

# <sup>1</sup> Ecological Network assembly: how the regional metaweb 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 applied  
<sup>5</sup> mostly to competitive interactions. Similar processes act in trophic networks, i.e. food webs: a regional pool  
<sup>6</sup> of species act as the source from which species colonize local areas, called the metaweb. Local food webs  
<sup>7</sup> are realizations of metawebs that result from assembly processes influenced by migration, habitat filtering,  
<sup>8</sup> stochastic factors, and dynamical constraints. We analyse how the structure of a metaweb influence local  
<sup>9</sup> food webs with different spatial scales, using an assembly model, a random model and properties at three  
<sup>10</sup> levels: emergent global properties that take into account the whole network e.g. modularity, sub-structural  
<sup>11</sup> properties that consider several nodes e.g. motifs, and properties related to one node e.g. topological roles.  
<sup>12</sup> Three independent data-sets were used: the marine Antarctic metaweb, built using a dietary database, the  
<sup>13</sup> Weddell Sea and Potter Cove food webs. We expected that local food webs show properties maximizing  
<sup>14</sup> stability and robustness. Looking at the global properties, we found that local food webs are more similar  
<sup>15</sup> to the random model than the metaweb. Local food webs showed almost no differences with the assembly  
<sup>16</sup> model. For sub-structural properties, the local food webs showed differences compared to the assembly model  
<sup>17</sup> that did not increase its stability. Topological roles showed differences between the metaweb and local food  
<sup>18</sup> webs that were not explained by the assembly model. We found that a great portion of the structure of  
<sup>19</sup> the food webs is inherited from the metaweb implying that evolutionary processes acting on large temporal  
<sup>20</sup> and spatial scales have a major influence. On the contrary, dynamical processes that favour stability have  
<sup>21</sup> a small influence, but habitat filtering or dispersal limitations seem to be important factors that determine  
<sup>22</sup> food web structure.

## <sup>23</sup> Introduction

<sup>24</sup> The characterization of ecological systems as networks of interacting elements has a long history (Paine 1966,  
<sup>25</sup> May 1972, Cohen and Newman 1985). Much of this work has been devoted to investigate network structure  
<sup>26</sup> and its effects on dynamics and stability (Thebault and Fontaine 2010). In recent years a renewed emphasis  
<sup>27</sup> on structural stability (Rohr et al. 2014, Grilli et al. 2017) and new developments in random matrix theory  
<sup>28</sup> has greatly expanded our capability to analyse ecological networks (Allesina et al. 2015). However, the  
<sup>29</sup> analyses of the effects of ecological dynamical processes on food web structure are not so well developed.

30 One such dynamic process is community assembly: how species from a regional pool colonize a site and  
31 build local interactions (Carstensen et al. 2013). Regional species pools are shaped by evolutionary and  
32 biogeographical processes that imply large spatial and temporal scales (Carstensen et al. 2013, Kortsch et al.  
33 2018). More specifically, the assembly of local communities is influenced by dispersal, environmental filters,  
34 biotic interactions and stochastic events (HilleRisLambers et al. 2012). These processes have been studied  
35 by means of metacommunity theory (Leibold et al. 2017), where different spatial assemblages are connected  
36 through species dispersal.

37 Metacommunity theory provides a framework for assessing the roles of local- and regional-scale dynamics  
38 (Leibold et al. 2004, Baiser et al. 2013). This approach has been applied mostly to competitive interactions,  
39 whereas trophic interactions have received less attention (Baiser et al. 2016). Recently, there has been an  
40 increase in food web assembly studies, integrating them with island biogeography (Gravel et al. 2011) and  
41 with metacommunity (Pillai et al. 2011, Liao et al. 2016). These were mainly focused on complexity-stability  
42 effects (Mougi and Kondoh 2016). Previous attempts to study the food web assembly process have used  
43 motifs as building blocks of local communities (Baiser et al. 2016). Motifs are sub-structures in networks  
44 composed of species and links whose frequency deviates from the expected in a random network (Milo et al.  
45 2002). By comparing motif representation at different spatial scales—from local to regional—the process of  
46 assembly of interactions may be revealed (Baiser et al. 2016), e.g. if the same processes structure the food  
47 web across scales, motif representation should be the same. Besides, as local food webs should have tighter  
48 links and stronger interaction rates, other structural properties should change as scale changes (Coll et al.  
49 2011).

50 The objective of the present study is to analyse the process of food web assembly addressing how multilevel  
51 network properties change across different spatial scales. For this we considered: the Antarctic metaweb,  
52 representing an area of 34.8 million Km<sup>2</sup>, and build from a dietary database (Raymond et al. 2011); the  
53 Weddell Sea food web that represents 3.5 million Km<sup>2</sup> (Jacob et al. 2011); and the Potter Cove network  
54 that represents 6.8 Km<sup>2</sup>, (Marina et al. 2018a).

55 There are several approaches to characterize the structure of ecological networks: emergent or global prop-  
56 erties that focus on averages over the entire network (e.g. modularity or connectance), and more local  
57 properties that focus on how one or several species are related to the whole. Global properties related to  
58 resilience and stability are fundamental to understand the response of ecological networks to global threats  
59 like climate change and biological invasions. One of these properties is the small-world pattern, associated  
60 with rapid responses to disturbances and resistance to secondary extinctions (Montoya and Solé 2002). The  
61 small-world pattern is related to two global properties: the average of the shortest distance between all

62 species, called the characteristic path length, and the clustering coefficient, the probability that two species  
63 linked to the same species are linked. Then, small-world patterns imply a high level of clustering and a short  
64 average path length compared to random networks (Watts and Strogatz 1998). This pattern comes from  
65 the general network theory, beyond ecological networks, and has been recently applied to marine food webs  
66 (Gray et al. 2016, Navia et al. 2016, Bornatowski et al. 2017, Marina et al. 2018b).

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

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

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

91 If we consider a subset of linked species inside the food web this forms a sub-network, when the abundance of  
92 one of these sub-networks deviates significantly from a null model network, this is called a motif (Milo et al.

93 2002). Besides this definition, in the ecological literature motif has been used as a synonym of sub-network.  
94 We analyse here the three-species sub-networks that have been most studied theoretically and empirically  
95 in food webs (Prill et al. 2005, Stouffer et al. 2007, Baiser et al. 2016). Specifically, we focused on four of  
96 the thirteen possible three-species sub-networks: apparent competition, exploitative competition, tri-trophic  
97 chain, and omnivory (Figure 1).

98 The frequency of motifs at different spatial scales (i.e over-represented, under-represented, or random) may  
99 reveal aspects about the process behind the assembly of interactions (Baiser et al. 2016). If the same processes  
100 structure the food web across scales, motif representation should be the same. Ecological interactions occur  
101 at the local scale so differences may show the importance of local interactions in the assembly of the food web.

102 During the assembly process those motif structures that are less dynamically stable tend to disappear from  
103 the food web (Borrelli 2015), this has been called non-adaptative systemic selection (Borrelli et al. 2015).

104 The process is non-adaptative because the selection process is not adapting the system to local conditions  
105 (Borrelli et al. 2015).

106 In this study, we analyze food web assembly from a metaweb to local networks with different spatial scales.  
107 To our knowledge, combining modularity, trophic coherence and motifs at different spatial scales has not  
108 been applied in food web studies up to now. First we compared the networks—including the metaweb—  
109 against a random network model (i.e. absence of ecological mechanisms), and a metaweb assembly model  
110 (i.e. representing an assembly process). We hypothesize that network properties will change from the metaweb  
111 to a local scale at which interactions are realized. We particularly expect global properties related to resilience  
112 and stability to be close to the random null model at the metaweb scale and significantly different at the  
113 local scale; a greater frequency of stable motifs in the local food webs; as well as a change in the frequency  
114 of topological roles since habitat filtering or dispersal limitation act at the local food web scale. These last  
115 two changes also should be reflected as differences from the metaweb assembly model.

## 116 Methods

117 The three datasets used in this study encompass a wide range of spatial scales and were collected inde-  
118 pendently. The Southern Ocean database compiled by Raymond et al. (2011) was used to construct the  
119 Antarctic metaweb selecting only species located at latitudes higher than 60°S. Raymond et al. (2011)  
120 compiled information from direct sampling methods of dietary assessment, including gut, scat, and bolus  
121 content analysis, stomach flushing, and observed feeding. We considered that the metaweb is the regional  
122 pool of species defined by the biogeographic Antarctic region. Next we analysed two local food webs: the

123 Weddell Sea food web dataset includes species situated between 74°S and 78°S with a West-East extension  
124 of approximately 450 km, and comprises all information about trophic interactions available for the zone  
125 since 1983 (Jacob et al. 2011). The Potter Cove dataset comes from a 4 km long and 2.5 km wide Antarctic  
126 fjord located at 62°14'S, 58°40'W, South Shetland Islands (Marina et al. 2018a). These food web datasets  
127 comprise benthic and pelagic habitats of the Antarctic ecosystem, few aggregated low-trophic level groups  
128 (e.g. detritus, diatoms, phytoplankton, zooplankton) and a high resolution of the macroalgae community  
129 (i.e. 24 biological species of red, brown and green macroalgae). The macroalgae community is responsible  
130 for the majority of the primary production and supports a large fraction of secondary production in Antarc-  
131 tic fjords (Quartino and Boraso de Zaixso 2008, Valdivia et al. (2015)). Higher trophic levels comprise:  
132 invertebrate (e.g. ascidians, sponges, isopods, amphipods, bivalves, gastropods, cephalopods, echinoderms)  
133 and vertebrate predator groups (e.g. demersal and pelagic fishes, penguins, seals and whales). For more  
134 information about these datasets we refer to the original publications. To make datasets compatible, we first  
135 checked taxonomic names for synonyms, and second, we added species (either prey or predator) with their  
136 interactions to the metaweb when the local food webs contain a greater taxonomic resolution. When the  
137 metaweb contained more detailed records, only for predators we added them to the local food webs checking  
138 for its geographic range. We removed cannibalistic (self-links) and double arrows (i.d. A eats B and B eats  
139 A).

## 140 Analysis

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

## 150 Null models

151 We considered two null models, the Erdős-Rényi random graph (Erdős and Rényi 1959), and the metaweb  
152 assembly model. An Erdős-Rényi network is constructed fixing the number of edges and nodes and assigning

153 at random the  $m$  edges to the  $n$  nodes with equal probability (Erdős and Rényi 1959, Baiser et al. 2016).  
 154 We restricted the random model eliminating double arrows and cannibalistic links. To calculate trophic level  
 155 and the coherence parameter (see below) we further restricted to random webs with at least one basal node,  
 156 to make these calculations possible. Since the random model represents the absence of any network assembly  
 157 mechanism, the comparison against it does not guarantee information on this aspect.  
 158 In order to consider network assembly mechanisms we designed a dynamic metaweb assembly model. In this  
 159 model species migrate from the metaweb to a local web with a uniform probability  $c$ , and become extinct from  
 160 the local web with probability  $e$ ; a reminiscence of the theory of island biogeography (MacArthur and Wilson  
 161 1967, Gravel et al. 2011), but with the addition of network structure. Species migrate with their potential  
 162 network links from the metaweb, then in the local web species can only survive if at least one of its preys is  
 163 present, or if it is a basal species. When a species goes extinct locally it may produce secondary extinctions;  
 164 we check that the local predators maintain at least one prey if not they become extinct independent of the  
 165 probability  $e$ . We simulated this model in time and it eventually reaches an equilibrium that depends on the  
 166 migration and extinction probabilities but also on the structure of the metaweb. The ratio of immigration  
 167 vs. extinction  $\alpha = c/e$  is hypothesized to be inversely related to the distance to the mainland (MacArthur  
 168 and Wilson 1967), and as extinction  $e$  should be inversely proportional to population size (Hanski 1999), the  
 169 ratio  $\alpha$  is also hypothesized to be related to the local area.  
 170 For the random model we simulated networks with the same number of nodes  $n$  and edges  $m$  as the empirical  
 171 networks; for the metaweb model we fitted the parameters  $g$  and  $e$  to obtain networks with  $n$  and  $m$  close  
 172 to the empirical networks. This implies that  $\alpha$  should reflect the differences in areas of the two local food  
 173 webs. For details of the fitting and simulations see Appendix.

#### 174 **Small-world topology**

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

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

180 where  $E_i$  is the number of edges between the neighbours of  $i$ . The clustering coefficient of the network is

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

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

185 and

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

186 where  $C_g$  and  $L_g$  are the clustering coefficient and the mean shortest path length of the network of interest  
 187  $G$ ;  $C_g$  and  $C_{null}$  are the same quantities for the corresponding null model. Thus, the quantitative small-  
 188 world-ness is defined as:

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

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

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

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

## 195 Coherence

196 The second global property is called trophic coherence (Johnson et al. 2014), and is related to stability in  
 197 the sense that small perturbations could get amplified or vanished, which is called local linear stability (May  
 198 1972, Rohr et al. 2014). We first needed to estimate the trophic level of a node  $i$ , defined as the average  
 199 trophic level of its preys plus 1. That is:

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

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

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

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

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

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

## 218 Modularity

219 An intermediate level property (i.e. between the whole network and the individual species) is modularity. It  
 220 measures how strongly sub-groups of species interact between them compared with the strength of interaction  
 221 with other sub-groups (Newman and Girvan 2004). These sub-groups are called compartments, and in order

222 to find the best partition we used a stochastic algorithm based on simulated annealing (Reichardt and  
 223 Bornholdt 2006). Simulated annealing allows to maximize modularity without getting trapped in local  
 224 maxima configurations (Guimerà and Nunes Amaral 2005). The index of modularity was defined as:

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

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

## 229 Motifs

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

## 236 Topological roles

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

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

242 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  
 243 deviation of  $k_{is}$  over all species in  $s$ . The participation coefficient  $PC$  estimates the distribution of the links  
 244 of species  $i$  among modules; thus it can be defined as:

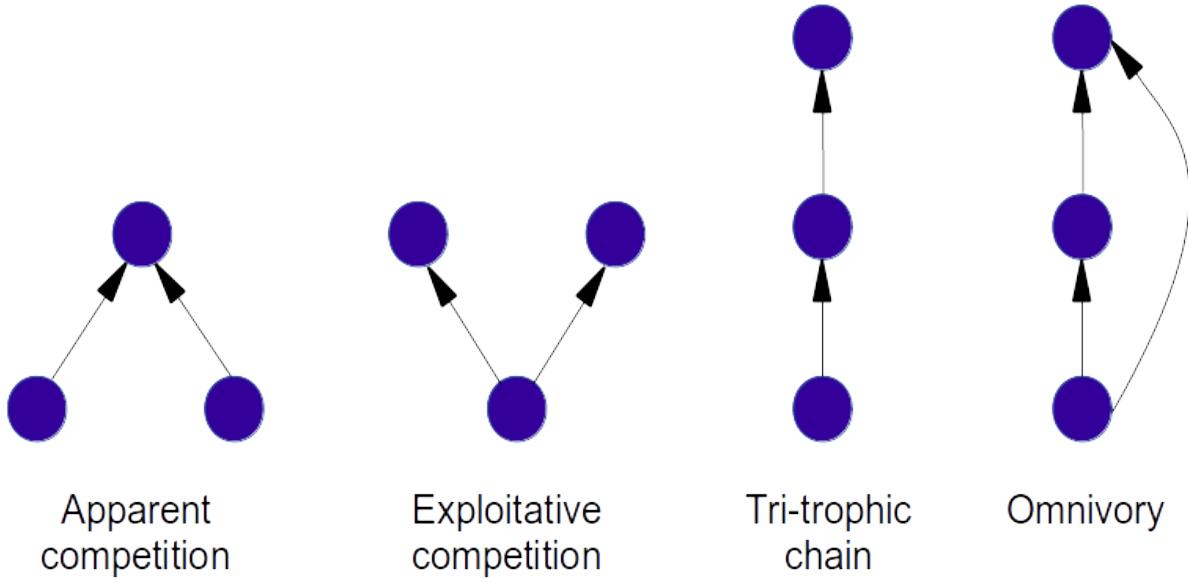


Figure 1: The four three-species sub-networks analysed: apparent competition, exploitative competition, tri-trophic chain, and omnivory. These four sub-networks have been explored both theoretically and empirically in ecological networks and are the most common sub-networks found in food webs

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

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

To determine each species' role the  $dz - PC$  parameter space was divided into four areas, modified from Guimerà and Nunes Amaral (2005), using the same scheme as Kortsch et al. (2015). Two thresholds were used to define the species' roles:  $PC = 0.625$  and  $dz = 2.5$ . If a species had at least 60% of links within 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 parameter space defines species with relatively high number of links, the majority within its own module. If a species had  $PC < 0.625$  and  $dz < 2.5$ , then it was called a peripheral or specialist; this refers to a species with relatively few links, mostly within its module. Species that had  $PC \geq 0.625$  and  $dz < 2.5$  were considered module connectors, since they have relatively few links, mostly between modules. Finally, if a species had  $PC \geq 0.625$  and  $dz \geq 2.5$ , then it was classified as a super-generalist or hub-connector, because

259 it has high between- and within-module connectivity. To test if the proportion of species' roles changed  
260 between networks we performed a Pearson's Chi-squared test with simulated p-value based on 10000 Monte  
261 Carlo replicates. Also, we tested if these proportions changed for one realization of the metaweb assembly  
262 model fitted for both local networks (i.e. Weddell Sea and Potter Cove food webs).

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

266 All analyses and simulations were made in R version 3.4.3 (R Core Team 2017), using the igraph package  
267 version 1.1.2 (Csardi and Nepusz 2006) for motifs and topological roles analyses, and NetIndices (Kones et  
268 al. 2009) for trophic level calculations. Source code and data is available at figshare <https://figshare.com/>  
269 ADD\_URL\_HERE and github [https://github.com//ADD\\_URL\\_HERE](https://github.com//ADD_URL_HERE).

## 270 Results

### 271 Global network properties

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

## 285 Sub-structural properties (motifs)

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

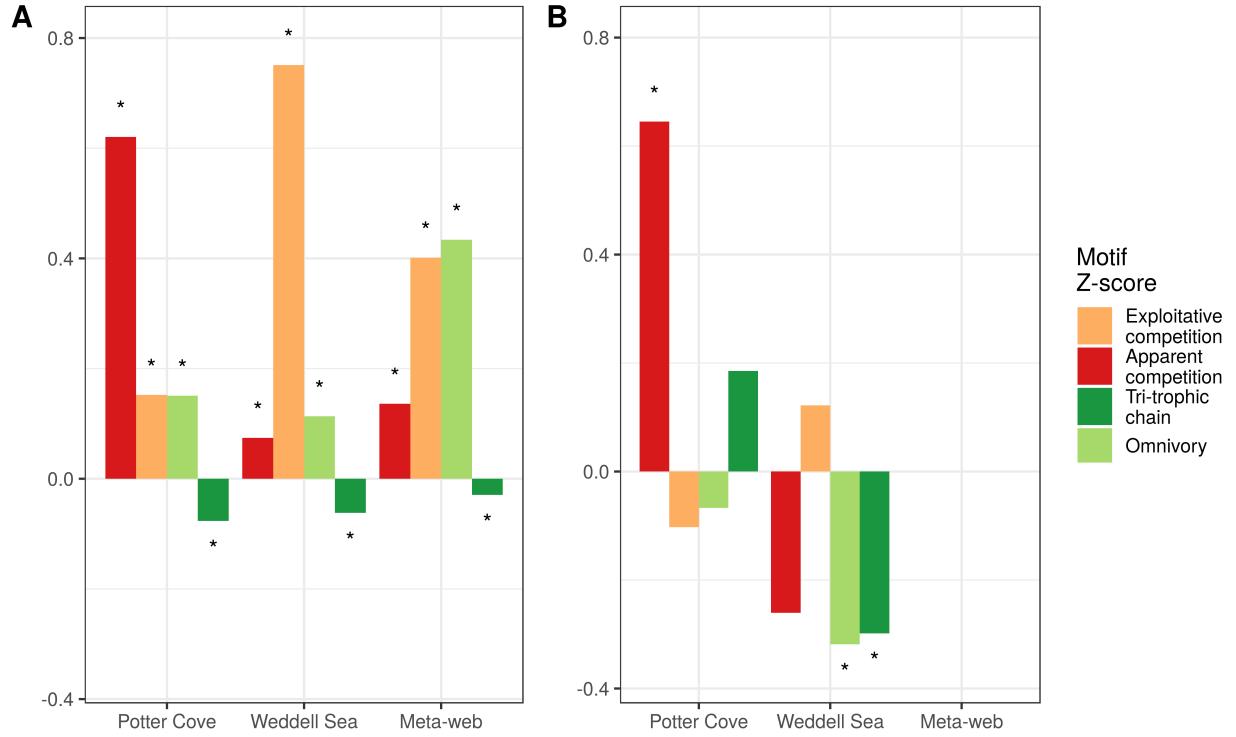


Figure 2: Network motifs z-scores across scales. Motifs are three-node sub-networks counted on each of the networks.: the *Metaweb* represents the marine predator-prey relationships of Antarctica (34.8 million Km<sup>2</sup>); the *Weddell Sea* (3.5 million Km<sup>2</sup>) and *Potter Cove* (6.8 Km<sup>2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

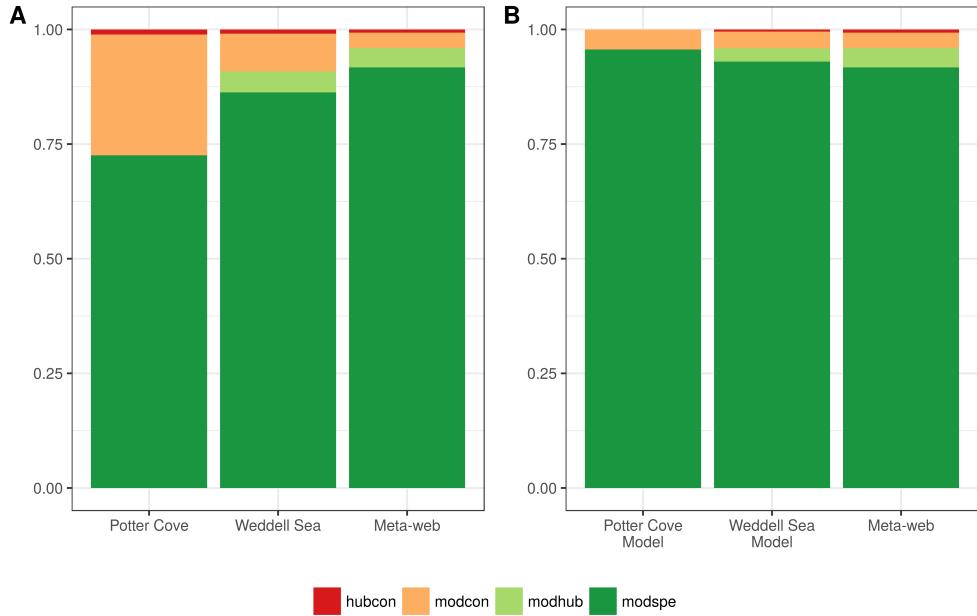


Figure 3: Proportion of topological roles across scales., the *Metaweb* represents the marine predator-prey relationships of Antarctica (34.8 million Km<sup>2</sup>); the *Weddell Sea* (3.5 million Km<sup>2</sup>) and *Potter Cove* (6.8 Km<sup>2</sup>) are local food webs. The topological roles are: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

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

296 The proportion of species displaying the four topological roles was different among food webs (Chi-squared  
297 = 79.31, p-value = 9.9e-05). A higher presence of module connectors (few links, mostly between modules)  
298 was observed in Weddell Sea, while a lack of module hubs (high number of links inside its module) was found  
299 in Potter Cove (Figure 3 A), which can be related to its low modularity value (Table 1). The proportions  
300 obtained with the metaweb assembly model were not different from the food webs (Chi-squared = 5.95,  
301 p-value = 0.41)(Figura 3 B).

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

314 **Discussion**

315 We expected the metaweb structure to reflect the evolutionary constraints of the species interactions, and  
316 the local networks to be influenced and determined by the assembly processes and the local environment.  
317 Our results showed that the structure of the metaweb does not change significantly in many properties as  
318 the spatial scale changes. We did not find a clear pattern in the properties expected to be maximized by  
319 dynamical assembly and local stability, but we found clear differences in the properties influenced by habitat  
320 filtering and dispersal limitation. As a consequence, food webs would be mainly shaped by evolutionary  
321 forces and local environment drivers and less constrained by dynamical and assembly processes.  
322 Global level network properties showed a similar pattern across scales; most of them were significantly  
323 different from the random null model but not from the assembly model. Modularity for Potter Cove food  
324 web was the only property that is similar to the random model. Studies suggest that modularity enhances

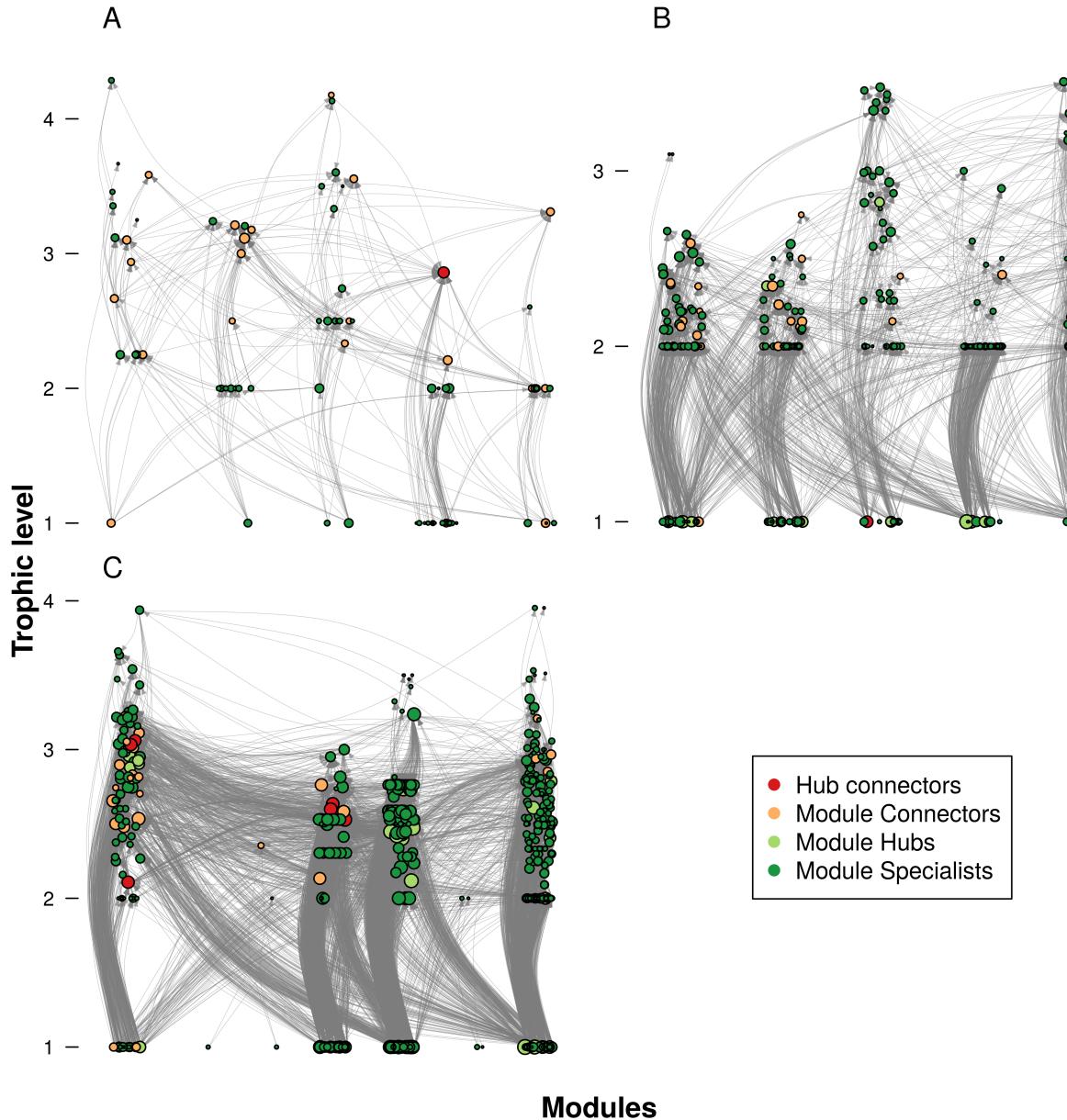


Figure 4: Plot of topological roles combined with trophic levels and modularity for each food web. The topological roles are: *Hub connectors* have a high number of between module links, *Module connectors* have a low number of links mostly between modules, *Module hubs* have a high number of links inside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

325 local stability (Stouffer and Bascompte 2011), even though stability strongly depends on the interaction  
326 strength configuration (Grilli et al. 2016) and on the existence of external perturbations (Gilaranz et al.  
327 2017). We did not find modularity is greater than the metaweb assembly model, the existence of a modular  
328 structure could be related to different habitats—in marine environments could be benthic and pelagic (Zhao  
329 et al. 2017). Thus we observed that the modular structure is present in the metaweb and not produced  
330 by a maximization of local stability. Dynamical stability is expected to be maximized at the local level but  
331 we only found that Weddell Sea food web exhibited a greater trophic coherence than the assembly model.  
332 Thus, although this evidence is not conclusive with regard to the importance of dynamical processes in the  
333 assembly of food webs, the structure of the local food webs examined here seem to be a consequence of the  
334 metaweb structure.

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

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

357 dynamical stability is not the main driver. This implies that other dynamical processes that influence the  
358 presence or absence of species like habitat filtering or dispersal limitation are acting and probably modifying  
359 motif frequencies in empirical food webs. This kind of structures that are a sub-product of processes that  
360 happen at a different level have been called spandrels of assembly (Solé and Valverde 2006).

361 As expected all the networks have a short mean trophic level (Williams et al. 2002, Borrelli and Ginzburg  
362 2014) compared with the random model. Different hypotheses were posed to explain this pattern: the low  
363 efficiency of energy transfer between trophic levels, predator size, predator behaviour, and consumer diversity  
364 (Young et al. 2013). These have contradictory support, reviewed by Ward and McCann (2017). Recently, it  
365 has been proposed that maximum trophic level could be related to productivity and ecosystem size depending  
366 on the context but related to energy fluxes that promote omnivory (Ward and McCann 2017). A different  
367 mechanism based on dynamic stability of the whole web was proposed: food webs with shorter trophic levels  
368 (between 2 and 4) that have more omnivore chains are more likely to be stable, which increase the probability  
369 of being observed in nature (Borrelli and Ginzburg 2014). We found that mean trophic level of the local food  
370 webs was not different from the assembly model, and omnivory was under-represented. This combination  
371 suggests that the trophic level could also be a spandrel of assembly, inherited from the metaweb structure.

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

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

<sup>389</sup> the diversity of patterns observed in the natural world.

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