Ecological Network assembly: how the regional meta web influence local food webs

Abstract

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

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Introduction

The characterization of ecological systems as networks of interacting elements has a long history (Paine 1966, May 1972, Cohen and Newman 1985), much of these work has been devoted to investigate network structure and its effects on dynamics and stability (Thebault and 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). Besides, 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). 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, where different spatial assemblages are connected through species dispersal.

Metacommunity theory provides a framework for assessing which are the roles of local and regional-scale dynamics (Leibold et al. 2004, Baiser et al. 2013) but has been applied mostly to competitive interactions, while trophic interactions received much less attention (Baiser et al. 2016). Recently, there was an increase in investigations that focused on food webs assembly, integrating it 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 and Kondoh 2016). Previous attempts to study the food web assembly process have used motifs as building blocks of local communities (Baiser et al. 2016). Motifs are sub-networks composed of species and links whose abundance deviates from the expected in a random network (Milo et al. 2002). By comparing motifs representation at different spatial scales—from regional to local—the process of assembly of interactions may be revealed (Baiser et al. 2016), e.g. if the same processes structure the food-web across scales, motifs representation should be the same. Besides, as local food-webs should have more tight links and stronger interaction rates, other structural properties should change as scale changes (Coll et al. 2011).

The objective of the present study is to analyse the process of food-web assembly using three datasets collected at different spatial scales: a marine Antarctic dietary database data-set representing an area of 34.8 million Km^2 that represent the meta-web (Raymond et al. 2011); the Weddell Sea data-set that represent 3.5 million Km^2 and is one of the most resolved marine food-webs obtained by a combination of field, laboratory analysis (Jacob et al. 2011); and the Potter Cove data-set that represent 6.8 Km^2, this was build using the results of

20 years of research in the area (Marina et al. 2018a). We analyse how this set of networks change across scales from the Antarctic to the two local food-webs.

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

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

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

There are species in ecological networks that have large effects on the whole ecosystem, like keystone species (Paine 1969), ecosystem engineers (Jones et al. 1994) and network hubs (Borthagaray et al. 2014). Species can participate in different ways with respect to modularity: depending on how many feed links they have within their own module and/or between the modules (Guimerà and Nunes Amaral 2005, Kortsch et al. 2015). This participation has been called the species' topological role; theoretical and empirical results suggest this roles are related to species traits like wide niche breadth, environmental tolerance, apex position in local communities and high motility (Rezende et al. 2009, Guimerà et al. 2010, Borthagaray et al. 2014). This is a local property at an individual species level.

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

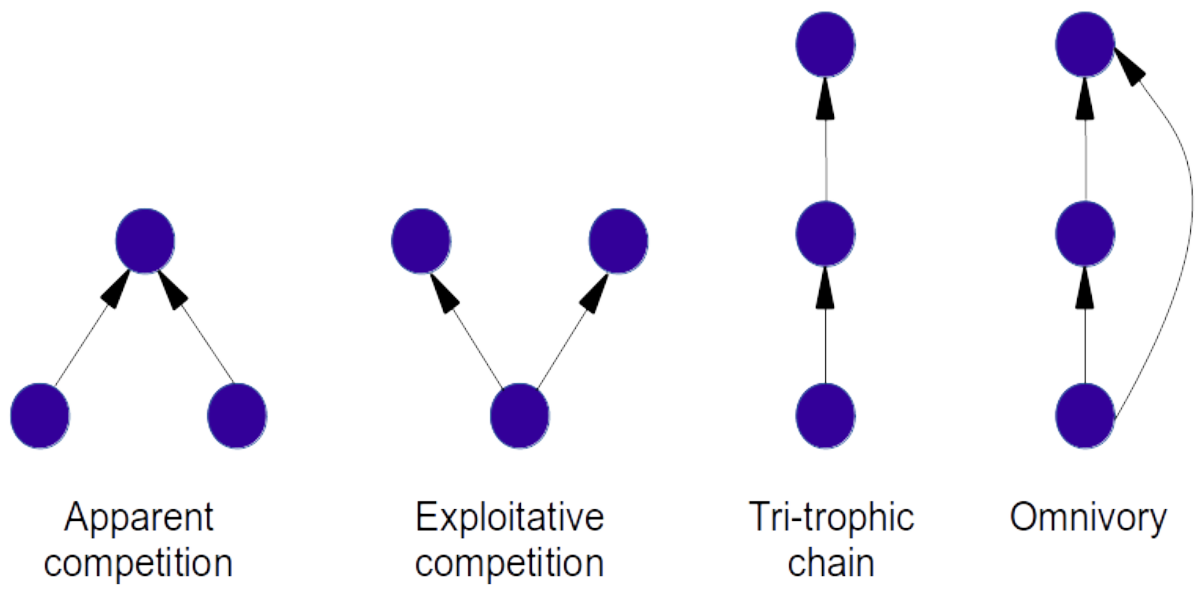

Figure 1: The four three-species sub-networks analysed: apparent competition, exploitative competition, tri-trophic chain, and omnivory. These four sub-networks have been explored both theoretically and empirically in ecological networks and are the most common sub-networks found in food webs

These motifs can show the process of assembly of interactions (Baiser et al. 2016) by comparing the representation of motifs at each scale (i.e over-represented, under-represented, or random). When the same processes structure of the food-web across scales, motifs representation should be the same. Ecological interactions

occur at the local scale so the differences may show the importance of local interactions in the assembly of the food web. During the assembly process the motif structures that are less dynamically stable tend to disappear from the food-web (Borrelli 2015), this has been called nonadaptative systemic selection (Borrelli et al. 2015). This process is nonadaptative because the selection process is not adapting the system to local conditions (Borrelli et al. 2015).

To our knowledge, the combination of network properties at three different levels has not been applied in food web studies up to now. All these properties would change from the meta-web to a more localized scale where interactions are realized; we will compare them against a random network null model, that represent the absence of ecological mechanisms, and to a meta-web assembly model that represent an assembly process. We expect that global properties related to resilience and stability should be close to the null model at the meta-web scale and different at the local food-webs; more stable motifs should be more frequent at local food-webs and the frequency of topological roles should change if habitat filtering or dispersal limitation is acting at local food-webs.

Methods

The three dataset used in this study encompass a wide range of spatial scales and they were collected independently. The Southern Ocean database compiled by Raymond et al. (2011) was used to construct the meta-web selecting only species located at latitudes higher than 60°S. Raymond et al. (2011) compiled information from direct sampling methods of dietary assessment, including gut, scat, and bolus content analysis, stomach flushing, and observed feeding. We considered that the meta-web is the regional pool of species defined by the biogeographic Antarctic region. Next we analysed two local food webs: the Weddell Sea dataset includes species situated between 74°S and 78°S with a West-East extension of approximately 450 km, comprises all information about trophic interactions available for the zone since 1983 (Jacob et al. 2011). The Potter Cove dataset comes from a 4 km long and 2.5 km wide Antarctic fjord located at 62°14'S, 58°40'W, South Shetland Islands (Marina et al. 2018a). These food web datasets comprise benthic and pelagic habitats of the Antarctic ecosystem, few aggregated low-trophic level groups (e.g. detritus, diatoms, phytoplankton, zooplankton) and a high resolution of the macroalgae community (i.e. 24 biological species of red, brown and green macroalgae). The macroalgae community is responsible for the majority of the primary production and supports a large fraction of secondary production in Antarctic fjords (Quartino and Boraso de Zaixso 2008, Valdivia et al. (2015)). The higher trophic levels comprise: invertebrate (e.g. ascidians, sponges, isopods, amphipods, bivalves, gastropods, cephalopods, echinoderms) and vertebrate predator groups (e.g. demersal

and pelagic fishes, penguins, seals and whales). For more information about these datasets we refer to the original publications. To make datasets compatible, first we checked taxonomic names for synonyms, and second, we added species (either prey or predator) with their interactions to the meta-web when the local food-webs contains more taxonomic resolution. When the meta-web contained more detailed records, only for predators we added them to the local food-web checking for its geographic range. We remove cannibalistic (self-links) and double arrows (i.d. A eats B and B eats A).

Analysis

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

Null models

We considered two null models, the Erdös-Rényi random graph (Erdős and Rényi 1959), and the meta-web assembly model. An Erdös-Rényi network is constructed fixing the number of edges and nodes and assigning at random the m edges to the n nodes with equal probability (Erdős and Rényi 1959, Baiser et al. 2016). We restrict the random model eliminating double arrows and cannibalistic links. To calculate trophic level and the coherence parameter (see below) we further restrict to random webs with at least one basal node, to make these calculations possible. The random model represents the absence of any mechanism, thus when we test our networks against it we do not obtain information about any hypothesized mechanism.

To consider the mechanism of network assembly we designed a dynamic meta-web assembly model. In this model species migrate from the meta-web to a local web with a uniform probability c, and become extinct from the local web with probability e, this is reminiscent of the theory of island biogeography (MacArthur and Wilson 1967, Gravel et al. 2011), but we added network structure. Species migrate with their potential network links from the meta-web, then in the local web, species can only survive if at least one of its preys is

present, or if it is a basal species. When a species goes extinct locally it may produce secondary extinctions; we check that the local predators maintain at least one prey if not they become extinct independent of the probability e. We simulate this model in time and it eventually reaches an equilibrium that depends on the migration and extinction probabilities but also on the structure of the meta-web. The ratio of immigration vs. extinction $\alpha = c/e$ is hypothesised to be inversely related to the distance to the mainland (MacArthur and Wilson 1967) and as extinction e should be inversely proportional to population size (Hanski 1999), the ratio α is also hypothesised to be related to local area.

For the random model we simulate networks with the same number of nodes n and edges m than the empirical networks, for the meta-web model we fitted the parameters g and e to obtain networks with n and m close to the empirical networks, this implies that α should reflect the differences in areas of the two local food webs. For details of the fitting and simulations see appendix.

Small-world topology

The first emergent property we used is the small world pattern, this relates the average distance between the nodes and the clustering of the network (Watts and Strogatz 1998). We first calculated the minimum path length, that is the minimum number of edges between two nodes. Then L is the mean value of the minimum path length across all pairs of nodes. The clustering coefficient of node i was defined as

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

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

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

and

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

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

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

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

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

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

Coherence

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

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

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

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

that is the standard deviation of the distribution of trophic distances. A food web is more coherent 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% CI using the 0.5% and 99.5% quantiles the distribution of q; we also calculated the CI for the mean trophic level tp. We calculated the z-scores as:

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

where q_{obs} is the observed coherence, q_{null} is the mean coherence from the null model networks and σ_{qnull} 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, that 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 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 is then 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 asses the significance of our networks we calculate the 99% confidence interval and z-scores based on 1000 null model networks as previously described.

Motifs

We consider here four of thirteen possible three-species subnetworks: the tri-trophic chain, omnivory, apparent competition, and exploitative competition (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.

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 and 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 is no statistical differences between the distributions of PC_i and dz_i in successive repetitions; to test that we used the k-sample Anderson-Darling test (Scholz and Stephens 1987). Then we calculate the mean and 95% CI of dz and PC.

To determine each species' role the $dz - PC$ parameter space is divided into four regions, this was modified from Guimerà and Nunes Amaral (2005), using the same scheme of Kortsch et al. (2015). There are two thresholds that define the roles: $dz = 2.5$ and $PC = 0.625$. If a species has at least 60% of links within its

own module then $PC < 0.625$ and if it also has $dz \geq 2.5$, it is classified as a module hub. These species have a relatively high number of links, but inside his own module. If a species has $dz < 2.5$ and $PC < 0.625$ is called peripheral or specialist, it means that it has relatively few links and most within its module. Species that have $dz < 2.5$ and $PC \geq 0.625$ are module connectors, they have relatively few links and most between modules. Finally if a species has $dz \geq 2.5$ and $PC \geq 0.625$ it is classified as super-generalist or hub-connector because it has high between- and within-module connectivity. To test if the proportion of species with each of the roles changes between networks we made a Pearson's Chi-squared test with simulated p-value based on 10000 Monte Carlo replicates. Also, we test if the proportions change for one realization of the meta-web assembly model fitted for both local networks.

We combined the topological roles with the trophic level of each species and the compartments in one plot to give an integrated visualization of these sub-structural and local properties of the food web.

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

Results

Global network properties

The networks have values for connectance, numbers of species (size) and links (Table 1), that are well inside the range found for marine food webs (Marina et al. 2018b). Based in the random null model, all networks present the small-world structure as their small-world-ness index is larger than the 99% CI (Table 1 & S1), but there is no difference between local food-webs and the assembly model (Table 1 & S2). By definition a network is more coherent when its q index is closer to zero, all networks have a negative random z-score and a significant smaller q value (Table 1 & S1); thus they are more locally stable as they are more coherent. Using the meta-web assembly model only Weddell food-web is more stable and Potter Cove food web have no differences with the model (Table 1 & S2). Mean trophic level is similar among networks and significantly lower than the random null model (Table 1 & S1), but compared with meta-web model trophic levels are not significant. Modularity is greater than the random model but not significant for Potter Cove. And modularity is not different compared with the meta-web model . In general the networks are different from the random null model and similar to the meta-web assembly model.

Table 1: Network global properties across scales, the *Meta-web* represents the marine predator-prey relationships of Antarctica, the *Weddell Sea* and *Potter Cove* are local food webs. Z-scores are 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^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
Modularity assembly z-score	-0.38	0.41	

Sub-structural properties (motifs)

The representation of three species sub-networks with respect to the random model showed similar patterns in all networks (Figure 2A). Exploitative competition, apparent competition, and omnivory are over-represented, three trophic chains are under-represented and all these patterns are significant (Table S3). The motifs proportions for the three scales are different (Chi-squared = 12612, p-value < 9.9e-05), this means that local and regional networks are not a random sample of the meta-web. With respect to the meta-web assembly model only some of them are significant (Table S4): apparent competition is higher for Potter Cove, and three trophic chains and omnivory are lower for Weddell Sea (Figure 2B). Contrary to our expectations Potter Cove is more similar to the meta-web than Weddell Sea food web.

Node level properties (Topological roles)

The proportion of species with the four topological roles is different as the spatial scale changes (Chi-squared = 79.31, p-value = 9.9e-05). This is observed as a higher presence of module connectors (few links, mostly

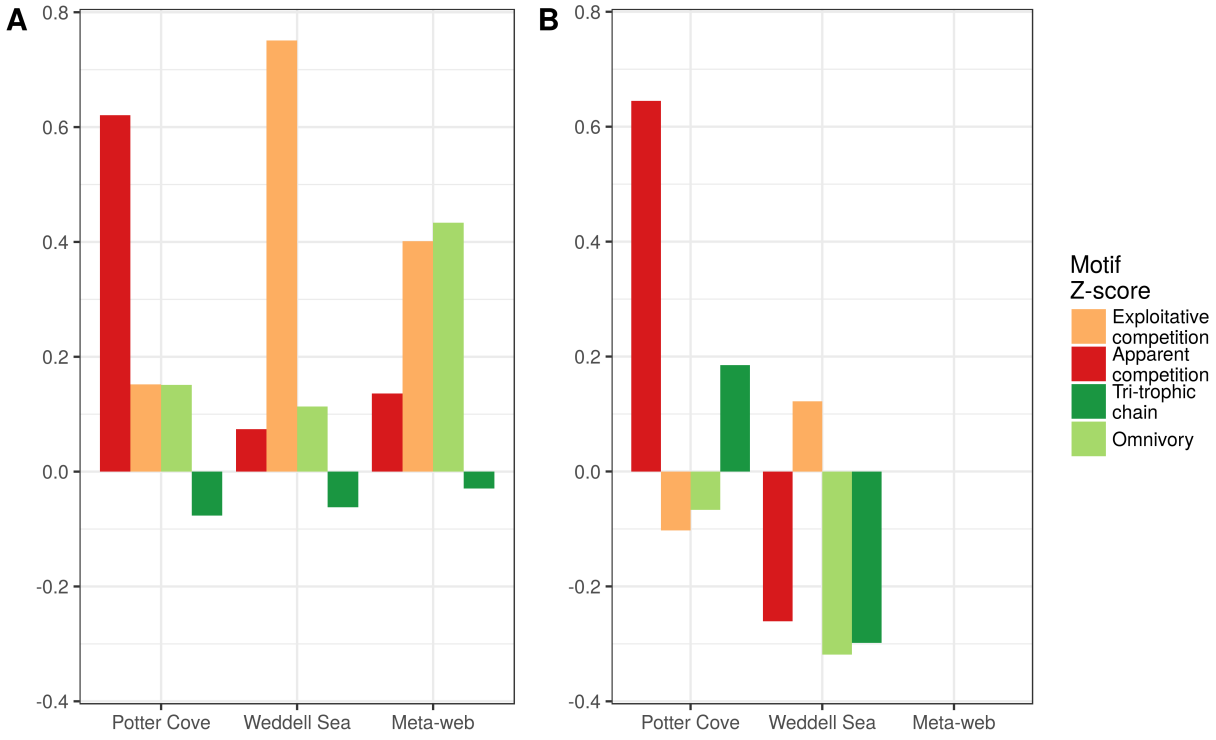

Figure 2: Network motifs z-scores across scales. Motifs are three-node sub-networks counted on each of the complete networks: the *Meta-web* represents the marine predator-prey relationships of Antarctica (34.8 million Km^2); the *Weddell Sea* (3.5 million Km^2) and *Potter Cove* (6.8 Km^2) are local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

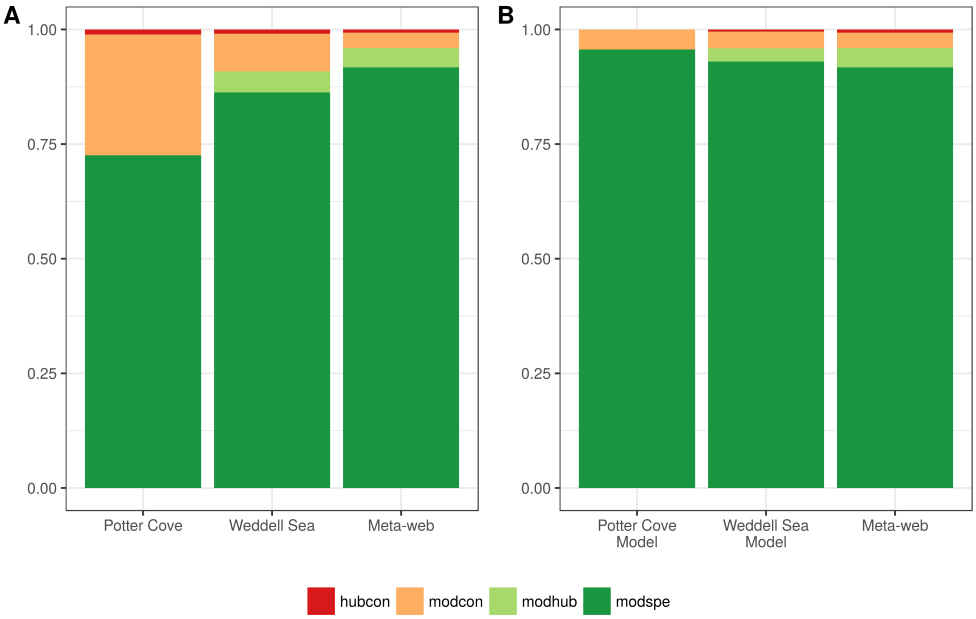

Figure 3: Proportion of topological roles across scales, the *Meta-web* represents the marine predator-prey relationships of Antarctica (34.8 million Km^2); the *Weddell Sea* (3.5 million Km^2) and *Potter Cove* (6.8 Km^2) are local food-webs. The topological roles are: *Hub connectors* have a high number 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. A. Observed proportions for the networks, these are different (Chi-squared = 79.31, p-value = 9.9e-05). B. Proportions obtained from the meta-web assembly model, there are no differences between them (Chi-squared = 5.95, p-value = 0.41)

between modules) in Weddell Sea, and the lack of module hubs (high number of links inside its module) in Potter Cove (Figure 3 A), which can be related to its low modularity value (Table 1). The proportions obtained with the meta-web assembly model are not different from the meta-web (Chi-squared = 5.95, p-value = 0.41)(Figura 3 B).

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

Discussion

We expect that the meta-web structure reflects the evolutionary constraints of the species interactions and the local networks should be influenced by assembly processes and also strongly determined by the local environment. Our results suggest that the structure of the meta-web does not change significantly as we change the scale, but there are indeed some evidences that the processes of dynamical assembly, habitat filtering and dispersal limitation are acting. Thus food-webs are mainly shaped by evolutionary forces and are less constrained by dynamical assembly processes and local environments.

Global level network properties showed the same patterns across scales; most of them are significantly different to the null random model but not different to the assembly model. Modularity for Potter Cove food-web is the only property not different from the random model, it was demonstrated that modularity enhance local stability (Stouffer and Bascompte 2011) besides this strongly depends on the interaction strengths configuration (Grilli et al. 2016) and on the existence of external perturbations (Gilarranz et al. 2017). This is consistent with the values we find for coherence, that is a proxy of dynamical local stability. All networks are more stable than a random one, but only Weddell Sea food-web is more coherent than the

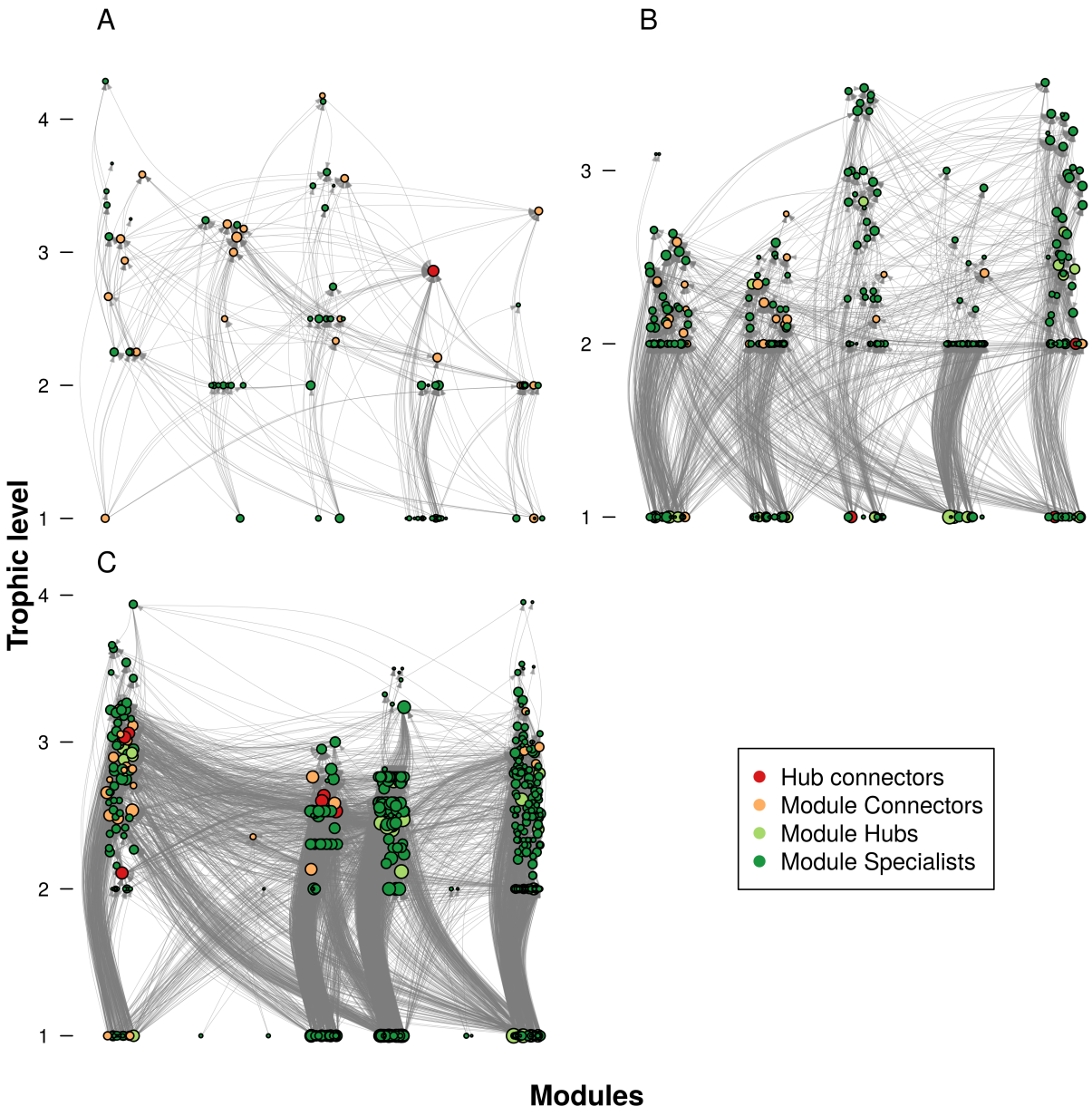

Figure 4: Food Web structure showing trophic level by compartments (modules) and topological roles. The topological are: *Hub connectors* have a high number of between module links, *Module connectors* have a low number of links mostly between modules, *Module hubs* have a high number of links inside its module. *Module specialists* have a low number of links inside its module. The size of the species nodes is proportional to the log of its degree.

assembly model and more modular than the random model. Dynamical stability is expected to be maximized at the local level but neither of the food webs is more modular than the assembly model, thus the evidence is not conclusive with regard to the importance of dynamical processes, most of the structure of local food-webs seems to be a consequence of meta-web structure.

All networks have a significant value of small-world-ness compared with the random model but the local food-webs are not different from the assembly model. In general food webs do not show small-world structure (Dunne et al. 2002, Marina et al. 2018b) this suggest that small-world property is inherited from the meta-web and that is not influenced by a greater percentage of realized interactions. If small-world-ness would be determinant for an increased resilience and robustness to secondary extinctions (Bornatowski et al. 2017), this value should be significantly higher than the meta-web assembly models.

Motifs also have the same representation patterns against the random model. Local food-webs should have motifs patterns that increase its persistence. The expected pattern based in dynamical models is an over-representation of omnivory and tri-trophic chains and under-representation of apparent competition and exploitative competition (Stouffer and Bascompte 2010). Other studies showed that tri-trophic chains, exploitative competition, and apparent competition should be expected more frequently (Borrelli 2015), but this was based on the stability of isolated three species sub-networks and the assumption that during the assembly process these 3 species sub-networks are selected because of their intrinsic stability (Borrelli et al. 2015). The fact that tri-trophic (or n-trophic) interactions cannot account fully for the properties of the food webs (Cohen et al. 2009) make the results based on isolated modules less convincing. Our results showed an over-representation of omnivory, exploitative competition and apparent competition, this configuration is not the most stable one based on either criteria. A first hypothetical explanation is that the structure observed in the meta-web is maintained at local food-webs. Almost all motif are not different from the assembly model but tri-trophic chains and onmivory that are lower in Weddell Sea, and apparent competition that is higher in Potter Cove, none of these followed the pattern expected from theoretical studies. Thus, the assembly process is not random, there are differences in the frequencies of motifs as the scale change, but the selection of motifs due to its dynamical stability is not the main driver, this implies that other dynamical processes that influence the presence or absence of species like habitat filtering or dispersal limitation are acting and probably modify the motifs frequencies. This kind of structures that are a sub-product of process that happen at a different level have been called spandrels of assembly (Solé and Valverde 2006).

As expected all the networks have a short mean trophic level (Williams et al. 2002, Borrelli and Ginzburg 2014) compared with the random model. Different hypothesis were posed to explain this pattern: the low efficiency of energy transfer between trophic levels, predator size, predator behaviour, and consumer diversity

(Young et al. 2013). These have contradictory support, reviewed by Ward and McCann (2017). Recently has been proposed that maximum trophic level could be related to productivity and ecosystem size depending on the context but related to energy fluxes that promote omnivory (Ward and McCann 2017). A different mechanism based on dynamic stability of the whole web was proposed: food-webs with shorter trophic levels (between 2 and 4) that have more omnivore chains are more probable to be stable which increase the probability of being observed in nature [Borrelli2014]. We found that mean trophic level of the local food webs is not different from the assembly model, and omnivory is under-represented, this combination suggest that the trophic level could be also be spandrels of assembly, inherited from meta-web structure.

Topological roles are useful to detect the existence of functional roles of species like super generalists (or hub connectors), these roles may change as the scales change. The simple explanation is that modules also change, modules are usually associated with habitats in Arctic and Caribbean marine food webs (Rezende et al. 2009, Kortsch et al. 2015). For example the Antarctic cod (*Notothenia coriiceps*) is a super generalist for the local food-web and a module hub—a species with most of their link between its module—for the meta web. This means that the same species can have different influences on the food-web depending on the type or extension of the habitat considered. The meta-web assembly model showed no change in the frequency of topological roles, our results showed that there is a change in topological roles with the scale. That means that in smaller areas there will be a smaller amount of different habitats, thus habitat filtering should be an important factor and will change the frequencies of species that represent a particular topological role.

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

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