 at the local scale so differences may show the importance of local interactions in the assembly of the food web.  
108 During the assembly process those motif structures that are less dynamically stable tend to disappear from  
109 the food web (Borrelli 2015), this has been called non-adaptative systemic selection (Borrelli et al. 2015).

110 This process is non-adaptive because the selection process is not adapting the system to local conditions  
111 (Borrelli et al. 2015).

112 To our knowledge, the combination of network properties at different spatial levels has not been applied in  
113 food web studies up to now. In addition, we compared the empirical food webs against a random network  
114 null model (i.e. absence of ecological mechanisms), and a meta-web assembly model (i.e. representing an  
115 assembly process). We hypothesize network properties to change from the meta-web to a local scale where  
116 interactions are realized. We particularly expect global properties related to resilience and stability to be  
117 close to the null model at the meta-web scale and significantly different at the local scale; a greater frequency  
118 of stable motifs in the local food webs; as well as a change in the frequency of topological roles since habitat  
119 filtering or dispersal limitation act at the local food web scale.

## 120 Methods

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

140 interactions to the meta-web when the local food webs contain a greater taxonomic resolution. When the  
141 meta-web contained more detailed records, only for predators we added them to the local food webs checking  
142 for its geographic range. We removed cannibalistic (self-links) and double arrows (i.d. A eats B and B eats  
143 A).

144 **Analysis**

145 We analysed the structure of the networks using properties that focus on different levels: emergent global  
146 properties that take into account the whole network, sub-structural properties that consider several nodes,  
147 and properties related to one node. To describe food webs as networks each species is represented as a node  
148 or vertex and the trophic interactions are represented as edges or links between de nodes. These links are  
149 directed, from the prey to the predator, as the flow of energy and matter. Two nodes are neighbours if they  
150 are connected by an edge and the degree  $k_i$  of node  $i$  is the number of neighbours it has. The food web  
151 can be represented by an adjacency matrix  $A = (a_{ij})$  where  $a_{ij} = 1$  if species  $j$  predares species  $i$ , else is 0.  
152 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  
153 predators of  $i$  or its out-degree. The total number of edges is  $E = \sum_{ij} a_{ij}$ .

154 **Null models**

155 We considered two null models, the Erdős-Rényi random graph (Erdős and Rényi 1959), and the meta-web  
156 assembly model. An Erdős-Rényi network is constructed fixing the number of edges and nodes and assigning  
157 at random the  $m$  edges to the  $n$  nodes with equal probability (Erdős and Rényi 1959, Baiser et al. 2016).

158 We restricted the random model eliminating double arrows and cannibalistic links. To calculate trophic level  
159 and the coherence parameter (see below) we further restricted to random webs with at least one basal node,  
160 to make these calculations possible. Since the random model represents the absence of any network assembly  
161 mechanism, the comparison against it does not guarantee information on this aspect.

162 In order to consider network assembly mechanisms we designed a dynamic meta-web assembly model. In this  
163 model species migrate from the meta-web to a local web with a uniform probability  $c$ , and become extinct  
164 from the local web with probability  $e$ ; a reminiscence of the theory of island biogeography (MacArthur  
165 and Wilson 1967, Gravel et al. 2011), but with the addition of network structure. Species migrate with  
166 their potential network links from the meta-web, then in the local web species can only survive if at least  
167 one of its preys is present, or if it is a basal species. When a species goes extinct locally it may produce  
168 secondary extinctions; we check that the local predators maintain at least one prey if not they become extinct

169 independent of the probability  $e$ . We simulated this model in time and it eventually reaches an equilibrium  
170 that depends on the migration and extinction probabilities but also on the structure of the meta-web. The  
171 ratio of immigration vs. extinction  $\alpha = c/e$  is hypothesized to be inversely related to the distance to the  
172 mainland (MacArthur and Wilson 1967), and as extinction  $e$  should be inversely proportional to population  
173 size (Hanski 1999), the ratio  $\alpha$  is also hypothesized to be related to the local area.

174 For the random model we simulated networks with the same number of nodes  $n$  and edges  $m$  as the empirical  
175 networks; for the meta-web model we fitted the parameters  $g$  and  $e$  to obtain networks with  $n$  and  $m$  close  
176 to the empirical networks. This implies that  $\alpha$  should reflect the differences in areas of the two local food  
177 webs. For details of the fitting and simulations see Appendix.

## 178 Small-world topology

179 The first global emergent property we used is the small-world pattern, which examines the average of the  
180 shortest distance between nodes and the clustering coefficient of the network (Watts and Strogatz 1998). We  
181 first calculated the characteristic path length that is the shortest path between any two nodes. Then  $L$  is  
182 the mean value of the shortest path length across all pairs of nodes. The clustering coefficient of node  $i$  was  
183 defined as

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

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

$$\gamma_g = \frac{C_g}{C_{null}}$$

189 and

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

190 where  $C_g$  and  $L_g$  are the clustering coefficient and the mean shortest path length of the network of interest

<sup>191</sup>  $G$ ;  $C_g$  and  $C_{null}$  are the same quantities for the corresponding null model. Thus, the quantitative small-  
<sup>192</sup> world-ness is defined as:

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

<sup>193</sup> and to determine if  $S$  is statistically significant Monte Carlo methods are used. We built 1000 null model  
<sup>194</sup> networks with the same number of nodes  $n$  and edges  $m$  than the empirical network; then we calculated  $S$   
<sup>195</sup> for each random network and the lower and higher 99% quantiles of the  $S$  distribution are called  $ql, qh$ :

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

<sup>196</sup> the upper 99% confidence limit is then  $CL^{0.01} = 1 + CI$ . Thus, if a network has  $S > CL^{0.01}$  it is considered  
<sup>197</sup> a small-world network (Humphries and Gurney 2008). We also calculated the small-world-ness and the CI  
<sup>198</sup> using the meta-web assembly model as a null model.

## <sup>199</sup> Coherence

<sup>200</sup> The second global property is called trophic coherence (Johnson et al. 2014), and is related to stability in  
<sup>201</sup> the sense that small perturbations could get amplified or vanished, which is called local linear stability (May  
<sup>202</sup> 1972, Rohr et al. 2014). We first needed to estimate the trophic level of a node  $i$ , defined as the average  
<sup>203</sup> trophic level of its preys plus 1. That is:

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

<sup>204</sup> where  $k_i^{in} = \sum_j a_{ji}$  is the number of preys of species  $i$ , basal species that do not have preys (then  $k_i^{in} = 0$ )  
<sup>205</sup> are assigned a  $tp = 1$ . Then the trophic difference associated to each edge is defined as  $x_{ij} = tp_i - tp_j$ .  
<sup>206</sup> The distribution of trophic differences,  $p(x)$ , has a mean  $E^{-1} \sum_{ij} a_{ij} x_{ij} = 1$  by definition. Then the trophic  
<sup>207</sup> coherence is measured by:

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

<sup>208</sup> that is the standard deviation of the distribution of all trophic distances. A food web is more coherent  
<sup>209</sup> when  $q$  is closer to zero, thus the maximal coherence is achieved when  $q = 0$ , and corresponds to a layered

network in which every node has an integer trophic level (Johnson et al. 2014, Johnson and Jones 2017). To compare coherence and trophic level we generated 1000 null model networks with at least one basal species and the same number of species and links—or approximately the same—than the network of interest. Then we calculated the 99% confidence interval using the 0.5% and 99.5% quantiles of the distribution of  $q$ ; we also calculated the confidence interval for the mean trophic level  $tp$ . We calculated the z-scores as:

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

where  $q_{obs}$  is the observed coherence,  $q_{null}$  is the mean coherence from the null model networks and  $\sigma_{q_{null}}$  is the standard deviation. The same formula is used for  $tp$ . The z-score thus measures the significance of deviations of the real network from the null hypothesis. If the distribution of the quantity ( $q$ ,  $tp$ ) under the null model is normal, a z-score greater than 2 is evidence than the observed quantity is significantly greater than its random counterpart, and a z-score less than 2 means that the quantity is significantly lower. If the distribution under the null model is skewed this is not necessarily true and thus we must rely on confidence intervals.

## Modularity

An intermediate level property (i.e. between the whole network and the individual species) is modularity. It measures how strongly sub-groups of species interact between them compared with the strength of interaction with other sub-groups (Newman and Girvan 2004). These sub-groups are called compartments, and in order to find the best partition we used a stochastic algorithm based on simulated annealing (Reichardt and Bornholdt 2006). Simulated annealing allows to maximize modularity without getting trapped in local maxima configurations (Guimerà and Nunes Amaral 2005). The index of modularity was defined as:

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

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

## Motifs

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

#### 240 Topological roles

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

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

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

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

249 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  
 250 species in module  $s$ . Due to the stochastic nature of the module detection algorithm we made repeated  
 251 runs of the algorithm until there were no statistical differences between the distributions of  $PC_i$  and  $dz_i$  in  
 252 successive repetitions; to test such statistical difference we used the k-sample Anderson-Darling test (Scholz  
 253 and Stephens 1987). Then we calculated the mean and 95% confidence interval of  $dz$  and  $PC$ .

254 To determine each species' role the  $dz - PC$  parameter space was divided into four areas, modified from  
 255 Guimerà and Nunes Amaral (2005), using the same scheme as Kortsch et al. (2015). Two thresholds were  
 256 used to define the species' roles:  $PC = 0.625$  and  $dz = 2.5$ . If a species had at least 60% of links within  
 257 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  
 258 parameter space defines species with relatively high number of links, the majority within its own module.

259 If a species had  $PC < 0.625$  and  $dz < 2.5$ , then it was called a peripheral or specialist; this refers to a  
260 species with relatively few links, mostly within its module. Species that had  $PC \geq 0.625$  and  $dz < 2.5$  were  
261 considered module connectors, since they have relatively few links, mostly between modules. Finally, if a  
262 species had  $PC \geq 0.625$  and  $dz \geq 2.5$ , then it was classified as a super-generalist or hub-connector, because  
263 it has high between- and within-module connectivity. To test if the proportion of species' roles changed  
264 between networks we performed a Pearson's Chi-squared test with simulated p-value based on 10000 Monte  
265 Carlo replicates. Also, we tested if these proportions changed for one realization of the meta-web assembly  
266 model fitted for both local networks (i.e. Weddell Sea and Potter Cove food webs).

267 With the aim of giving an integrated visualization of the sub-structural and local properties of the food webs,  
268 we combined in a single plot information about compartments and the topological roles with the trophic  
269 level for each species.

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

## 274 Results

### 275 Global network properties

276 The number of trophic species (size), links and connectance (Table 1), were in concordance with values found  
277 for marine food webs (Marina et al. 2018b). Based on the random null model, all networks presented the  
278 small-world topology as their small-world-ness index was larger than the 99% confidence interval (Table 1  
279 & S1). However, we did not find differences between the local food webs and the assembly model (Table  
280 1 & S2). Regarding trophic coherence, all networks presented negative random z-scores and significantly  
281 smaller  $q$  values (Table 1 & S1). thus they are more locally stable as they are more coherent. Using the  
282 meta-web assembly model, the Weddell Sea food web showed negative z-scores lower than 2, and Potter Cove  
283 food web exhibited no significant differences (Table 1 & S2). Mean trophic level results were similar among  
284 networks and significantly lower than the random null model (Table 1 & S1), though were not significantly  
285 different when compared to the meta-web model trophic levels . Modularity values for the empirical food  
286 webs were greater than the random model, but not significantly higher in the Potter Cove web. No differences  
287 were found when compared to the meta-web assembly model (Table 1). Overall, networks differed from the  
288 random null model though presented similarities with the meta-web assembly model.

Table 1: Network global properties across scales. *Meta-web* represents the marine predator-prey relationships of Antarctica, the *Weddell Sea* and *Potter Cove* are local food webs. Z-scores were calculated against 1000 null model networks (random or meta-web assembly models). Quantities marked with '\*' are significant at 1% level. A negative z-score means that the quantity is smaller than the expectation for null model networks; a positive z-score means that is greater.

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

## 289 Sub-structural properties (motifs)

290 The representation of three-species sub-networks with respect to the random model showed similar patterns  
 291 in all networks (Figure 2A). While exploitative competition, apparent competition, and omnivory were over-  
 292 represented, tri-trophic chains were under-represented; all these patterns were significant (Table S3). We  
 293 found that motifs proportions for the three examined spatial scales were different (Chi-squared = 12612,  
 294 p-value < 9.9e-05). this means that local and regional networks are not a random sample of the meta-web.  
 295 With respect to the meta-web assembly model only some of them were significant (Table S4): tri-trophic  
 296 chains and omnivory were under-represented for Weddell Sea, and apparent competition was over-represented  
 297 for Potter Cove (Figure 2B). Contrary to our expectations Potter Cove was more similar to the meta-web  
 298 than Weddell Sea food web.

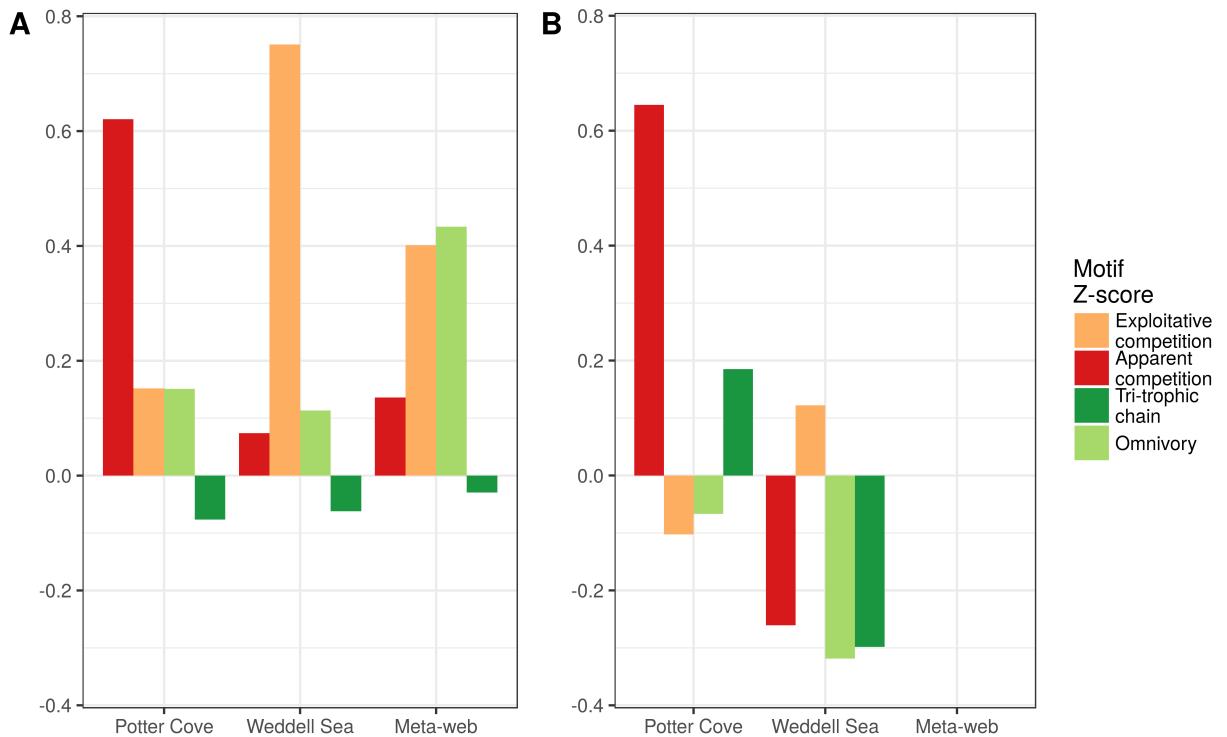


Figure 2: Network motifs z-scores across scales. Motifs are three-node sub-networks counted on each of the networks.: the *Meta-web* represents the marine predator-prey relationships of Antarctica (34.8 million Km<sup>2</sup>); the *Weddell Sea* (3.5 million Km<sup>2</sup>) and *Potter Cove* (6.8 Km<sup>2</sup>) are local food-webs. A. Z-scores estimated with the random null model. B. Z-scores estimated with the meta-web assembly model. Z-scores were normalized by the square root of the sum of the squared z-scores for that food web.

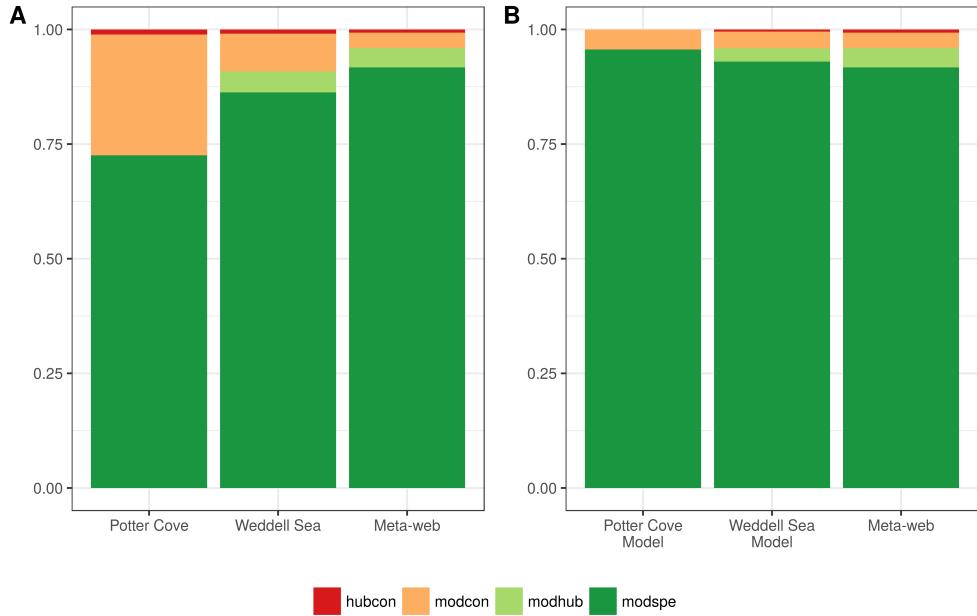


Figure 3: Proportion of topological roles across scales., the *Meta-web* represents the marine predator-prey relationships of Antarctica (34.8 million Km<sup>2</sup>); the *Weddell Sea* (3.5 million Km<sup>2</sup>) and *Potter Cove* (6.8 Km<sup>2</sup>) are local food-webs. The topological roles are: *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 (Chi-squared = 79.31, p-value = 9.9e-05). B. Proportions obtained from the meta-web assembly model; no differences were found (Chi-squared = 5.95, p-value = 0.41)

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

300 The proportion of species displaying the four topological roles was different among food webs (Chi-squared  
301 = 79.31, p-value = 9.9e-05). A higher presence of module connectors (few links, mostly between modules)  
302 was observed in Weddell Sea, while a lack of module hubs (high number of links inside its module) was found  
303 in Potter Cove (Figure 3 A). Which can be related to its low modularity value (Table 1). The proportions  
304 obtained with the meta-web assembly model were not different from the food webs (Chi-squared = 5.95,  
305 p-value = 0.41)(Figura 3 B).

306 The plot of topological roles combined with trophic levels and modularity revealed important details of the  
307 food webs (Figure 4): the meta-web has densely connected compartments but some of them have few low-  
308 connected species (module connectors or module specialists). Additionally, we observed in the Weddell Sea  
309 food web hub connectors with a basal trophic level (Table S5). These are aggregated nodes that represent  
310 generic preys, e.g. fish or zooplankton, they only have incoming links or predators and they cannot have  
311 outgoing links or preys because they comprise several species. Different fish species are present in the Weddell  
312 Sea food web with correctly specified preys and predators, but this reflects the fact that for some predators  
313 there is insufficient knowledge of its preys and aggregated nodes must be added. Thus the existence of  
314 these basal hub connectors is a spurious result of aggregating prey species. The other non-aggregated hub  
315 connectors are highly mobile species with an intermediate trophic level like krill (Table S5). The variation  
316 of maximum trophic levels is evidenced in Figure 4, where both Potter Cove and Meta-web networks had  
317 similar values and Weddell Sea food web exhibited a lower maximum trophic level. this is consistent with  
318 the motifs results.

319 **Discussion**

320 We expected the meta-web structure to reflect the evolutionary constraints of the species interactions, and  
321 the local networks to be influenced and determined by the assembly processes and the local environment.  
322 Our results suggest that the structure of the meta-web does not change significantly as the spatial scale  
323 changes, although there is indeed evidence that the processes of dynamical assembly, habitat filtering and  
324 dispersal limitation are acting. As a consequence, food webs are mainly shaped by evolutionary forces and  
325 less constrained by dynamical assembly processes and local environmental drivers.

326 Global level network properties showed a similar pattern across scales; most of them were significantly  
327 different to the null random model but not to the assembly model. Modularity for Potter Cove food web  
328 was the only property not to differ from the random model. Studies suggest that modularity enhances local

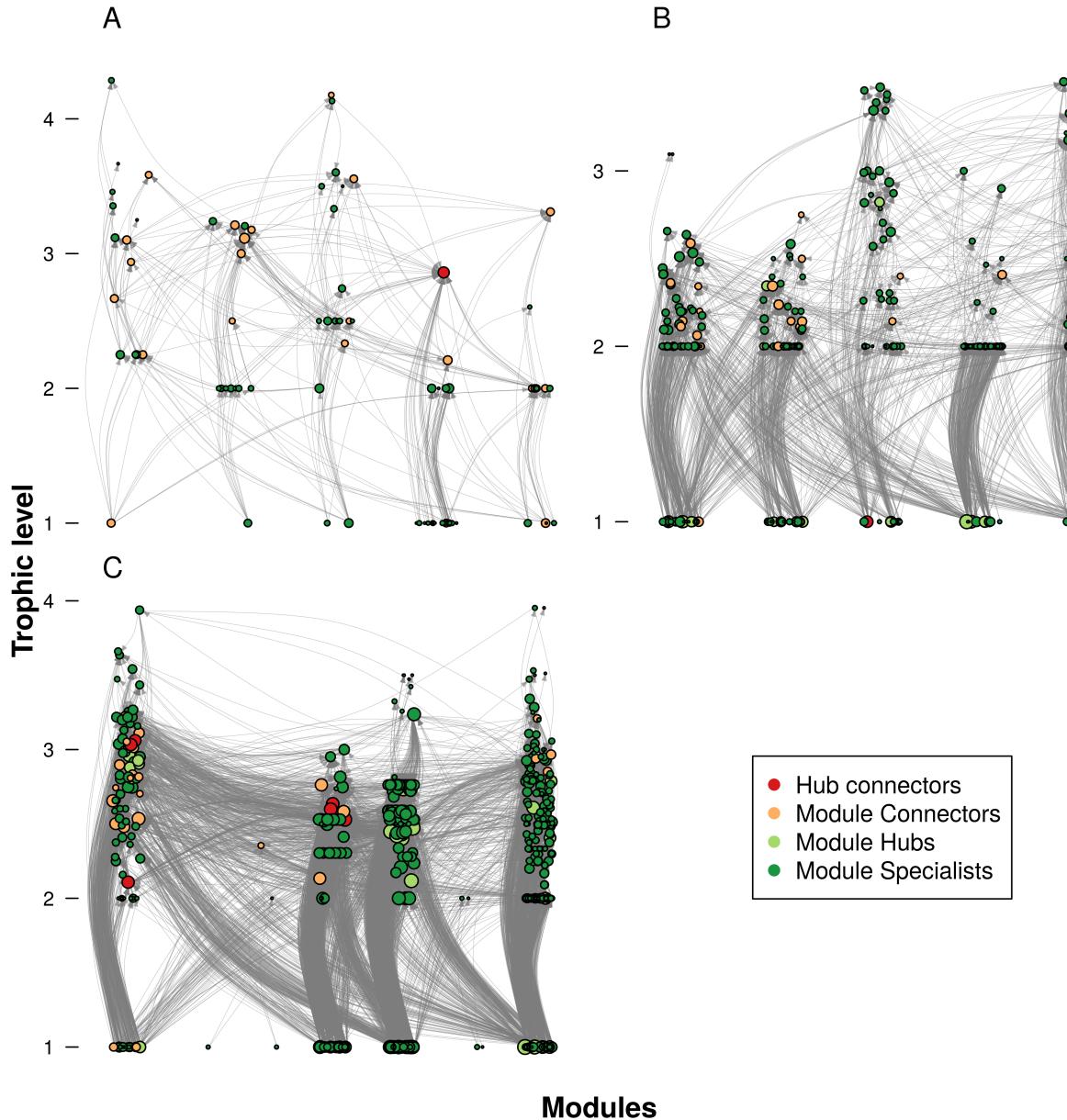


Figure 4: Plot of topological roles combined with trophic levels and modularity for each food web. The topological roles are: *Hub connectors* have a high number of between module links, *Module connectors* have a low number of links mostly between modules, *Module hubs* have a high number of links inside 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.

329 stability (Stouffer and Bascompte 2011), even though stability strongly depends on the interaction strength  
330 configuration (Grilli et al. 2016) and on the existence of external perturbations (Gilaranz et al. 2017). This  
331 is consistent with the values we find for coherence, that is a proxy of dynamical local stability. All networks  
332 are more stable than a random one, but only Weddell Sea food web exhibited a greater trophic coherence  
333 than the assembly model and a higher modularity than the random model. Dynamical stability is expected  
334 to be maximized at the local level but neither of the local food webs presented higher modularity values  
335 than the assembly model. Thus, although this evidence is not conclusive with regard to the importance of  
336 dynamical processes in the assembly of food webs, the structure of the local food webs examined here seem  
337 to be a consequence of the meta-web structure.

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

345 Motifs also have the same representation patterns against the random model. Local food webs should have  
346 motif patterns that increase its persistence. The expected pattern, based in dynamical models, is an over-  
347 representation of omnivory and tri-trophic chains and an under-representation of apparent and exploitative  
348 competition (Stouffer and Bascompte 2010). Other studies showed that tri-trophic chains, exploitative and  
349 apparent competition should be displayed more frequently (Borrelli 2015), but this was based on the stability  
350 of isolated three-species sub-networks and the assumption that during the assembly process these 3 species  
351 sub-networks were selected because of their intrinsic stability (Borrelli et al. 2015). The fact that tri-trophic  
352 (or n-trophic) interactions cannot account fully for the properties of the food webs (Cohen et al. 2009) make  
353 the results based on isolated modules less convincing. Our results showed an over-representation of omnivory,  
354 exploitative competition and apparent competition, this configuration is not the most stable one based on  
355 either criteria. A first hypothetical explanation is that the structure observed in the meta-web is maintained  
356 in local food webs. Despite the fact that almost all motifs were not different from the assembly model,  
357 neither tri-trophic chains and omnivory (lower in Weddell Sea) nor apparent competition (higher in Potter  
358 Cove) followed the pattern expected from theoretical studies. Thus, the assembly process is not random,  
359 there are differences in the frequencies of motifs as the scale change, but the selection of motifs due to its  
360 dynamical stability is not the main driver. This implies that other dynamical processes that influence the

361 presence or absence of species like habitat filtering or dispersal limitation are acting and probably modifying  
362 motif frequencies in empirical food webs. This kind of structures that are a sub-product of process that  
363 happen at a different level have been called spandrels of assembly (Solé and Valverde 2006).

364 As expected all the networks have a short mean trophic level (Williams et al. 2002, Borrelli and Ginzburg  
365 2014) compared with the random model. Different hypothesis were posed to explain this pattern: the low  
366 efficiency of energy transfer between trophic levels, predator size, predator behaviour, and consumer diversity  
367 (Young et al. 2013). These have contradictory support, reviewed by Ward and McCann (2017). Recently, it  
368 has been proposed that maximum trophic level could be related to productivity and ecosystem size depending  
369 on the context but related to energy fluxes that promote omnivory (Ward and McCann 2017). A different  
370 mechanism based on dynamic stability of the whole web was proposed: food webs with shorter trophic levels  
371 (between 2 and 4) that have more omnivore chains are more likely to be stable, which increase the probability  
372 of being observed in nature [Borrelli2014]. We found that mean trophic level of the local food webs was not  
373 different from the assembly model, and omnivory was under-represented. This combination suggests that  
374 the trophic level could also be a spandrel of assembly, inherited from the meta-web structure.

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

386 The spatial scales involved in our study do not represent a continuity; the meta-web and regional web have  
387 a 10 to 1 ratio but the local web is  $10^6$  smaller, besides that most of the global network properties and the  
388 motif structure showed no changes relative to the null model. Thus, we found evidence that local processes  
389 that limit species from the meta-web to local scales are influencing the assembly process but the structure of  
390 the food web originated through an emergent process from evolutionary or co-evolutionary forces seems to  
391 be more important. This could guide us to find a unified theory of ecological interactions that could describe  
392 the diversity of patterns observed in the natural world.

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