

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

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¹⁵ Data accessibility statement: all the raw data is from public repositories, the data supporting the results
¹⁶ will be archived at figshare public repository

¹⁷ **Abstract**

¹⁸ The idea that ecological networks are built in a sequence of colonization events is not new but has been applied
¹⁹ mostly to competitive interactions. Similar processes act in trophic networks, i.e. food webs: a regional pool
²⁰ of species act as the source from which species colonize local areas, called the metaweb. Local food webs
²¹ are realizations of metawebs that result from assembly processes influenced by migration, habitat filtering,
²² stochastic factors, and dynamical constraints. We analyse how the structure of a metaweb influence local
²³ food webs with different spatial scales, using an assembly model, a random model and properties at three
²⁴ levels: emergent global properties that take into account the whole network e.g. modularity, sub-structural
²⁵ properties that consider several nodes e.g. motifs, and properties related to one node e.g. topological roles.

²⁶ Three independent data-sets were used: the marine Antarctic metaweb, built using a dietary database and
²⁷ representing 34.8 million Km², the Weddell Sea (3.5 million Km²) and Potter Cove (6.8 Km²) food webs. We

expected that local food webs show properties maximizing stability and robustness. Looking at the global properties, we found that local food webs are more similar to the random model than the metaweb. The assembly model only takes into account migration, local extinction and secondary extinctions, local food webs showed almost no differences with the assembly model. For sub-structural properties the local food webs showed differences compared to the assembly model that did not increase its stability. Topological roles showed differences between the metaweb and local food webs that were not explained by the assembly model. We found that a great portion of the structure of the food webs is inherited from the metaweb implying that evolutionary processes acting on large temporal and spatial scales have a major influence. On the contrary, dynamical processes that favour stability have a small influence, but habitat filtering or dispersal limitations seem to be important factors that determine food web structure.

Introduction

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

Metacommunity theory provides a framework for assessing the roles of local- and regional-scale dynamics (Leibold *et al.* 2004; Baiser *et al.* 2013). This approach has been applied mostly to competitive interactions, whereas trophic interactions have received less attention (Baiser *et al.* 2016). Recently, there has been an increase in food web assembly studies, integrating them with island biogeography (Gravel *et al.* 2011) and with metacommunity (Pillai *et al.* 2011; Liao *et al.* 2016). These were mainly focused on complexity-stability effects (Mougi & Kondoh 2016). Previous attempts to study the food web assembly process have used motifs

58 as building blocks of local communities (Baiser *et al.* 2016). Motifs are sub-structures in networks composed
59 of species and links whose frequency deviates from the expected in a random network (Milo *et al.* 2002). By
60 comparing motif representation at different spatial scales—from local to regional—the process of assembly
61 of interactions may be revealed (Baiser *et al.* 2016), e.g. if the same processes structure the food web across
62 scales, motif representation should be the same. Besides, as local food webs should have tighter links and
63 stronger interaction rates, other structural properties should change as scale changes (Coll *et al.* 2011).

64 The objective of the present study is to analyse the process of food web assembly addressing how multilevel
65 network properties change across different spatial scales. For this we considered: the Antarctic metaweb,
66 representing an area of 34.8 million Km², and build from a dietary database (Raymond *et al.* 2011); the
67 Weddell Sea food web that represents 3.5 million Km² (Jacob *et al.* 2011); and the Potter Cove network
68 that represents 6.8 Km², (Marina *et al.* 2018a).

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

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

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

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

105 If we consider a subset of linked species inside the food web this forms a sub-network, when the abundance of
106 one of these sub-networks deviates significantly from a null model network, this is called a motif (Milo *et al.*
107 2002). Besides this definition, in the ecological literature motif has been used as a synonym of sub-network.
108 We analyse here the three-species sub-networks that have been most studied theoretically and empirically
109 in food webs (Prill *et al.* 2005; Stouffer *et al.* 2007; Baiser *et al.* 2016). Specifically, we focused on four of
110 the thirteen possible three-species sub-networks: apparent competition, exploitative competition, tri-trophic
111 chain, and omnivory (Figure 1).

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

120 In this study, we analyze food web assembly from a metaweb to local networks with different spatial scales.

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

130 Methods

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

152 for its geographic range. We removed cannibalistic (self-links) and double arrows (i.d. A eats B and B eats
153 A).

154 **Analysis**

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 de 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 predaes 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 **Null models**

165 We considered two null models, the Erdős-Rényi random graph (Erdős & Rényi 1959), and the metaweb
166 assembly model. An Erdős-Rényi network is constructed fixing the number of edges and nodes and assigning
167 at random the m edges to the n nodes with equal probability (Erdős & Rényi 1959; Baiser *et al.* 2016). We
168 restricted the random model eliminating double arrows and cannibalistic links. To calculate trophic level
169 and the coherence parameter (see below) we further restricted to random webs with at least one basal node,
170 to make these calculations possible. Since the random model represents the absence of any network assembly
171 mechanism, the comparison against it does not guarantee information on this aspect.

172 In order to consider network assembly mechanisms we designed a dynamic metaweb assembly model. In this
173 model species migrate from the metaweb to a local web with a uniform probability c , and become extinct from
174 the local web with probability e ; a reminiscence of the theory of island biogeography (MacArthur & Wilson
175 1967; Gravel *et al.* 2011), but with the addition of network structure. Species migrate with their potential
176 network links from the metaweb, then in the local web species can only survive if at least one of its preys is
177 present, or if it is a basal species. When a species goes extinct locally it may produce secondary extinctions;
178 we check that the local predators maintain at least one prey if not they become extinct independent of the
179 probability e . We simulated this model in time and it eventually reaches an equilibrium that depends on the
180 migration and extinction probabilities but also on the structure of the metaweb. The ratio of immigration

181 vs. extinction $\alpha = c/e$ is hypothesized to be inversely related to the distance to the mainland (MacArthur
182 & Wilson 1967), and as extinction e should be inversely proportional to population size (Hanski 1999), the
183 ratio α is also hypothesized to be related to the local area.

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

188 **Small-world topology**

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

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

194 where E_i is the number of edges between the neighbours of i . The clustering coefficient of the network is the
195 average of c_i over all nodes. The original definition of small-world networks is conceptual (Watts & Strogatz
196 1998), a network G is small-world when it has a similar mean shortest path length but greater clustering
197 than an Erdős-Rényi random network with the same number of nodes n and edges m . For the quantitative
198 version of the small-world pattern we followed Humphries & Gurney (2008); we need to define:

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

199 and

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

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

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

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

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

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

209 Coherence

210 The second global property is called trophic coherence (Johnson *et al.* 2014), and is related to stability in
 211 the sense that small perturbations could get amplified or vanished, which is called local linear stability (May
 212 1972; Rohr *et al.* 2014). We first needed to estimate the trophic level of a node i , defined as the average
 213 trophic level of its preys plus 1. That is:

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

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

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

218 that is the standard deviation of the distribution of all trophic distances. A food web is more coherent
 219 when q is closer to zero, thus the maximal coherence is achieved when $q = 0$, and corresponds to a layered
 220 network in which every node has an integer trophic level (Johnson *et al.* 2014; Johnson & Jones 2017). To
 221 compare coherence and trophic level we generated 1000 null model networks with at least one basal species

222 and the same number of species and links—or approximately the same—than the network of interest. Then
 223 we calculated the 99% confidence interval using the 0.5% and 99.5% quantiles of the distribution of q ; we
 224 also calculated the confidence interval for the mean trophic level tp . We calculated the z-scores as:

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

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

232 Modularity

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

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

239 where s is the number of modules or compartments, I_s is the number of links between species in the module
 240 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
 241 assess the significance of our networks we calculate the 99% confidence intervals and z-scores based on 1000
 242 null model networks as previously described.

243 Motifs

244 We considered four of the thirteen possible three-species sub-networks: apparent competition, exploitative
 245 competition, tri-trophic chain, and omnivory (Figure 1). These are the only motifs present in all networks

analysed here. We compared the frequency of these motifs to 1000 null model networks using the 99% confidence interval and the z-score as previously described. To determine if the proportions of motifs change across networks we use the Pearson's Chi-squared test with simulated p-value based on 10000 Monte Carlo replicates.

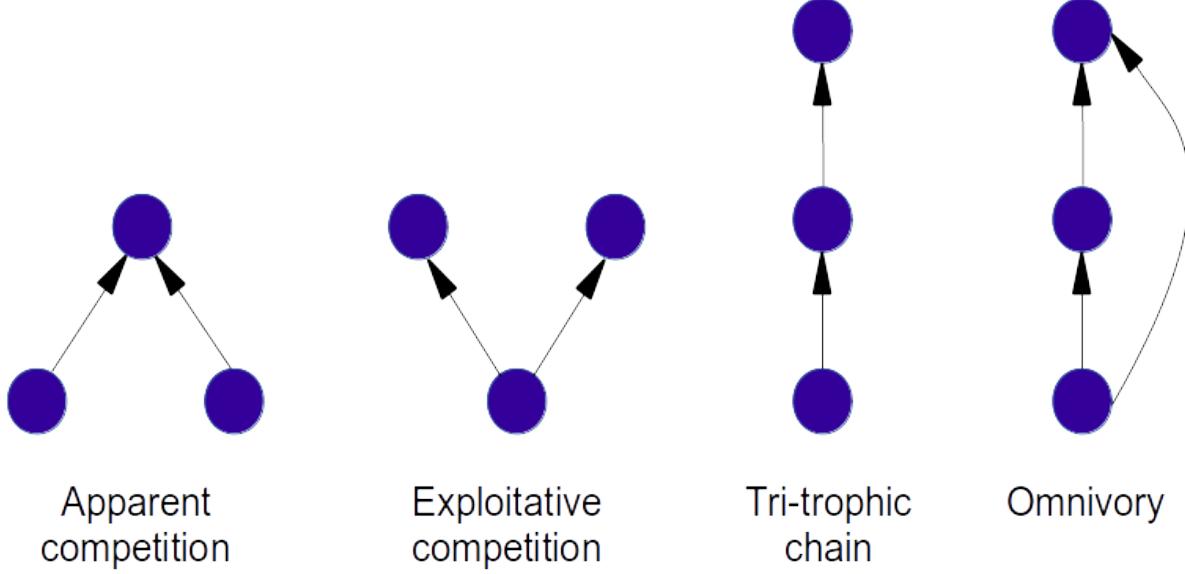


Figure 1: The four three-species sub-networks analysed: apparent competition, exploitative competition, tri-trophic chain, and omnivory. These four sub-networks have been explored both theoretically and empirically in ecological networks and are the most common sub-networks found in food webs

250 Topological roles

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

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

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

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

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

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

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

284 **Results**

285 **Global network properties**

286 The number of trophic species (size), links and connectance (Table 1), were in concordance with values found
287 for marine food webs (Marina *et al.* 2018b). Based on the random null model, all networks presented the
288 small-world topology as their small-world-ness index was larger than the 99% confidence interval (Table 1 &
289 S1). However, we did not find differences between the local food webs and the assembly model (Table 1 &
290 S2). Regarding trophic coherence, all networks presented negative random z-scores and significantly smaller
291 q values (Table 1 & S1). thus they are more locally stable as they are more coherent. Using the metaweb
292 assembly model, the Weddell Sea food web showed negative z-scores lower than 2, and Potter Cove food web
293 exhibited no significant differences (Table 1 & S2). Mean trophic level results were similar among networks
294 and significantly lower than the random null model (Table 1 & S1), though were not significantly different
295 when compared to the metaweb model trophic levels . Modularity values for the empirical food webs were
296 greater than the random model, but not significantly higher in the Potter Cove web. No differences were
297 found when compared to the metaweb assembly model (Table 1). Overall, networks differed from the random
298 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 z-score	1.29	1.09	
Modularity	0.37	0.48	0.45
Modularity random z-score	0.89	*18.97	*85.75

Network	Potter Cove	Weddell Sea	Metaweb
Modularity assembly z-score	-0.38	0.41	

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

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

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

310 The proportion of species displaying the four topological roles was different among food webs (Chi-squared
 311 = 79.31, p-value = 9.9e-05). A higher presence of module connectors (few links, mostly between modules)
 312 was observed in Weddell Sea, while a lack of module hubs (high number of links inside its module) was found
 313 in Potter Cove (Figure 3 A), which can be related to its low modularity value (Table 1). The proportions
 314 obtained with the metaweb assembly model were not different from the food webs (Chi-squared = 5.95,
 315 p-value = 0.41) (Figura 3 B).

316 The plot of topological roles combined with trophic levels and modularity revealed important details of the
 317 food webs (Figure 4): the metaweb has densely connected compartments but some of them have few low-
 318 connected species (module connectors or module specialists). Additionally, we observed in the Weddell Sea
 319 food web hub connectors with a basal trophic level (Table S5). These are aggregated nodes that represent
 320 generic preys, e.g. fish or zooplankton, they only have incoming links or predators and they cannot have
 321 outgoing links or preys because they comprise several species. Different fish species are present in the
 322 Weddell Sea food web with detailed information about preys and predators, but for some predators there is
 323 insufficient knowledge of its preys and aggregated nodes must be added. Thus the existence of these basal
 324 hub connectors is a spurious result of aggregating prey species. The other non-aggregated hub connectors
 325 are highly mobile species with an intermediate trophic level like krill (Table S5). The variation of maximum

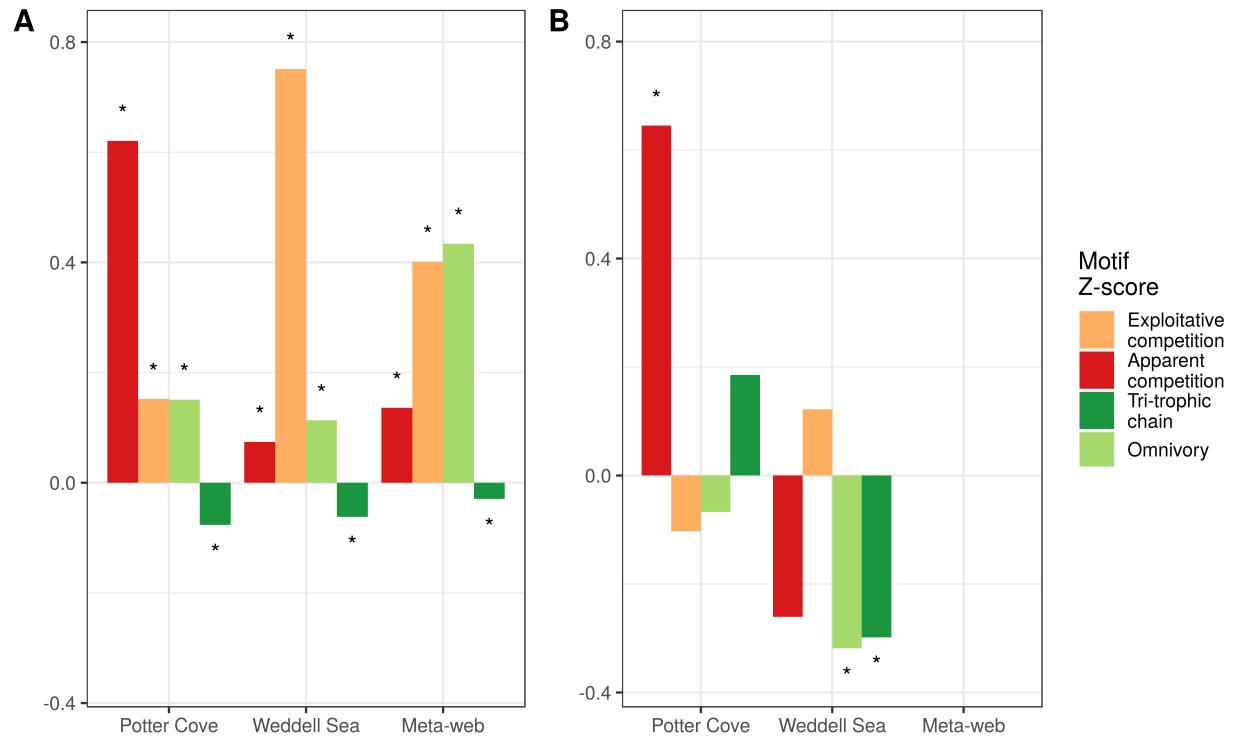


Figure 2: Network motifs z-scores across scales. Motifs are three-node sub-networks counted on each of the networks.: the *Metaweb* represents the marine predator-prey relationships of Antarctica (34.8 million Km²); the *Weddell Sea* (3.5 million Km²) and *Potter Cove* (6.8 Km²) are local food webs. 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.

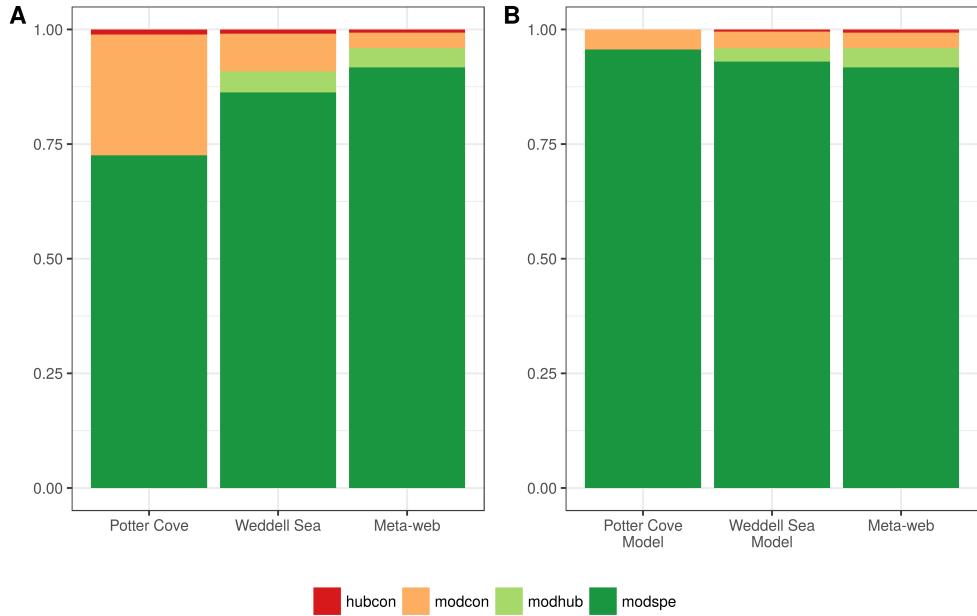


Figure 3: Proportion of topological roles across scales., the *Metaweb* represents the marine predator-prey relationships of Antarctica (34.8 million Km²); the *Weddell Sea* (3.5 million Km²) and *Potter Cove* (6.8 Km²) are local food webs. The topological roles are: *Hub connectors*, high number of 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)

326 trophic levels is evidenced in Figure 4, where both Potter Cove and Metaweb networks had similar values
327 and Weddell Sea food web exhibited a lower maximum trophic level.

328 Discussion

329 We expected the metaweb structure to reflect the evolutionary constraints of the species interactions, and
330 the local networks to be influenced and determined by the assembly processes and the local environment.
331 Our results showed that the structure of the metaweb does not change significantly in many properties as
332 the spatial scale changes. We did not find a clear pattern in the properties expected to be maximized by
333 dynamical assembly and local stability, but we found clear differences in the properties influenced by habitat
334 filtering and dispersal limitation. As a consequence, food webs would be mainly shaped by evolutionary
335 forces and local environment drivers and less constrained by dynamical and assembly processes.

336 Global level network properties showed a similar pattern across scales; most of them were significantly
337 different from the random null model but not from the assembly model. Modularity for Potter Cove food web
338 was the only property that is similar to the random model. Studies suggest that modularity enhances local
339 stability (Stouffer & Bascompte 2011), even though stability strongly depends on the interaction strength
340 configuration (Grilli *et al.* 2016) and on the existence of external perturbations (Gilarrañz *et al.* 2017). We
341 did not find modularity is greater than the metaweb assembly model, the existence of a modular structure
342 could be related to different habitats —in marine environments could be benthic and pelagic (Zhao *et al.*
343 2017). Thus we observed that the modular structure is present in the metaweb and not produced by a
344 maximization of local stability. Dynamical stability is expected to be maximized at the local level but we
345 only found that Weddell Sea food web exhibited a greater trophic coherence than the assembly model. Thus,
346 although this evidence is not conclusive with regard to the importance of dynamical processes in the assembly
347 of food webs, the structure of the local food webs examined here seem to be a consequence of the metaweb
348 structure.

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

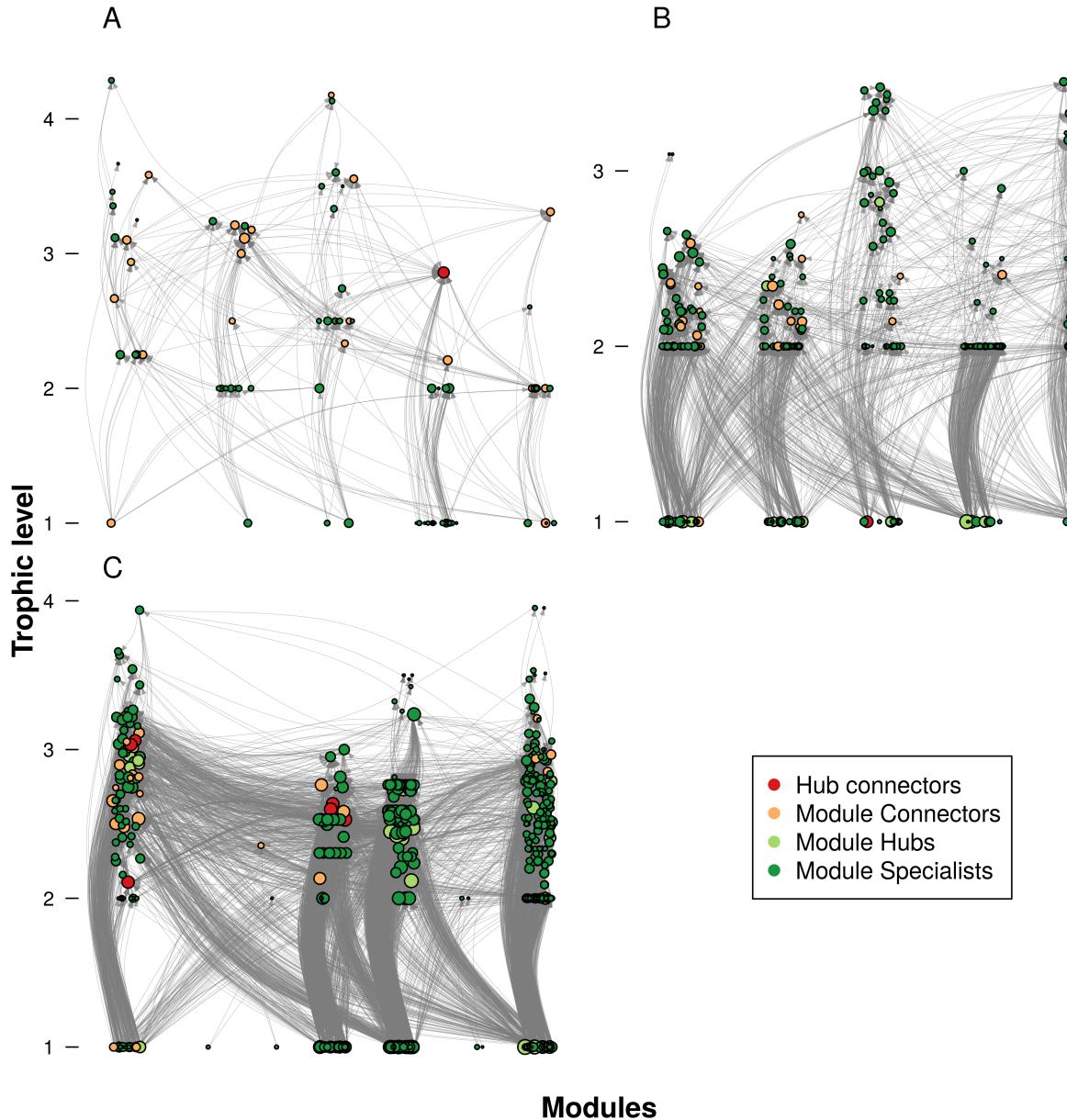


Figure 4: Plot of topological roles combined with trophic levels and modularity for each food web. The topological roles are: *Hub connectors* have a high number of between module links, *Module connectors* have a low number of links mostly between modules, *Module hubs* have a high number of links inside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

356 Motifs also have the same representation patterns against the random model. Local food webs should have
357 motif patterns that increase its persistence. The expected pattern, based on dynamical models, is an over-
358 representation of omnivory and tri-trophic chains and an under-representation of apparent and exploitative
359 competition (Stouffer & Bascompte 2010). Other studies showed that tri-trophic chains, exploitative and
360 apparent competition should be displayed more frequently (Borrelli 2015), but this was based on the stability
361 of isolated three-species sub-networks and the assumption that during the assembly process these 3 species
362 sub-networks were selected because of their intrinsic stability (Borrelli *et al.* 2015). The fact that tri-trophic
363 (or n-trophic) interactions cannot account fully for the properties of the food webs (Cohen *et al.* 2009) make
364 the results based on isolated modules less convincing. Our results showed an over-representation of omnivory,
365 exploitative competition and apparent competition, this configuration is not the most stable one based on
366 either criterion. A first hypothetical explanation is that the structure observed in the metaweb is maintained
367 in local food webs. Despite the fact that almost all motifs were not different from the assembly model,
368 neither tri-trophic chains and omnivory (lower in Weddell Sea) nor apparent competition (higher in Potter
369 Cove) followed the pattern expected from theoretical studies. Thus, the assembly process is not random,
370 there are differences in the frequencies of motifs as the scale change, but the selection of motifs due to its
371 dynamical stability is not the main driver. This implies that other dynamical processes that influence the
372 presence or absence of species like habitat filtering or dispersal limitation are acting and probably modifying
373 motif frequencies in empirical food webs. This kind of structures that are a sub-product of processes that
374 happen at a different level have been called spandrels of assembly (Solé & Valverde 2006).

375 As expected all the networks have a short mean trophic level (Williams *et al.* 2002; Borrelli & Ginzburg 2014)
376 compared with the random model. Different hypotheses were posed to explain this pattern: the low efficiency
377 of energy transfer between trophic levels, predator size, predator behaviour, and consumer diversity (Young
378 *et al.* 2013). These have contradictory support, reviewed by Ward & McCann (2017). Recently, it has been
379 proposed that maximum trophic level could be related to productivity and ecosystem size depending on the
380 context but related to energy fluxes that promote omnivory (Ward & McCann 2017). A different mechanism
381 based on dynamic stability of the whole web was proposed: food webs with shorter trophic levels (between 2
382 and 4) that have more omnivore chains are more likely to be stable, which increase the probability of being
383 observed in nature (Borrelli & Ginzburg 2014). We found that mean trophic level of the local food webs
384 was not different from the assembly model, and omnivory was under-represented. This combination suggests
385 that the trophic level could also be a spandrel of assembly, inherited from the metaweb structure.
386 Topological roles are valuable to detect the existence of functional roles of species, like super-generalists (or
387 hub connectors). These roles may change as the scale changes. A simple explanation is that modules also

388 change. It was demonstrated in Arctic and Caribbean marine food webs that modules are usually associated
389 with habitats (Rezende *et al.* 2009; Kortsch *et al.* 2015). For example, the Antarctic cod (*Notothenia*
390 *coriiceps*) is a super-generalist for Potter Cove and a module hub—a species with most of their links within
391 its module—for the metaweb. This means that the same species can have different influences on the food
392 web depending on the type or extension of the habitat considered. Although the metaweb assembly model
393 showed no change in the frequency of topological roles, we found a change in topological roles with the scale.
394 That means that in smaller areas there will be a smaller amount of different habitats, thus habitat filtering
395 should be an important factor and will change the frequency of species that represent a particular topological
396 role.

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

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409 Conflict of interest disclosure

410 The authors of this preprint declare that they have no financial conflict of interest with the content of this
411 article

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