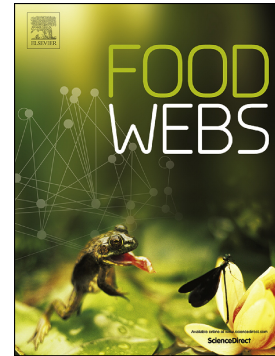


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Green vs Brown food web: Effects of habitat type on multidimensional stability proxies for a highly-resolved Antarctic food web

Georgina Cordone ¹, Vanesa Salinas ², Tomás I. Marina ^{2,4}, Santiago R. Doyle ^{2,3}, Francesca Pasotti ⁵, Leonardo A. Saravia ^{2,3}, Fernando R. Momo ^{2,3}

¹ Centro Para el Estudio de Sistemas Marinos (CESIMAR), Centro Nacional Patagónico (CCT CONICET-CENPAT). Boulevard Brown 2915, (U9120) Puerto Madryn, Chubut, Argentina.

² Instituto de Ciencias (ICI), Universidad Nacional de General Sarmiento. J.M. Gutierrez 1150, (B1613), Los Polvorines, Buenos Aires, Argentina.

³ Instituto de Ecología y Desarrollo Sustentable (INEDFS), Universidad Nacional de Luján. CC 221, (B6700), Luján, Buenos Aires, Argentina.

⁴ Centro Austral de Investigaciones Científicas (CADIC-CONICET). B.A. Houssay 200, (V9410), Ushuaia, Tierra del Fuego, Argentina

⁵ Marine Biology Laboratory, Biology Department, Ghent University. Krijgslaan 281/S8, B-9000, Ghent, Belgium.

e-mail address: gcordone@cenpat-conicet.gob.ar

Abstract

Food web analyses are powerful tools to understand the structure, dynamics and stability of communities. Potter Cove (25 de Mayo / King George Island) is one of the most biodiverse and studied fjords on the West Antarctic Peninsula (WAP), where climate change is affecting benthic and pelagic communities. This fjord ecosystem presents a considerable degree of environmental and species distribution heterogeneity across space: the outer portion of the cove is dominated by hard

bottoms meanwhile the inner portion is dominated by soft bottoms. In this work, we have incorporated habitat type to a highly-resolved Antarctic food web, and evaluated its effects on different network metrics and proxies for various dimensions of stability. We considered a multidimensional perspective and employed simulation techniques to encompass variability. Our results showed that the incorporation of habitat type to Potter Cove food web analysis led to two different functional types of networks segregated on space: a green food web (in the outer cove) and a brown food web (in the inner cove). The green and the brown food webs showed significant differences in network structure and in some proxies for multidimensional stability (i.e. quasi sign-stability and omnivory), suggesting that these two food webs have different resilience to perturbations. However, there were no changes in network robustness when *in silico* experiments were performed. We conclude that habitat type plays a significant role in the structure and stability of Antarctic food webs, and should be taken into account to design effective conservation strategies.

Keywords

Hard bottom; Soft bottom; Quasi Sign Stability; Strona curve-ball algorithm; West Antarctic Peninsula; Climate Change

1. Introduction

Space is an undeniable dimension in the life of organisms, communities and ecosystems. It has been a central theme in ecology and it is deeply-rooted in various fields of such discipline, including food-web studies (Polis et al., 1997; Holt, 2002; Baiser et al., 2012; Kortsch et al., 2019). Food webs represent energy and matter flows among organisms, which relate to each other in consumer-resource relationships (Bascompte, 2009). Many environmental variables correlate with space, characterizing and defining with their distribution different habitats (e.g. Tolonen et al., 2001; Dalkiran et al., 2020). On marine benthos, a key environmental variable is the substratum type, since sessile species depend on substrata for attachment and feeding (Sebens, 1991). Thus,

substratum type (i.e. hard/soft or rocks/sediments) determines the composition of the benthic community, the species that predate on them and the species that live on these engineered environments (e.g. Albrecht 1998; Thiel & Ullrich, 2002). Hard bottoms are typically dominated by macroalgae assemblages and suspension-feeders organisms, while soft bottoms are typically dominated by infauna and deposit-feeders (Wilson, 1990; Wahl, 2009). These differences in community composition are reflected in the food web structure and may have consequences for food-web stability. Food webs are usually characterized as “green” or “brown” relying on the dominant energy pathway (Hairston et al., 1960; Polis & Strong, 1996; Evans-White & Halvorson, 2017). A green food web is based on energy obtained from plants or algae (i.e. by photosynthesis and posterior herbivores consumption), whereas a brown food web is based on the consumption of decaying biomass by detritivores (Odum, 1969).

While herbivores ingest organic carbon and nutrients directly from their prey, in brown food webs detrital organic carbon is repackaged and consumed several times, resulting in a “microbial loop” or “detrital processing chain” (Azam et al., 1983; Fenchel 2008; Evans-White & Halvorson, 2017). Modeling experiments show that adding complexity such as mixotrophic interactions to the microbial loop may enhance food-web stability (Jost et al., 2004). However, the relationship between stability and complexity has been the subject of a long debate in ecology that is still in force (May, 1973; McCann et al., 1998; Montoya et al., 2006; van Altena et al., 2016). Brown food webs are hypothesized to be more stable than green food webs because detritus dynamic is little affected by predator dynamic (i.e. donor-control) (Odum 1969; Pimm 1982; Neutel et al. 1994; Moore et al. 2004). Indeed, the incapacity of detritus to show compensatory dynamic (i.e. detritus cannot grow and reproduce) suggests that bottom-up effects on detrital-based food webs are quite different from that of producer-based food webs (Srivastava et al., 2009). Omnivory is a food web property related to stability, which may differ between green and brown food webs, and is expected to be higher on those habitats with greater primary production (McCann & Hastings, 1997; Clay et

al., 2017; Wootton, 2017). Despite these differences, green and brown food webs are not isolated. In fact, these networks are typically coupled by nutrient cycling and mobile predators. Predator coupling is thought to confer stability to food webs by reducing variability on resources, and nutrient cycling to promote the propagation of cascading effects between green and brown webs (Rooney et al., 2006; Dolson et al., 2009; McCann & Rooney, 2009; Zou et al., 2016). But not only predators of high trophic levels participate in the green-brown coupling: species at low consumer levels, such as herbivores or detritivores, are generally omnivorous linking grazing and detrital resource channels (i.e. multichannel feeding) (Wolkovich et al., 2014). The impact of first-level consumer omnivory on food-web stability depends on how strongly the omnivores fed on resources and the ecosystem type (i.e. terrestrial or aquatic) (Wolkovich et al., 2014). Several studies have focused on brown and green energy pathways and their implication to food-web stability by employing simple models with few components due to dynamical constraints (Moore et al., 2004; Wolkovich et al., 2014; Zou et al., 2016). In this sense, less is known about how brown and green pathways impact food-web structure from a topological perspective and the possible implications that this brings on the stability of highly-resolved networks.

Ecological stability is understood as a complex concept with various facets such as variability, resilience, resistance, persistence or robustness (Pimm, 1984). However, the majority of ecological research has usually focused on a single component or dimension of stability (Donohue et al., 2013). In this regard, the complexity of ecological interactions demands researchers to take a multidimensional approach for studying stability in ecological systems; not doing so implies a high risk in underestimating the effects of perturbations and human impacts on ecosystems (Donohue et al., 2016). Domínguez-García et al. (2019) have explored the relationship between different metrics of stability in ecological networks and highlighted the importance of selecting metrics that accurately reflect the reaction of food webs to different disturbance lengths. Recent network research has developed useful metrics, which combined with simulations techniques can be a

powerful tool to explore food-web ecological stability from a multidimensional perspective (Dunne et al., 2002b; Krause et al., 2003; Newman & Girvan, 2004; Allesina & Pascual, 2008). Simulation techniques such as *in silico* extinction experiments are widely used in food-web studies with different purposes and are a good proxy for community stability (Memmott et al., 2004; Allesina et al., 2006; Curtsdotter et al., 2011; Eklöf et al., 2013; Bellingeri & Bodini, 2013). Besides, other simulation techniques like the curve-ball algorithm for generating networks might help to solve a long debated issue: how to compare food webs (Strona et al., 2014). In any case, the comparison between different ecological networks is constrained by the quality of the networks under consideration and the possibility of network replication (Ma et al., 2018). Nowadays, new techniques developed in the context of trophic ecology such as stable isotopes, fatty acids and DNA analyses enable researchers to have a more detailed description of predator-prey relationships (e.g. Cordone et al., 2020). However, these types of relationships are determined by a multiplicity of factors that keep them naturally variable (Chesson, 1978; Carreon-Martinez & Heath, 2010; Traugott et al., 2013). Since natural variability is of vital importance for comparing networks, the simulation of food web replication is of great help for studying variability in predator-prey interactions when network replication is not possible (Yen et al., 2016). Traditionally, null models such as the curve-ball have been used to study networks not in order to generate variability and compared networks, but rather to demonstrate that a certain structure or property is not explained by the null model (Veech, 2012; Ma et al., 2018). The advantage of the curve-ball algorithm is that it creates simulated networks that maintain important network features related to trophic ecology (such as the percentage of top/base/intermediate species) but allowing other network metrics to vary (as characteristic path length or clustering coefficient). In this sense, curve-ball algorithm generates simulated networks with ecological significance that can be employed to mimic natural variability and make statistical inference (Strona et al., 2014; Kéfi et al., 2015).

In this work we employed two types of simulation techniques, *in silico* extinctions and the curve-ball algorithm, combined with network metrics to test the effects of habitat type on proxies for multidimensional stability in a highly-resolved Antarctic food web. The food web in question is located in the West Antarctic Peninsula (WAP), and more precisely in Potter Cove (25 de Mayo / King George Is., South Shetlands). Potter Cove food-web structure was recently analyzed, and one dimension of its stability tested but only at the basal assemblage, though neither a multidimensional stability assessment was performed nor the habitat type was considered (Marina et al., 2018a; Cordone et al., 2018). Potter Cove is one of the most biodiverse fjords of the WAP, where drastic environmental and ecological changes have been documented as a consequence of a rapid temperature rise (Schloss et al., 2012; Grange & Smith, 2013; Quartino et al., 2013; Sahade et al., 2015; Hernández et al., 2019). An accurate assessment of the structure and stability of such food web is of paramount importance in understanding how WAP fjords will respond to these environmental changes (Vaughan et al., 2003; Turner et al., 2005; Meredith & King, 2005; Bromwich et al., 2013; Nicolas & Bromwich, 2014). Our previous studies showed that Potter Cove food web is relatively robust to perturbations on macroalgae species (Cordone et al., 2018). However, Potter Cove ecosystem presents a significant degree of environmental and species distribution spatial heterogeneity, where hard and soft bottoms are clearly segregated in space (Klöser et al., 1994; Klöser et al., 1996; Pasotti et al., 2015b; Jerosch et al., 2018; Alurralde et al., 2020). This is an ideal study case to gain insight into the effects of habitat type in empirical food webs in general, and in the Antarctic shallow water marine fjord in particular.

Thus, our main aim was to analyze the effects of habitat type in Potter Cove food web. We hypothesized that the incorporation of habitat type in the description of this food web will reveal differences in its multidimensional stability proxies with respect to an analysis that ignores spatial variation in habitat types. In addition, we hypothesized that the soft bottom (brown) food web displays greater stability proxies than the hard bottom (green) food web.

2. Materials and Methods

2.1 Study site

Potter Cove is a tributary inlet of Maxwell Bay, on the Southern coast of 25 de Mayo / King George Island ($62^{\circ}14'S$, $58^{\circ}40'W$) (Figure 1). It is a spatially heterogeneous fjord-like bay divided into an outer and inner cove, which strongly differs in its bottom characteristics (Klöser et al., 1994; Klöser et al., 1996). While the outer cove consists of hard substrate formed by solid rocks and big boulders, the inner cove is dominated by soft sediments with a high presence of muddy substrate. The rocky shores of the outer cove are densely colonized by macroalgae (Klöser et al., 1996; Quartino et al., 2005), whereas the inner cove has one of the largest concentrations of benthic filter feeders found in Antarctic coastal areas. Therefore Potter Cove ecosystem represents a hotspot of Antarctic biodiversity (Sahade et al., 1998; Tatián et al., 1998; Tatián et al., 2004; Grange & Smith, 2013).

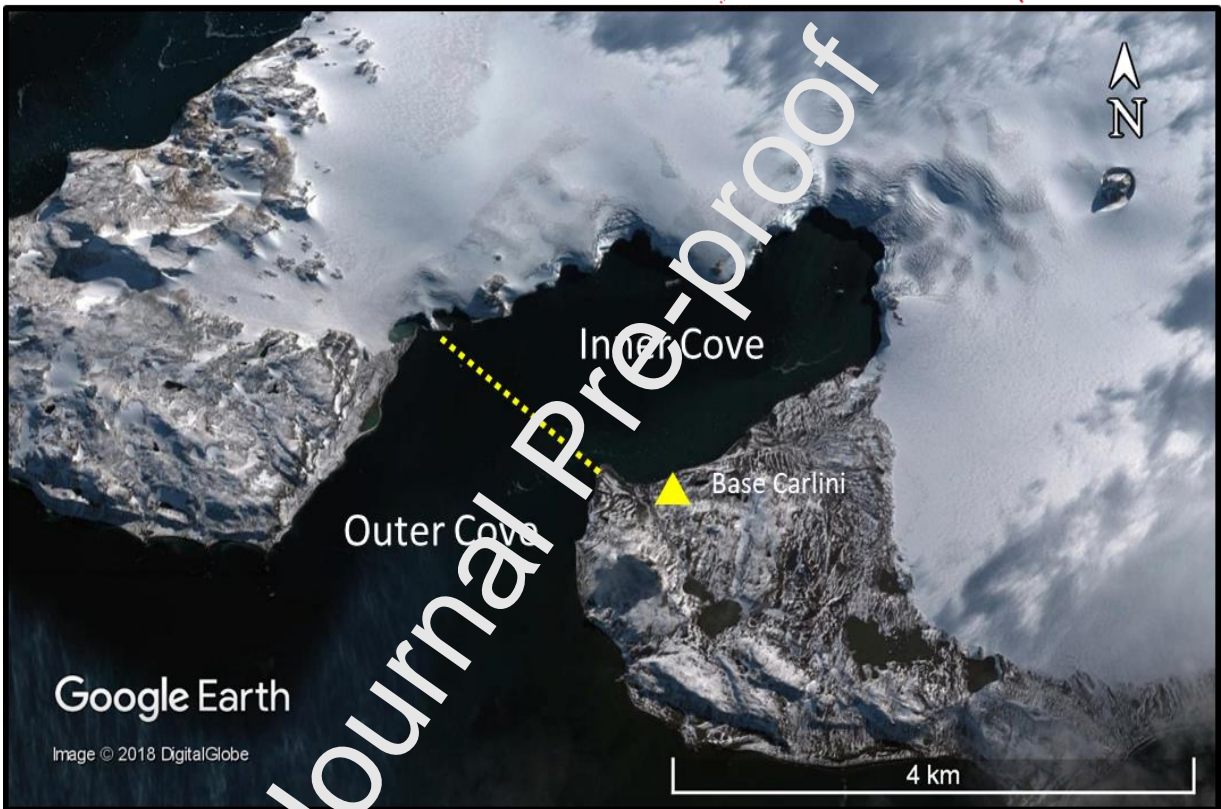
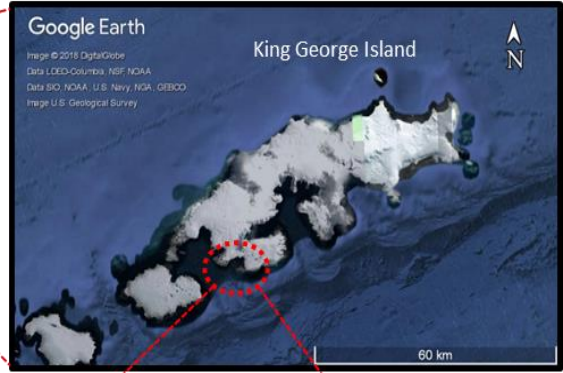
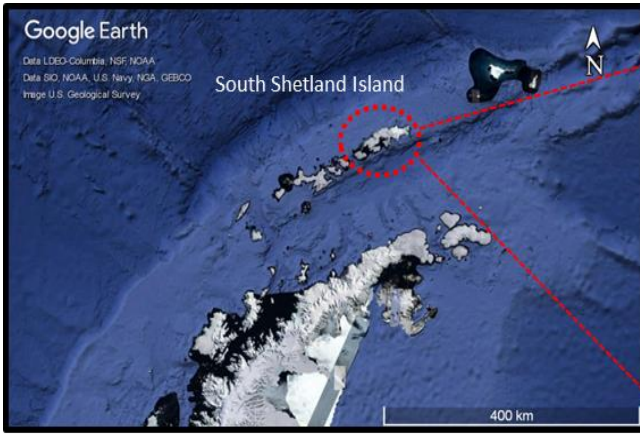


Figure 1. Map of Potter Cove at 25 de Mayo / King George Island where the outer and the inner coves, and the scientific research station Carlini are highlighted. Google. (s.f.). [Map of Potter Cove, 25 de Mayo / King George Is. in Google maps]

2.2 Food web assembly and topological description

The food-web assembly was established from a previous work performed by Marina et al. (2018a), where 91 trophic species and 307 interactions were registered at Potter Cove. Trophic species are represented as nodes in the network and can correspond to: biological species (e.g. macroalgae: *Palmaria decipiens* (Reinsh) Ricker, 1987; bivalve: *Laternulla elliptica* P. P. King, 1832; fish: *Notothenia coriiceps* Richardson, 1844), groups or organisms that share the same sets of predators and prey (e.g. hyperiids, copepods, phytoplankton), and non-living compartments of matter and energy (i.e. fresh and aged detritus, necromass). Henceforth, we will use the term “species” as synonymous of “trophic species” (Briand & Cohen, 1984). Further details on Potter Cove food web assembly can be found in Marina et al. (2018a). Since our main objective was to study the habitat type of Potter Cove food web, we incorporated the meiobenthos assemblage that is heterogeneously distributed in space and it represents a key player in the detritivorous pathway (Pasotti et al., 2015a,b). Thus a total of 20 new species and 139 new trophic interactions were added to the first

description of Marina et al. (2018a). Each species was classified according to the type of bottom they live on: soft bottom, hard bottom, or both. This was done based on the species biology and feeding behavior, literature search and expert knowledge (Appendix: Table A.1). Once the species were classified we built three food webs: 1) Full food web (FW), corresponding to the whole cove ; 2) Hard Bottom web (HB); and 3) Soft Bottom web (SB). The last two networks represent the incorporation of habitat type to the analysis: one for the outer cove/hard bottom habitats (HB) and the other for the inner cove/soft bottom (SB). In this manner, i) FW encompassed all species and interactions in the cove, ii) HB was represented by those species only present on the hard bottom habitat, and iii) SB was based on species only present in the soft bottom habitat. Mobile species that connect soft-bottom and hard-bottom habitats were included in both food webs (see scheme in the Appendix: Figure A.1).

We described the topology of the three analyzed networks based on network metrics widely used in food-web studies (Pimm, 1982; Cohen, 1990; Pascual & Dunne, 2006; Bascompte, 2009). We calculated connectance (C), mean trophic level (*mean TL*), percentage of top/base/intermediate species (%Top, %Basal, %Intermediate), clustering coefficient (CC), and characteristic path length (CPL) (Table 1, Appendix for equations). We compared these network metrics (C , *mean TL*, %Top, %Base, %Intermediate, CC , CPL) following Kortsch et al. (2015), by calculating the percentage difference $((B-A/A) * 100)$ between metrics for the three possible comparison: HB-FW, SB-FW and HB-SB. We calculated the cumulative degree distribution (DD) for the three food webs. For these purposes, node degree (Di) was calculated for each species (i) as the sum of all in and out trophic interactions. Then we fitted the cumulative degree distributions (DD) to Poisson, exponential and power-law functional forms by maximum likelihood and performed model selection procedure by the Akaike's Information Criterion for each food web (Burnham & Anderson, 2003; Clauset et al., 2009).

2.3 Multidimensional stability proxies

In order to analyze the effect of habitat type on the stability of the food webs, we employed two types of simulation techniques: *in silico* extinctions and the curve-ball algorithm combined with proxies of network stability (Memmott et al., 2004; Bellingeri & Bodini, 2013; Strona et al., 2014). *In silico* extinctions were performed considering thresholds of extinction in a topological approach (Bellingeri & Bodini, 2013; Schleuning et al., 2016; Cordone et al., 2018). This approach consists in defining a threshold as the minimum number of prey necessary for species' survival. After each random removal, the prey number for each species was calculated. If this number was lower than the threshold then the species became secondarily extinct. This procedure was repeated iteratively until any species had a prey number below the threshold (for a detailed description of this method refer to Cordone et al., 2018). The threshold was increased from 0 to 0.9 by 0.10 and the robustness ($R50$) was recorded. The $R50$ is a standardized measure of robustness proposed by Dunne et al. (2002b). It represents the fraction of species that has to be removed in order to result in a total loss of 50% of the original set of species (S). The $R50$ has proven to be a reliable measure of network robustness (Jonsson et al., 2015). We performed 100 simulations randomly selecting the species to be removed, and produced primary extinctions. This procedure was repeated for each threshold, as well as the $R50$. A real collapse in the food web, as a product of nonlinear relationships between species, would be seen as an abrupt decrease in $R50$ while the threshold increases (Cordone et al., 2018).

The second type of simulation we used was the curve-ball algorithm, which randomizes network structure maintaining the number of *in* and *out* trophic interactions. Curve-ball algorithm preserves the prey and predator number for each species resulting in simulated food webs with ecological significance (Strona et al., 2014; Kéfi et al., 2015). To characterize network stability we simulated 1000 networks and calculated for the Full (FW), Hard Bottom (HB) and Soft Bottom webs (SB) three measures proxies for stability: Quasi Sign-Stability (QSS), Omnivory (O) and Modularity

(*Mod*) (Table 1). These network metrics are proxies of multidimensional stability as they do not constitute a direct assessment of stability, as local stability analysis, but they are related to different dimensions of stability and are typically used as stability indicators (Allesina & Pascual, 2008; Grilli et al., 2016; Wootton, 2017). Afterwards, we tested if the empirical values of these stability proxies and other network metrics (mean *TL*, *CC* and *CPL*) were within the distribution of the simulated food webs (mean \pm 1 std). If this condition was fulfilled, we considered that our simulations fitted the empirical values and that it could be used to make comparisons. Then, we compared the distributions obtained for each stability proxy by two-sided Kolmogorov-Smirnov test, and calculated Cohen's *d* to estimated effect size for each comparison HB-FW, SB-FW and SB-HB (Massey, 1951; Cohen, 1992; Crawley, 2012).

All analyses and simulations were performed in R version 3.6.1 (R Core Team 2019). The *PowerLaw* R package was used to fit power law and heavy-tailed distributions (Gillespie, 2014), and the *multiweb* R package to estimate all network metrics and food web simulations (Saravia, 2019). Visone (version 2.9.2) software was used to make plots of the networks (Brandes & Wagner, 2004).

Table 1. List of network metrics analyzed, abbreviations, definitions and relevant ecological information related to food web structure and stability.

Network metric	Abbreviation	Definition and ecological meaning	Reference
Number of species	<i>S</i>	Number of trophic species (= nodes) in the food web. <i>S</i> measures the species richness of the community described by the network. It has been deeply related to the famous “complexity-stability” debate.	May, 1973.
Number of interactions or links	<i>L</i>	Number of trophic interactions in a food web. It is related to food web complexity and energy pathways.	Dunne et al., 2002a
Connectance	<i>C</i>	<i>C</i> is a standard food web measure that reveals the proportion of real interactions among possible ones. It is considered as an estimator of community sensitivity to	Martinez, 1992; Dunne et al., 2002a; Montoya et al., 2006; Vermaat et al., 2009;

		perturbations and it strongly covaries with many network properties. See Eq. A.1 in Appendix.	Poisot & Gravel 2014
Mean Trophic Level	$mean TL$	Trophic Level (TL) is an indicator of the position a species occupies in a food web resuming the distance of each species to the source of matter and energy. Low values of $mean TL$ indicate efficient energy transfer from basal assemblage to top predators. It contributes to food-web stability. See Eq. A.2 in Appendix.	Lindeman, 1942; Odum & Heald, 1975; Borrelli & Ginzburg, 2014
Percentage of top species	$\% Top$	Percentage of species with prey but without predators. Top predators may have indirect effects on other species in the food web and may hold top-down control (i.e. by trophic cascades).	Briand & Cohen, 1984; Frank et al., 2005; Kortsch et al., 2019.
Percentage of basal species	$\% Basal$	Percentage of species without prey. A high proportion of basal species is related to a food web dominated by living-autotroph ("green world") in contrast to a detritus-based food web ("brown world").	Briand & Cohen, 1984; Pimm, 1982; Moore et al., 2004.
Percentage of intermediate species	$\% Intermediate$	Percentage of species with prey and predators. Intermediate species determine the connectivity of lower and upper trophic levels and positively correlates with omnivory.	Briand & Cohen, 1984; Dunne et al., 2004; Romanuk et al., 2006; Kortsch et al., 2019.
Clustering coefficient	CC	CC is a measure of grouping that reflects how likely is that two connected species are part of a larger highly connected group. High values of CC are thought to promote network stability since it would imply the existence of compartments. Compartments may buffer the spread of perturbations. See Eq. A.3 in Appendix.	Albert & Barabási, 2002; Newman 2003; Stouffer & Bascompte, 2011.
Characteristic Path Length	CPL	CPL is the average distance, accounted by the number of interactions, between any pair of species. It is related to stability in a complex way. Food webs with low CPL values are shown to be more stable, though short chains might also contribute to a rapid propagation of disturbances. See Eq. A.4 in Appendix.	Kaunzinger & Morin, 1998; Albert & Barabási, 2002; Newman, 2003; Borrelli & Ginzburg, 2014.
Quasi Sign-Stability	QSS	QSS is the proportion of community matrices that are locally stable preserving the sign structure. It is directly related to network local stability, which can reveal the amplification or not of small perturbations near the equilibrium point. QSS ranges from 0 to 1 indicating a more stable food web when it is closer to 1.	Allesina & Pascual, 2008.
Omnivory	O	O is the fraction of species that feed at different trophic levels. The effects of O on stability might be positive or negative depending on the interaction strength	McCann & Hastings, 1997; Kuijper et al., 2003; Gellner & McCann, 2012;

		distribution. A predominance of weak interactions promote stability when O values are high.	Wootton, 2017.
Modularity	<i>Mod</i>	<i>Mod</i> reflects how strongly sub-groups of species interact with each other compared to species from other sub-groups. A high value promotes stability by preventing the spread of perturbations across sub-groups. See Eq. A.5 in Appendix.	Krause et al., 2003; Newman & Girvan, 2004; Stouffer & Bascompte, 2011; Grilli et al., 2016.

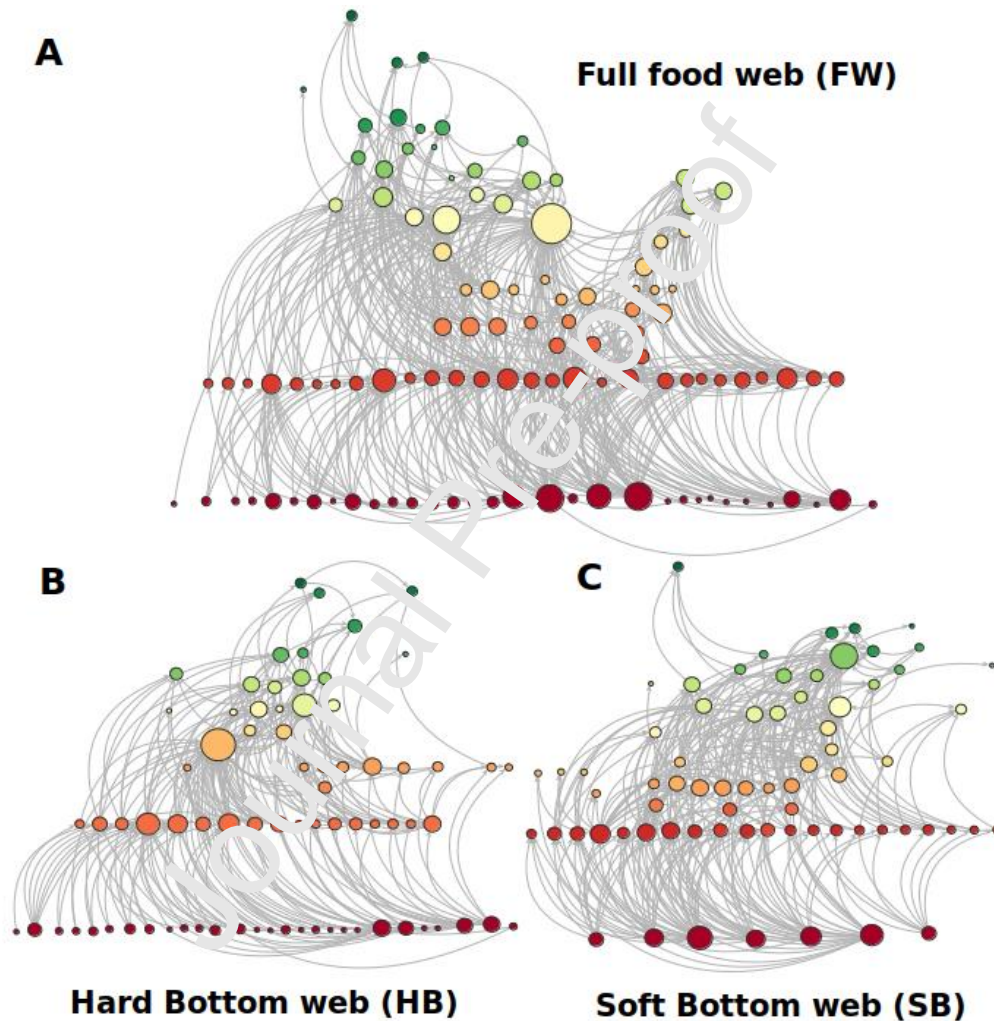
3. Results

3.1 Food web assembly and topological description

Potter Cove food web (FW) included 111 species representing predators and prey, with a total of 446 trophic interactions and a connectance (C) of 0.036. Instead, Hard Bottom web (HB) comprised 76 species and 221 trophic interactions, and Soft Bottom web (SB) 71 species and 293 trophic interactions (Figure 2). HB and SB networks shared 36 species, approximately 30% of all species. The three analyzed food webs presented some similarities and differences regarding the empirical values, depending on the identity of the web and the network metric analyzed (Table 2). Following the ordering of Table 2 we first mention the HB-FW comparison: there were no substantial changes in C (+5.6%), *mean TL* (-4.8%) and CP (+4.5%). However, some moderate changes in CC (-8.4%) were observed while HB displayed an important difference in the percentage of basal species in comparison with FW (+27.8%). The SB-FW comparison displayed various differences, especially in C (+57.9%) and CC (-37.4%), and in the percentage of basal species (-65.8%). Regarding the comparison of both habitat type webs (HB-SB), we observed large differences in C (-52.6%), CC (-50%) and strong differences in the percentage of basal (+73.3%), intermediate (-42.7%) and top species (-50%). At this point, it would be worth noting that both FW and HB showed a larger proportion of basal species than SB; though the three analyzed webs had a majority of species at intermediate positions.

The degree distributions of each of the three networks were positively skewed, with few species presenting a high degree and most species with a low degree (Figure 3). In all cases, the best fit was

achieved when exponential distribution was tested (Appendix Table A.2). *Notothenia coriiceps* (Richardson 1844; Cordata, Perciformes) displayed the highest value of degree D_i for the three analyzed webs (FW: 61, HB: 44 and SB: 32). *Ophionotus victoriae* (Bell 1902; Ophiurida) also presented a high value of D_i in the three food webs (FW: 29, HB: 22 and SB: 21), ranking among the first three species with the highest degree along with Phytoplankton (FW: 29, HB: 12 and SB: 27).



representation of **A**) the Full food web of Potter Cove (FW) without considering habitat type and **B-C**) the two habitat type food webs: Hard Bottom and Soft Bottom (HB and SB, respectively). Each node represents a species and each arrow symbolizes a trophic interaction (flow of matter and energy from prey to predator). Node size is relative to node degree (D_i); vertical scale represents trophic level (TL).

Table 2. Structural properties and differences $(B-A/A)*100$ of empirical food webs: the Full food web (FW), the Hard Bottom (HB) and Soft Bottom (SB) food webs.

Network metric	Abbreviation	Full food web	Hard Bottom web	Soft Bottom web	Diff HB-FW (%)	Diff SB-FW (%)	Diff HB-SB (%)
Number of species	<i>S</i>	111	76	71	(-) 31.5	(-) 36	(+) 6.6
Number of trophic interactions	<i>L</i>	446	221	293	(-) 50.5	(-) 34.3	(-) 32.6
Connectance	<i>C</i>	36	38	58	(+) 5.6	(+) 57.9	(-) 52.6
Mean Trophic Level (std)	Mean <i>TL</i>	2.1 (0.9)	2.0 (0.9)	2.5 (0.8)	(-) 4.8	(+) 19	(-) 25
Percentage of basal species	% Basal	28.82	36.84	9.86	(+) 27.8	(-) 65.8	(-) 73.2
Percentage of intermediate species	% Intermediate	54.97	47.38	67.61	(-)13.8	(+) 23	(-) 42.7
Percentage of top species	% Top	16.21	15.79	22.53	(-) 2.6	(+) 39	(-) 42.7
Clustering Coefficient	<i>CC</i>	107	98	147	(-) 8.4	(+) 37.4	(-) 50
Characteristic Path Length	<i>CPL</i>	1.77	1.85	1.57	(+) 4.5	(-) 11.3	(+) 15.1

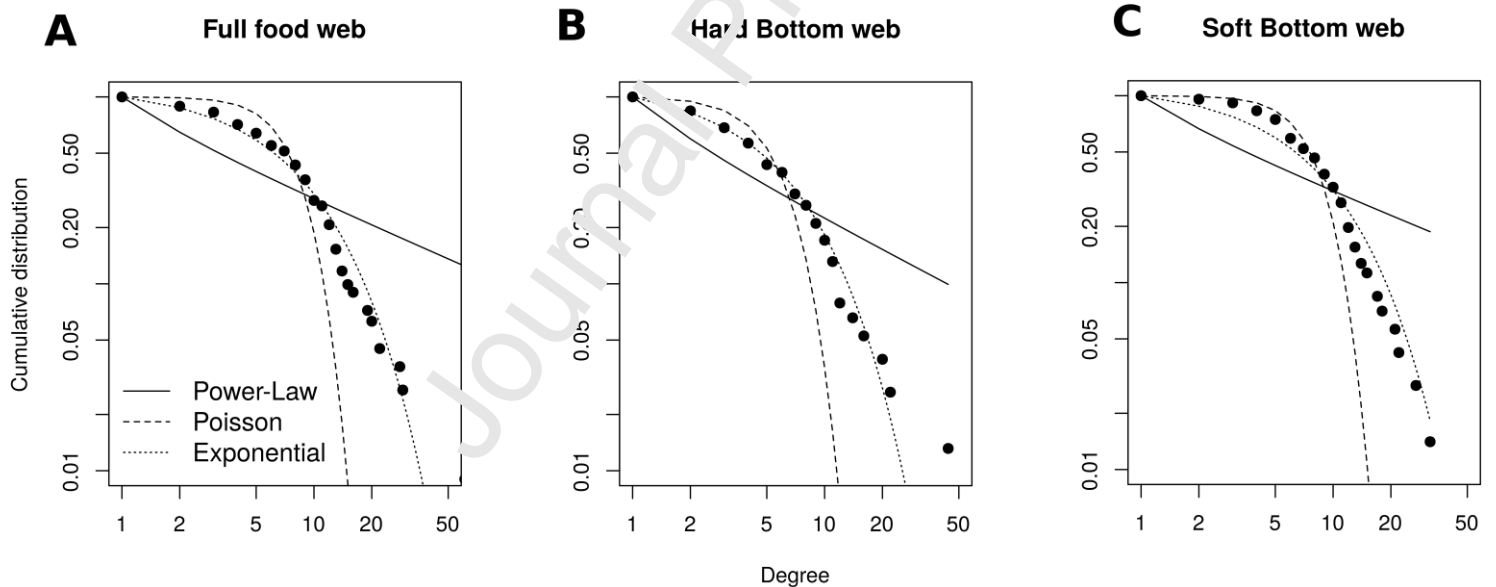


Figure 3. Log-Log cumulative degree distributions of **A)** Potter Cove Full (FW) and **B)** Hard Bottom (HB) and **C)** Soft Bottom (SB) food webs. The model with best fit was the exponential distribution.

3.2 Multidimensional stability proxies

In silico extinctions showed the same general pattern for the three analyzed webs (Figure 4). We observed that the fraction of species that has to be removed in order to result in a total loss of 50% of the original set of species (i.e. $R50$) descended as the threshold increased for FW, HB and SB. This decrease in robustness ($R50$) is expected because as the threshold increased the food web becomes more vulnerable to species loss; therefore $S/2$ is reached in less extinction steps. For smaller thresholds (0-0.2) the effect was minor (i.e. a plateau was observed in the y axis) but then (around 0.3) the curves for the three food webs started to descend monotonously. It is worth noting that abrupt changes were not observed, and simulations (quartile 25-75) overlapped for the three networks: FW, HB and SB (Figure 4).

Regarding the curve-ball algorithm, the other simulation technique that was used, it is important to notice that the empirical values of the three food webs fell within the distributions of the simulated networks, and were found near the means of these distributions for stability proxies (Figure 5.). The same occurred for the other network metrics analyzed: *mean TL*, *CC* and *CPL* (Appendix Figure A.2). Only the modularity did not differ significantly between SB-HB (Appendix Table A.3), though omnivory and quasi sign-stability showed significant differences between the three food webs. The greatest Cohen's effect size values were observed at SB-HB comparison for omnivory and HB-FW and SB-HB comparisons for quasi sign-stability (Appendix Table A.4).

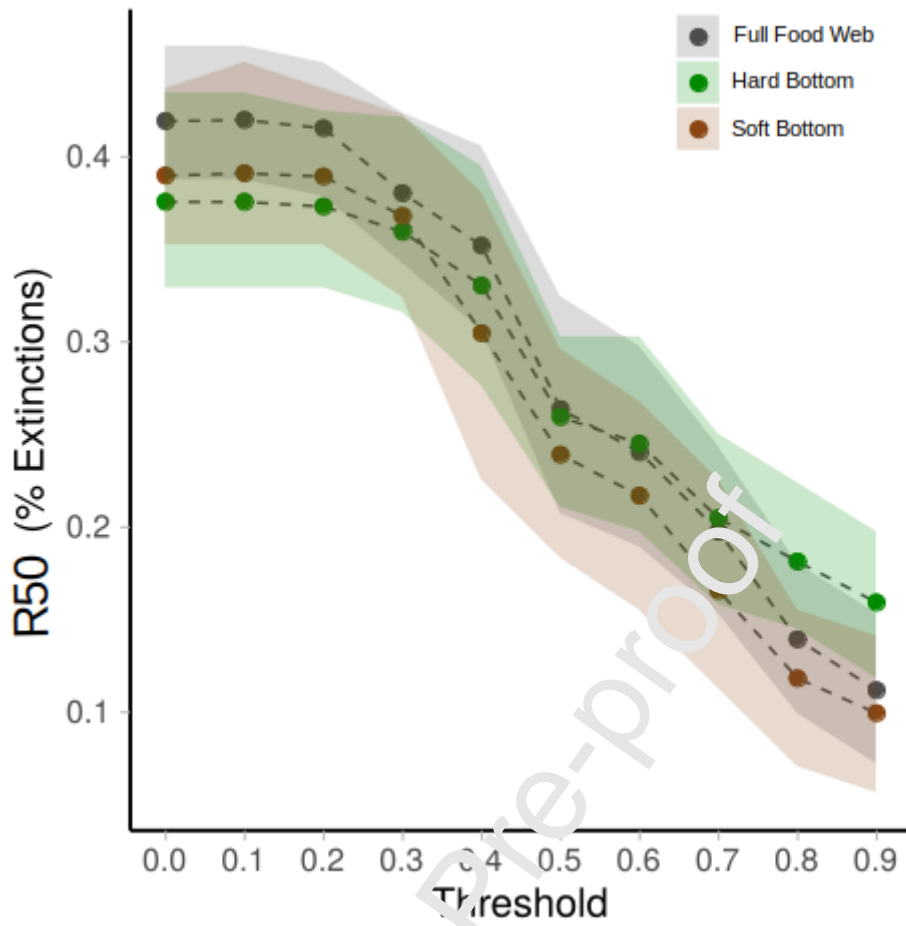


Figure 4. Food webs response *in silico* extinctions ($R50$: % of primary extinctions required to reach $S/2$) with threshold variations (from 0 to 0.9 by 0.1). Colors represent the Full food web (FW) in gray, the Hard Bottom (HB) in green and the Soft Bottom (SB) in brown. Colored points are means of 100 random simulations and shaded areas represent quartiles 25-75.

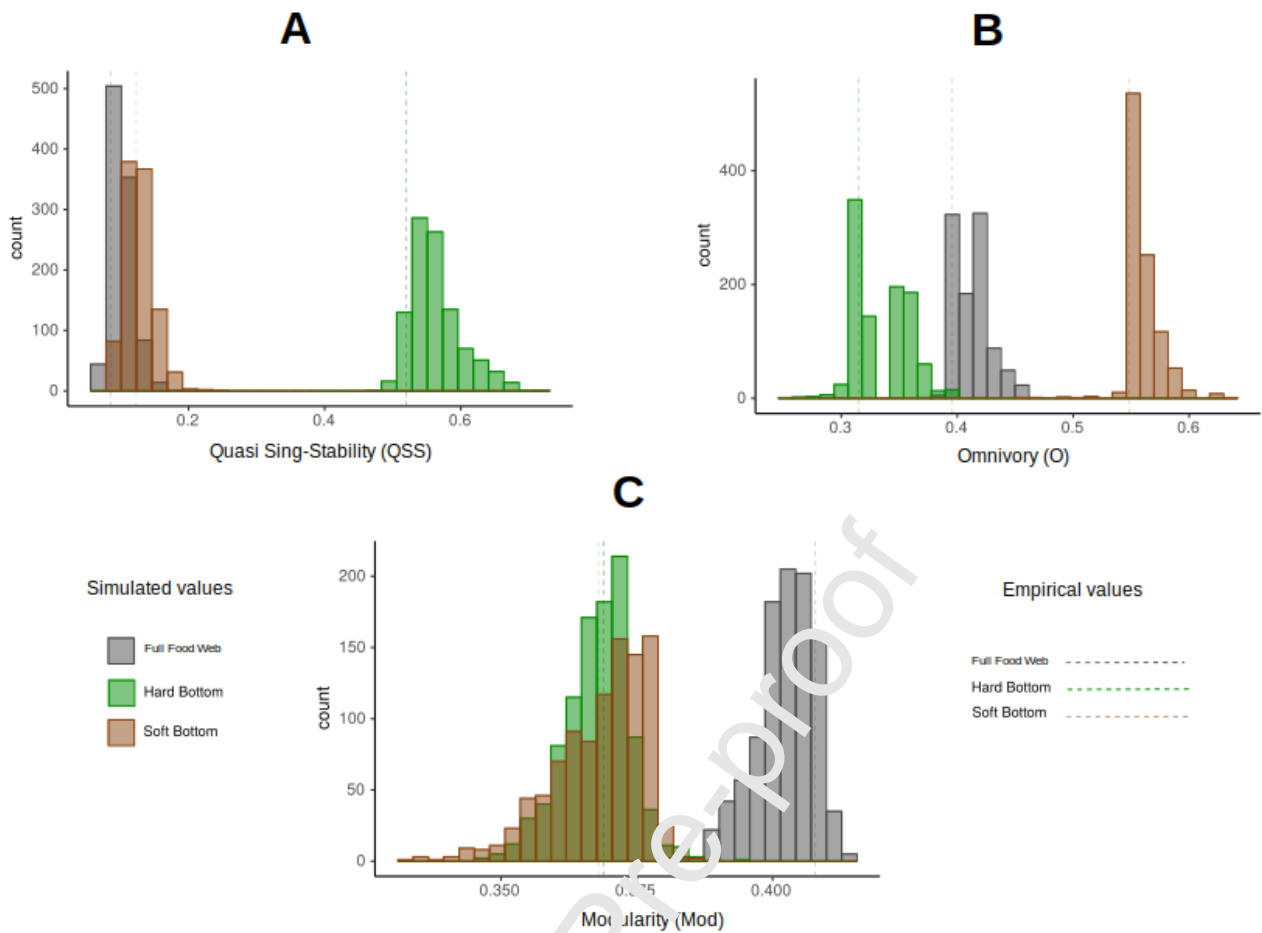


Figure 5. Histograms showing stability metrics of simulated networks for the Full (FW), the Hard Bottom (HB) and the Soft Bottom (SB) food webs. Empirical values are shown as dotted lines (FW: gray, HB: green and SB: brown). Stability proxies displayed here are: **A)** Quasi Sign-Stability QSS , **B)** Omnivory O , and **C)** Modularity Mod .

4. Discussion

4.1 Food web assembly and topological description

The topological description showed how the incorporation of habitat type has consequences on network metrics such as connectance and distribution of species. In previous studies, connectance has been pointed out as one of the most important metrics regarding variation between food webs and, in particular, along environmental gradients (Vermaat et al., 2009, Baiser et al., 2012; Kortsch

et al., 2019). Accordingly, we found major differences in connectance when taking into account habitat type: Soft Bottom food web (SB) exhibited a higher C value than the Full food web (FW). Also, it is worth noting that Hard and Soft Bottom food webs displayed a clear difference in the percentage of basal/intermediate/top species. In this sense, the Hard Bottom food web (HB) is a green food web where the low trophic level is dominated by macroalgae species, while the Soft Bottom food web (SB) is a brown food web with a considerable low percentage of basal species where detritus might play an important role since most species are not autotroph. Indeed, it has been hypothesized that the Soft Bottom food web is subsidized by the Hard Bottom web through macroalgae decomposition and detritus accumulation in the inner cove (Tatián et al., 2004; Quartino et al., 2008; Braeckman et al., 2019). It has been observed in other Antarctic food webs that the carbon flux product of macroalgae decomposition plays an important role in benthic fauna and soft-sediment communities (Dunton 2001; Norkko et al., 2004; Norkko et al., 2007; Gillies et al., 2012). Baruzzi et al. (2018) have shown that an increase in carrion biomass led to higher diversity values of primary and secondary consumers participating in carrion recycling on food webs. In this sense, an increase in algae mortality on hard bottoms can lead to changes in the Soft Bottom food web due to a greater availability of detritus. Also, mobile predators from higher trophic levels usually couple different energy channels in space. Predators coupling has been detected on terrestrial, marine, and freshwater food webs (Rocney et al. 2006, Dolson et al. 2009), and recently, on food webs from high latitudes in the Arctic ecosystem (McMeans et al., 2013). In this regard, Potter Cove is not the exception; the Hard Bottom and the Soft Bottom food webs are coupled by mobile predators. Fish such as *Nothothenia coriiceps* and *Harpagifer antarcticus* (Nybelin, 1947) and other mobile species as sea stars (e.g. *Odontaster validus* Koehler, 1906) and crustacea (e.g. *Glyptonotus antarcticus* Eights, 1852) couple HB and SB on space (inner and outer cove) and across habitats (hard and soft bottoms). In this sense, the green and the brown food webs described here are clearly interrelated and disturbances on one of them could probably propagate to the other.

It is not yet clear if food webs display a universal functional form of degree distribution. Indeed, marine food webs tend to fit mostly to power-law and exponential degree distributions, though even the Poisson degree distribution (i.e. random network) was registered to be the case in some empirical marine food webs (Montoya & Solé 2002; Bornatowski et al., 2017; Marina et al., 2018b). In our case, degree distribution of both the Full food web and the Hard and Soft Bottom food webs showed an exponential fit. Such degree distribution form is associated with some vulnerability to primary removals of species. A network with this degree distribution is more fragile to the removal of the most connected species than a random network, but not as fragile as a power-law network (Albert et al., 2000; Dunne et al., 2002a; Estrada, 2007). These results could explain why the three food webs exhibited an apparent robustness to primary extinctions (i.e. response to *in silico* extinctions).

4.2 Multidimensional stability proxies

We understand network stability as a complex concept. This is why we approached it in a multidimensional way incorporating two types of simulation techniques and different network metrics. Firstly, when analyzing *in silico* extinctions we found no differences between the three studied food webs. The absence of a real collapse in this analysis suggests an apparent robustness to species lost. In concordance, a previous study showed an apparent robustness to macroalgae lost (Cordone et al., 2018). Here we extended this to other species beyond the lower trophic levels. Secondly, when applying the curve-ball algorithm we observed that the Full food web, the Hard Bottom, and Soft Bottom food webs displayed differences in the multidimensional stability proxies. The curve-ball algorithm was consistent in the generation of simulated networks with topological parameters compatible with empirical food webs and allowed us to make reliable comparisons between networks. This fact highlights the importance of in- and out-degree distributions in the generation of simulated webs, which displayed topological structure coherent with a trophic network. The HB displayed a higher significant value of QSS , suggesting that HB could be more

locally stable than FW and SB. In this sense, we expect HB to exhibit a higher probability to recover after a perturbation event such as a local loss of a particular species (Allesina & Pascual, 2008). This result contradicts our hypothesis that brown webs (Soft Bottom food web) displays proxies related to higher stability than green food webs (Hard Bottom food web). In the case of omnivory (O), we observed that SB showed a higher value than FW and HB indicating that SB could potentially be more robust to variations in prey abundances since predators can refuge on alternative preys (Borrvall et al., 2000). However, in order to better know the effect of higher O values in Potter Cove stability (i.e. stabilizer or destabilizing), the distribution of interactions strength would be required (McCann, 2012; Wootton, 2017). To achieve this, estimations of the interaction strengths should be performed. Higher O values in the Soft Bottom food web might be related to a higher productivity; it has recently been observed that microalgal primary production on soft sediments is higher than on rocky substrata on the Baltic Sea (Ask et al., 2016). With regard to modularity, the FW showed higher values than the HB and the SB food webs. This is an expected and logical result since ignoring habitat type in food web description makes the presence of modules more likely. However, it is interesting to note that the HB and SB food webs showed similar values of Mod (i.e. with non-significant differences), which implies that both networks would have the same capacity to contain disturbances (Newman & Girvan, 2004; Stouffer & Bascompte, 2011).

The existence of differences between network metrics on FW and between the HB and the SB food webs is a clear evidence that habitat type could determine important aspects of network structure with consequences on the estimation of food-web stability. In particular, the Full food web might be an inaccurate representation of what happens in Potter Cove system since habitat type food webs are not considered in the full picture (FW). Recently, Hutchinson et al. (2019) highlighted the need to understand ecological networks as entities, which constitute higher structures as multilayer networks. Accordingly, a multilayer framework will allow us to incorporate space, time and other

types of species interactions in food-web studies. This approach is truly recent in ecology research and requires further empirical and theoretical work (Hutchinson et al., 2019). Adding habitat type to Potter Cove food web description was the first step needed to generate a multilayer structure. Future studies should take into account other factors such as seasonality or different types of interactions in order to better understand the structure and stability of this Antarctic ecosystem.

4.3 Multidimensional stability proxies and their relevance for local climate change impacts

Both Hard and Soft Bottom food webs are currently threatened by environmental changes at Potter Cove ecosystem related to climate change (Schloss et al., 2012; Pers et al., 2013; Ducklow et al., 2013). These environmental changes are a potential source of disturbances that can spread through the two food webs and may affect the Hard and the Soft Bottom food webs in different ways. One recently observed change is the release of new ice-free areas induced by glacial retreat (Lagger et al., 2018). This kind of disturbance could produce an increase on macroalgal production by the colonization of new ice-free hard bottom areas, but also increase the amount of suspended particulate matter with negative effects on photosynthesis rates (Quartino et al., 2013; Deregibus et al., 2016). Changes on macroalgal assemblage may be reflected in the Hard Bottom food web and indirectly in the Soft Bottom web by changes on the detritus stock as observed in other Antarctic food webs (Dunton 2001; Norkko et al., 2004; Norkko et al., 2007; Gillies et al., 2012). Also, glacial retreat seems to be associated with a decrease in net primary production of the microphytobenthos community in Potter Cove, which may negatively impact the Soft Bottom food web capacity to maintain its high O values (Hoffmann et al., 2019). Despite this, it has been shown that there is a degree of adaptation in trophic niches of meio- and macrofauna assemblages where more recent ice-free soft bottom areas may host a less redundant trophic assemblage (Pasotti et al., 2015b). This finding would suggest that the meiofauna community has a good capacity to adapt and consequently the overall stability of the Soft Bottom food web would be expected to be higher. Other disturbances related to temperature rise (e.g. iceberg scour frequency) seem to have negative

effect on diversity at hard bottoms but not at soft bottoms on other Antarctic ecosystems (Vause et al., 2019). In this sense, to predict the consequences of climate change in Potter Cove, in-depth investigations about the energy subsidies and the coupling between the Hard and the Soft Bottom food webs are needed and should be the next step to conquer.

5. Conclusions

Our results showed that habitat type is an important aspect for the understanding of food-web structure. Ignoring the differences between habitat type in Potter Cove food web has consequences on network proxies for multidimensional stability and it can lead to an overestimation of robustness and false predictions about how perturbations affect this Antarctic ecosystem. In addition, we found differences on network metrics between green and brown food webs, which suggested that food webs based on different energy pathways (producer-based or detritus-based) exhibit differences in their network structure and on different aspects of their stability. In this sense, habitat type and particularly bottom type at marine ecosystems should not be neglected *a priori* in future network studies. Our work highlights the need to take into account the habitat structure to design more appropriate conservation strategies, since each habitat has different characteristics on food-web stability dimensions.

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Authors' contributions

Georgina Cordone contributed to data collection, performed data analysis and manuscript writing. Vanesa Salinas contributed to data collection and manuscript writing. Tomás Ignacio Marina contributed to data collection and manuscript writing. Santiago Raul Doyle contributed to data collection and manuscript writing. Francesca Pasotti contributed to data collection and manuscript writing. Leonardo Ariel Saravia contributed to data collection, data analysis and manuscript writing. Fernando Momo provided the idea, contributed to data collection and manuscript writing.

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Appendix

2. Materials and Methods

2.2. Food web assembly and topological description

Table A1. Trophic species and characteristic type of bottom (soft, hard and both) are presented here.

* *Hippomedon kergueleni* and *Orchomene plebs* were considered as one trophic species because they share all predators and prey items; both of them are amphipods. *Mycale acerata* and *Stylocordyla borealis* are sponges and also were considered as one trophic species for the same reason.

Trophic Species	Bottom	Trophic Species	Bottom
<i>Adenocystis utricularis</i>	Hard	<i>Eatoniella</i> sp.	Both
<i>Aequiyoldia eightsii</i>	Soft	Epiphyte diatoms	Hard
<i>Agalophamus trissophyllus</i>	Soft	<i>Euphausia superba</i>	Both
Aged detritus	Soft	<i>Eurytemora nonticulosa</i>	Hard
Asciadiacea	Both	Fresh detritus	Soft
<i>Ascoseira mirabilis</i>	Hard	<i>Parrukia cristata</i>	Soft
Benthic copepods	Soft	<i>Ceminocarpus geminatus</i>	Hard
Benthic diatoms	Both	<i>Georgiella confluens</i>	Hard
<i>Bovallia gigantea</i>	Hard	<i>Gigartina skottsbergii</i>	Hard
Bryozoa	Both	<i>Gitanopsis squamosa</i>	Both
<i>Callophyllis atosanguinea</i>	Hard	<i>Glyptonotus antarcticus</i>	Both
<i>Chaenocephalus aceratus</i>	Hard	<i>Gondogeneia antarctica</i>	Hard
<i>Cheirimedon femoratus</i>	Soft	<i>Haliclonidae</i> sp.	Soft
Cirratulidae	Soft	<i>Harpagifer antarcticus</i>	Both
Copepods	Both	<i>Hemiarthrum setulosum</i>	Hard
Cumacea	Soft	Hiperiids	Hard
<i>Curdiea racovitzae</i>	Hard	<i>Hippomedon kergueleni</i> *	Both
<i>Dacrydium</i> sp.	Hard	Hydrozoa	Hard
<i>Dendrilla antartica</i>	Soft	<i>Iridaea cordata</i>	Hard
<i>Desmarestia anceps</i>	Hard	<i>Laevilacunaria antarctica</i>	Hard
<i>Desmarestia antarctica</i>	Hard	<i>Lambia antarctica</i>	Hard
<i>Desmarestia menziesii</i>	Hard	<i>Laternulla elliptica</i>	Soft
<i>Diplasterias brucei</i>	Both	<i>Lepidonotothen nudifrons</i>	Both
<i>Doris kerguelensis</i>	Both	<i>Malacobelmnnon daytoni</i>	Soft
		Maldanidae	Soft

<i>Margarella antarctica</i>	Soft	<i>Parborlasia corrugatus</i>	Soft
Meiofaunal Cumacea	Soft	<i>Pariphimedia integricauda</i>	Both
Meiofaunal Polychaetes	Soft	<i>Perknaster aurorae</i>	Soft
<i>Monostroma hariotii</i>	Hard	<i>Perknaster fuscus antarcticus</i>	Both
<i>Mycale acerata*</i>	Soft	<i>Phaeurus antarcticus</i>	Hard
Microphythobentos	Soft	Phytoplankton	Both
<i>Myriogramme manginii</i>	Hard	<i>Picconiella plumosa</i>	Hard
<i>Mysella sp.</i>	Soft	<i>Plakarthrium puncattissimum</i>	No information
Mysidacea	Both	<i>Plocamium cartilagineum</i>	Hard
<i>Nacella concinna</i>	Hard	<i>Pontogeneia sp.</i>	Hard
Nauplii	Soft	<i>Porphyra plocumiestris</i>	Hard
Necromass	Both	Priapula	Both
Nematodes	Soft	<i>Prosiobbingia gracilis</i>	Hard
<i>Neobuccinum eatoni</i>	Both	<i>Protoryctophum sp.</i>	No information
Nereidae	Hard	<i>Ptilosarcus gurneyi</i>	Soft
<i>Neuroglossum delesseriae</i>	Hard	<i>Rosella sp.</i>	Soft
<i>Notothenia coriiceps</i>	Both	Salps	Both
<i>Notothenia rossii</i>	Both	<i>Serolis sp.</i>	Both
Octopus	Both	Spionidae	Soft
<i>Odontaster validus</i>	Both	SPM	Soft
<i>Odontaster meridionalis</i>	Both	Squids	Both
Oligochaeta	Both	<i>Sterechinus neumayeri</i>	Both
Ophaeliidae	Soft	<i>Stylocordyla borealis*</i>	Soft
<i>Ophionotus victoriae</i>	Both	Tanaidacea	Soft
<i>Oradarea bidentata</i>	Hard	Terebellidae	Soft
Orbiniidae	Soft	<i>Trematocarpus antarcticus</i>	Hard
<i>Orchomene plebs*</i>	Both	<i>Trematomus bernacchi</i>	Hard
Ostracoda	Soft	<i>Trematomus newnesi</i>	Both
<i>Palmaria decipiens</i>	Hard	<i>Ulothrix sp.</i>	Hard
<i>Pantoneura plocamioides</i>	Hard	<i>Urospora penicilliformis</i>	Hard
<i>Parachaenichthys charcoti</i>	Both	<i>Urticinopsis antartica</i>	Soft
<i>Paradexamine sp.</i>	Both	<i>Waldeckia obesa</i>	Both
<i>Paraserolis polita</i>	Soft	Zooplankton	Both

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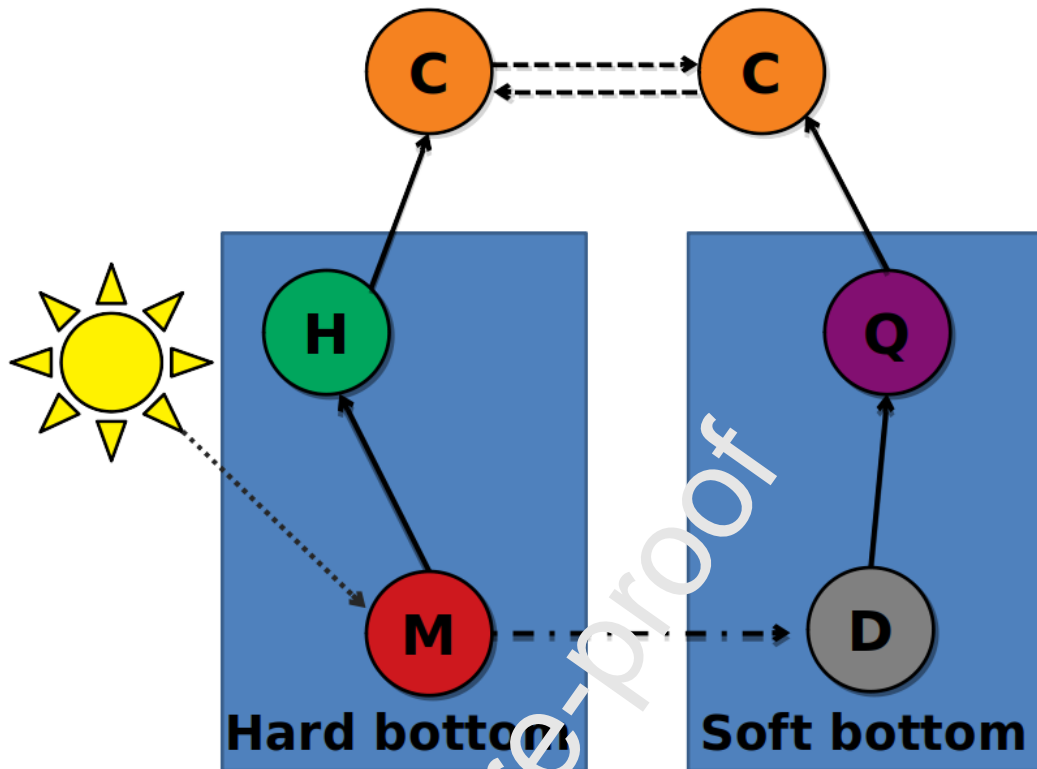


Figure A1. Simplified representation of the main flows of matter and energy in Potter Cove food web considering the two habitat types: Hard Bottom food web is dominated by macroalgae species as food source while Soft Bottom food web depends on detritus stock. Both food webs are coupled by higher trophic levels with greater mobility (top predators). Macroalgae (M), herbivores (H), detritus (D), filters (Q), top predators (C).

Equation A.1: Connectance (C)

$$C = L/S^2 \text{ (Eq. A.1.)}$$

Where L is the number of trophic interactions and S the number of species.

Equation A.2: Trophic Level (TL)

$$TL_i = 1 + \sum_{j=1}^S TL_j DC_{ij} \text{ (Eq. A.2)}$$

Where TL_j is the trophic level of j prey and DC_{ij} is the fraction of prey j in predator i diet. For basal species TL is equal to 1 given that they have not preys.

Equation A.3: Clustering Coefficient (CC)

$$CC_i = \frac{2E_i}{k_i(k_i-1)} \text{ (Eq. A.3)}$$

This is a measure of the probability that any two nodes connected with a third be also connected each to other. K_i are all the edges which connect the focal node (i) and other K_i nodes being $2K_i (K_i - 1)$ the maximum value if all K_i are neighbours and E_i the real number of neighbours. When all K_i nodes are neighbours CC is 1 (complete clustering).

Equation A.4: Characteristic Path Length (CPL)

$$CPL = \frac{2}{S(S-1)} \sum_{i=1}^S \sum_{j=1}^S CPL_{min}(i, j) \text{ (Eq. A.4)}$$

Where $CPL_{min}(i, j)$ is the minimum path between i and j nodes, averaged over $S(S-1)/2$ nodes.

Equation A.5: Modularity (Mod)

$$M = \sum_s \frac{l_s}{L} - \left(\frac{d_s}{2L} \right) \text{ (Eq. A.5)}$$

Where s is the number of modules or compartment, l_s is the number of links between species in the modules, d_s is the sum of degrees for all species in module s and L is the total number of links.

3. Results**3.1 Food web assembly and topological description**

Table A2. Observations of the degree distributions of Full, Hard Bottom and Soft Bottom food webs comparing the fit with three common statistical models (Power-Law, Exponential and Poisson distributions).

Distribution	Full food web			Hard Bottom web			Soft Bottom web		
	Estimate (SD)	AIC	Δ AIC	Estimate (SD)	AIC	Δ AIC	Estimate (SD)	AIC	Δ AIC
Power-Law	1.46 (0.02)	760.54	106.94	1.53 (0.03)	471.08	57.21	1.44 (0.02)	501.95	90.56
Poisson	7.62 (0.74)	987.90	334.30	5.84 (0.71)	592.39	178.52	7.66 (0.70)	509.39	98.00
Exponential	0.14 (0.01)	653.60	0	0.19 (0.02)	413.87	0	0.14 (0.01)	411.39	0

3.2 Multidimensional stability proxies

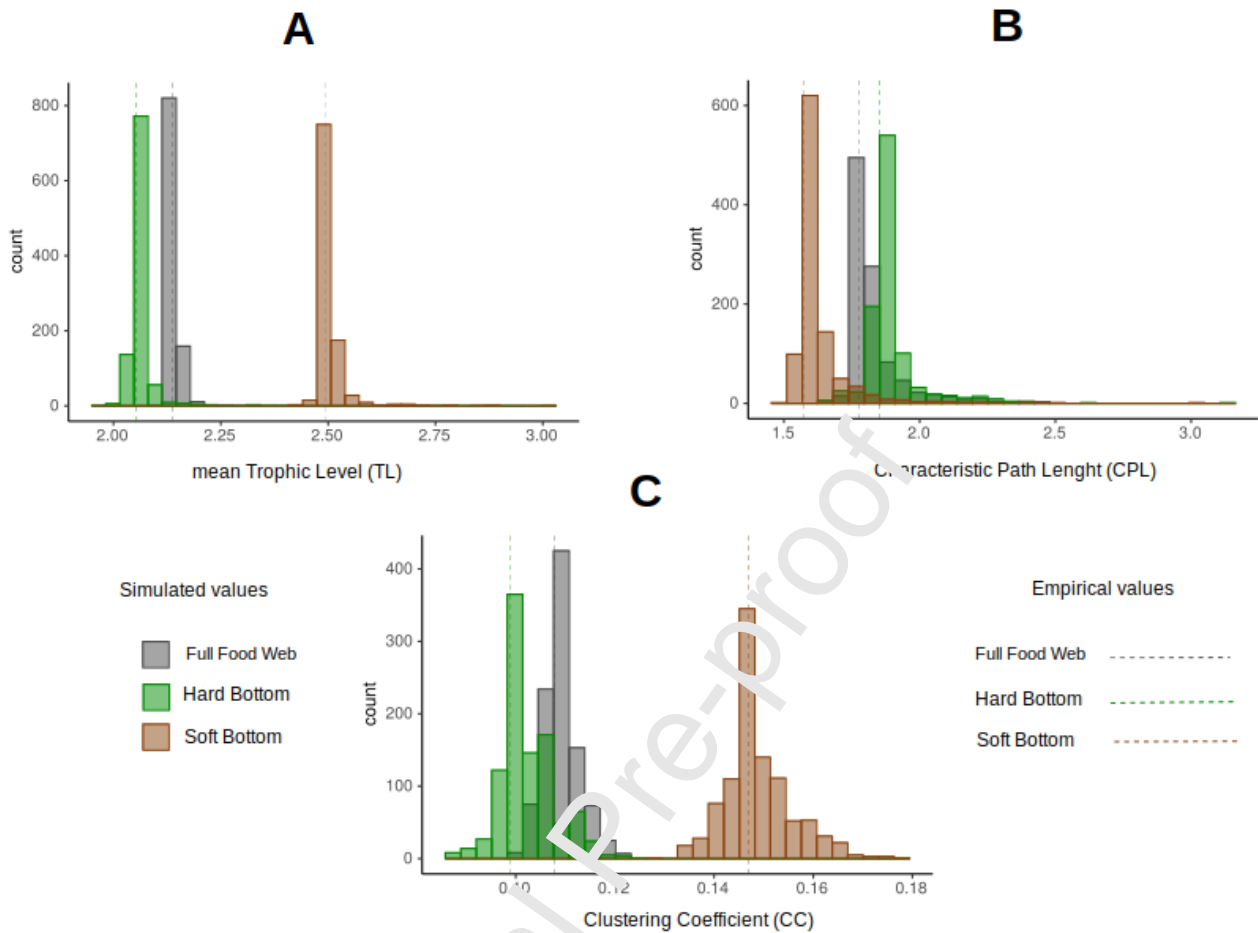


Figure A.2. Histograms showing topological parameters of simulated networks for Full food web (FW), Hard Bottom (HB) and, Soft Bottom (SB) food webs. Empirical values are shown as dotted lines (FW: gray, HB: green and SB: brown). Network metrics displayed here are: mean Trophic Level (A), Characteristic Path Length (B) and Clustering Coefficient (C).

Table A.3. Estimates D and P-values from two-sides Kolmogorov-Smirnov test for Hard Bottom-Full food web (HB-FW), Soft Bottom-Full food web (SB-FW) and Soft Bottom-Hard Bottom (SB-HB) comparisons of simulated values ($n=30$ for each simulated web). * for p-values significantly different (<0.05).

Network metric	Abbreviation	HB-FW		SB-FW		SB-HB	
		D	P-value	D	P-value	D	P-value
Quasi Sing-Stability	QSS	1	$1.872e-13^*$	0.5333	0.0004^*	1	$1.872e-13^*$
Omnivory	O	1	$1.872e-13^*$	1	$1.872e-13^*$	1	$1.872e-13^*$

Modularity	<i>Mod</i>	1	1.872e-13*	1	1.872e-13*	0.2667	0.2365
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Table A.4. Estimates for Cohen's d effect size for Hard Bottom-Full food web (HB-FW), Soft Bottom-Full food web (SB-FW) and Soft Bottom-Hard Bottom (SB-HB) comparisons of simulated values. * for p-values significantly different (<0.05).

Network metric	Abbreviation	HB-FW	SB-FW	SB-HB
Quasi Sing-Stability	<i>QSS</i>	16.2212*	1.3840*	-14.6547*
Omnivory	<i>O</i>	-4.1855*	9.3008*	11.9872*
Modularity	<i>Mod</i>	-6.0003*	-4.7449*	-0.07514

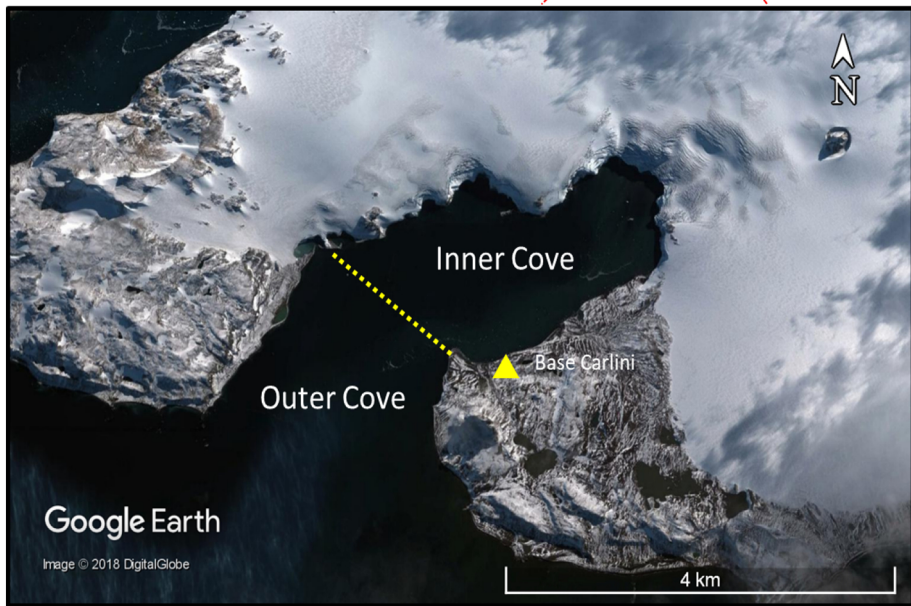
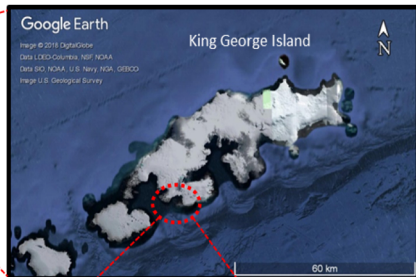
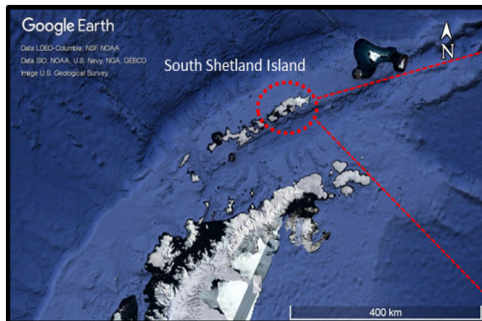
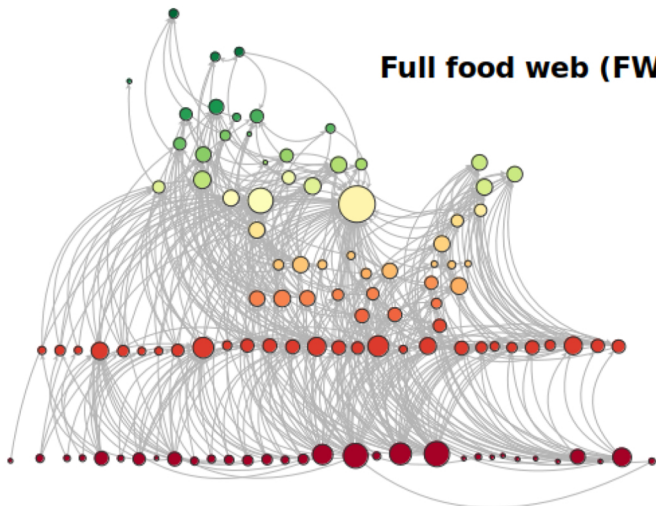
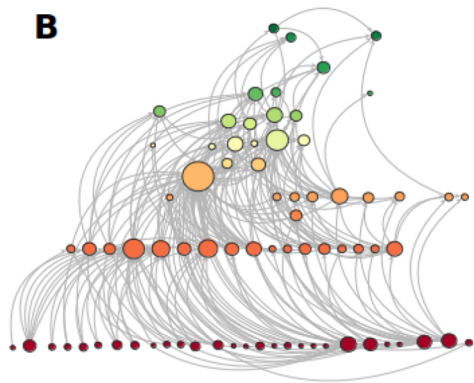


Figure 1

A Full food web (FW)

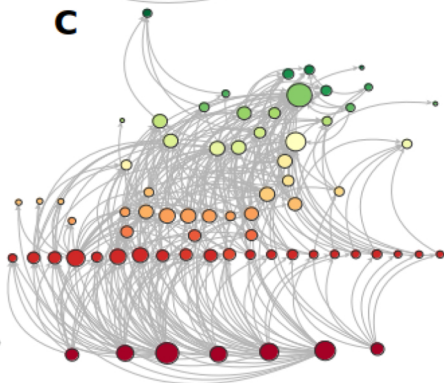


B



Hard Bottom web (HB)

C



Soft Bottom web (SB)

Figure 2

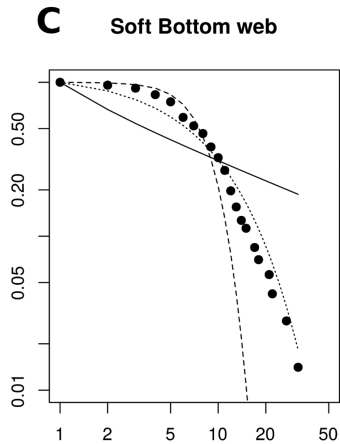
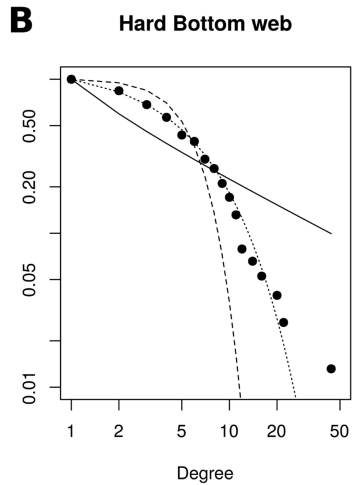
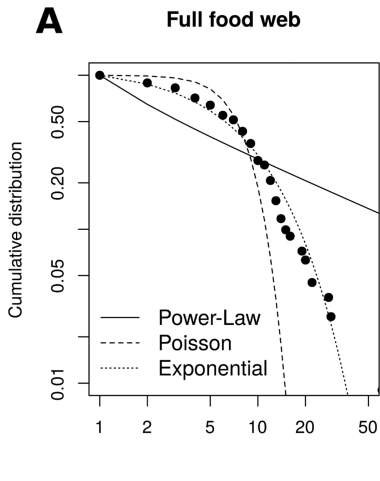


Figure 3

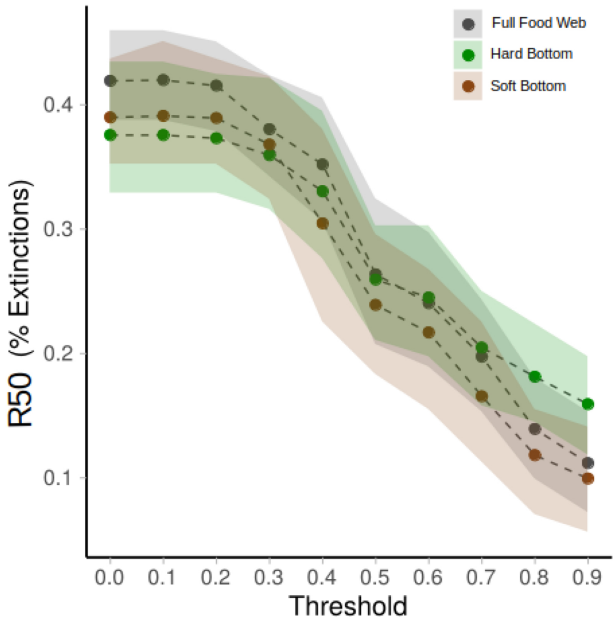
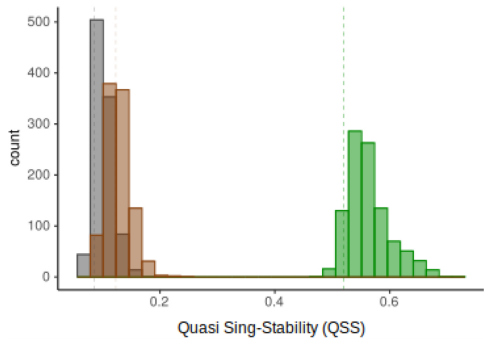
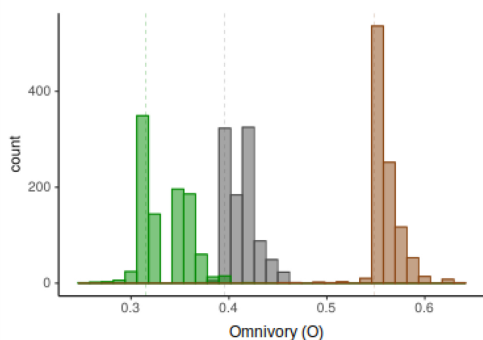
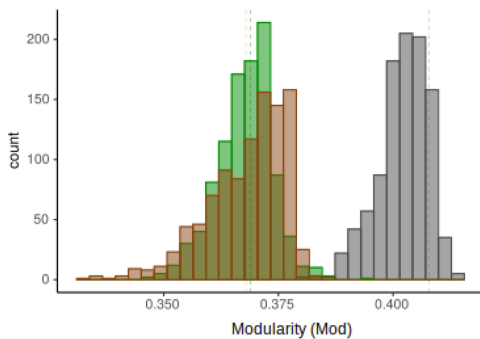


Figure 4

A**B****C**

Simulated values



Empirical values



Figure 5