Potter Cove's Heavyweights: Estimation of species' interaction strength of an Antarctic food web

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Abstract

Understanding the complex interplay between structure and stability of marine food webs is crucial for assessing ecosystem resilience, particularly in the context of ongoing environmental changes. In the West Antarctic Peninsula, global warming has led to severe alterations in community composition, species distribution, and abundance over the last decades. In this study, we estimate the interaction strength within the Potter Cove (South Shetland Islands, Antarctica) food web to elucidate the roles of species in its structure and functioning. We use these estimates to calculate food web stability in response to perturbations, conducting sequential extinctions to quantify the importance of individual species based on changes in stability and food web fragmentation. We explore connections between interaction strength and key topological properties of the food web. Our findings reveal an asymmetric distribution of interaction strengths, with a prevalence of weak interactions and a few strong ones. Species exerting greater influence within the food web displayed higher degree and trophic similarity but occupied lower trophic levels and displayed lower omnivory levels (e.g., macroalgae and detritus). Extinction simulations revealed the key role of certain species, particularly amphipods and the black rockcod

Notothenia coriiceps, as their removal led to significant changes in food web stability and network fragmentation. This study highlights the importance of considering species interaction strengths in assessing the stability of polar marine ecosystems. These insights have crucial implications for guiding monitoring and conservation strategies aimed at preserving the integrity of Antarctic marine ecosystems.

Keywords: Antarctic ecosystem, Marine food web, Species interaction strength, Climate change.

Introduction

Within an ecosystem, species are interconnected through feeding relationships, which shape energy flows and create complex food webs. The exploration of food webs has significantly enhanced our comprehension of species' ecological roles and their impact on ecosystem functionality and resilience (Belgrano et al., 2005; Landi et al., 2018). Most food web studies have focused on binary representations, primarily examining species' presence or absence and their interactions (Dunne et al., 2002; Kortsch et al., 2015; Marina, Salinas, et al., 2018; Olivier & Planque, 2017). However, a deeper understanding recognizes that food webs possess inherent complexities in the form of weighted interactions, where the strengths of species interactions vary. Integrating weighted links based on interaction strengths in food web studies provides valuable ecological insights, especially when examining ecosystem function and stability. Understanding the pattern of these interaction strengths becomes pivotal in assessing and predicting food web stability.

Interaction strength in food webs estimates the magnitude of one species' effect on another and allows for differentiating the importance of species interaction. Several methodologies have been applied to estimate interaction strength in food webs that can require a great variety of empirical data, most of them using species biomass (Calizza et al., 2021; Gauzens et al., 2019; Gellner et al., 2023). Here, we applied the method proposed by Pawar et al. (2012) that combines data on consumer and resource body masses, resource density and consumer search space (interaction dimensionality) to obtain interaction strengths estimates for each pair-wise predator-prey interaction. The novelty of this method is that it changes the coefficients that relate body size to metabolism according to whether the species moves in 2D or 3D, and it has the advantage that resource density and species biomass or density are not mandatory.

One of the greatest challenges is to predict the effect of human activity on the complex webs of interactions among species. These species interactions mediate how changes in the physical and chemical environment play out throughout the ecosystem. Impacts affecting one species can have cascade effects on others, either directly or indirectly, depending on the pattern of strength of these connections. In the face of increasing mean global temperature caused by global climate change, understanding the effect of species on the stability of ecological communities is a pressing issue.

The West Antarctic Peninsula has experienced the most intense warming on the planet in the last fifty years (Ducklow et al., 2013; Turner et al., 2014), with direct impacts on the cryosphere. As a result, the glacier in Potter Cove has been rapidly receding since 1950 (Rückamp et al., 2011), which has generated cascading effects in terms of freshwater input with sediment run-off (Schloss et al., 2012), leading to profound changes on the benthic and pelagic communities(Braeckman et al., 2021; Deregibus et al., 2023; Garcia et al., 2019; Sahade et al., 2015).

While the Potter Cove food web topology, complexity and stability have been largely studied (Cordone et al., 2018, 2020; Marina, Salinas, et al., 2018; Marina, Saravia, et al., 2018; Rodriguez et al., 2022), this study aims to go beyond a purely topological (presence/absence) assessment of who eats whom in the Potter Cove ecosystem. Our goal is to analyze the trophic network structure quantitatively by estimating the interaction strength for each trophic interaction. We aim to evaluate the species' role in the food web structure and stability, considering the strength of interactions.

Materials and methods

I. Description of the study area

Potter Cove (62° 14’ S, 58° 38’ W) is a ~9 km^2 fjord located at Isla 25 de Mayo/King George Island, South Shetland Islands, on the West Antarctic Peninsula (Figure 1). Potter Cove's high-latitude location results in fluctuating environmental conditions driven by the strong seasonality in the photoperiod length. The winter reduction in irradiance and temperature regulates several environmental variables, including incident radiation, sea-ice extent, mixing layer depth, water column particulate matter, and nutrient concentration.

II. Potter Cove food web dataset

We used a well-resolved food web that documents 649 feeding links between 110 species that inhabit Potter Cove (Rodriguez et al., 2022). The species diet information was collected and compiled from gut content studies and personal communication with experts. The Potter Cove food web can be considered representative of the summer season since data were collected during austral summer months when most research campaigns are carried out. More detailed information on Potter Cove food web assembly can be found in Rodriguez et al. (2022) and Marina, Salinas, et al. (2018)

III. Interaction strength estimation

We estimated the strength of each pairwise interaction in the food web following Pawar et al. (2012) methodology, considering consumer (predator) and resource (prey) body mass and the interaction dimensionality (ID). First, we compiled information about resources and consumers' body mass m_R and m_C. Then the ID was classified as 2 or 3 dimensions based on the species movement space and habitat. We assign 2D when both predator and prey move in 2D (e.g., both are benthic) or if a predator moves in 3D and a prey in 2D (e.g., pelagic predator on benthic prey). The ID was classified as 3D when both predator and prey move in 3D (e.g., both pelagic) or if the predator moves in 2D and the prey in 3D (e.g., benthic predator, pelagic prey) (Pawar et al., 2012).

The main equation we used to estimate the interaction strength (IS) was:

$$IS = \frac{\alpha \, x_R \, m_R}{m_C}$$

where α is the search rate, x_R the resource density and m_R and m_C the body mass for the resource and the consumer, respectively (Pawar et al., 2012).

We obtained estimates for the search rate (α) from the power-law scaling relationship with the consumer mass, determined by ordinary least squares regression, but with different coefficients for both dimensional search space (Pawar et al., 2012). When available, we used empirical resource density (x_R) acquired from bibliography, otherwise, we estimated it from the scaling relationship with the resource body mass, since it scales as power-law with different exponents in 2D and in 3D (Pawar et al., 2012). For resources such as macroalgae, sponges, necromass, fresh and aged detritus, where body mass and/or density are independent from the consumer, a value of 1 was assigned m_R and m_C. Consequently, the interaction strength was solely dependent on consumer biomass (Pawar et al., 2012). The equations for estimating the search rate and the resource density are specified in the Supporting Information.

Since the exponents reported by Pawar et al. (2012) have associated standard deviations from the estimation through linear regressions, we used these uncertainties to measure the variability in interaction strength estimates. We generated 1000 random samples of the exponents, assuming a normal distribution with a mean based on the estimated exponent and a standard deviation equal to the reported standard error. Then, we calculated interaction strength values for each sample, leading to distributions of interaction strength estimates for each pair-wise interaction. Since these interaction strength distributions showed right-skewed tendencies, we used the median IS to describe the central tendency.

We fitted the interaction strength distribution (i.e., medians for each interaction) to various models including exponential, gamma, log-normal, normal, power-law, and uniform using maximum likelihood (McCallum, 1999) and chose the best model using the Akaike Information Criterion (Burnham & Anderson, 2002).

IV. Species properties

To characterize the species' role in food web structure and stability, we calculated unweighted food web properties. Unweighted properties are topology-based metrics applied to binary food webs that only describe species presence/absence, where all trophic links are considered equally important in the food web. We calculated four commonly used topological species properties in food web studies: a) trophic level, b) degree, c) omnivory, and d) trophic similarity. Trophic level represents the number of feeding links separating a species from the base of production in a food web. Top predators and primary producers are expected to have large effects on their communities through top-down and bottom-up control (Cirtwill et al., 2018). The degree of a species is calculated as the sum of all in- (number of prey) and out- (number of predators) trophic interactions. It has been linked to a species' importance for the structure and functioning of a food web. Species with high degree are important because perturbations can directly affect many other species (Cirtwill et al., 2018). Omnivory is a feeding strategy in which a consumer feeds at multiple trophic levels. Omnivore species can adapt faster to variation in prey abundances, and it gives trophic flexibility to an ecosystem by presenting alternative energy pathways in the face of perturbations (K. L. Wootton, 2017). Trophic similarity is an index of overlap in species feeding relationships as both consumers and resources, representing species trophic niches

(Delmas et al., 2019; Morlon et al., 2014). Formulas used to obtain the above species' properties are described in Supporting Information.

To study the relationship between species topological properties and interaction strength, we performed quantile regression at quantile 0.25, 0.5 (the median) and 0.75 between the log total interaction strength, representing the sum of the interaction strength for all interactions (both in and out) involving a given species, and each of the species topological properties. Slope significance of the quantile regressions was assessed using the bootstrap method (Koenker, 2005).

V. Species impact on food web stability and fragmentation

To analyze the individual impact of species on food web stability, we performed species removal simulations, sequentially deleting the first 50 species in decreasing order of total interaction strength, trophic level, degree, omnivory and trophic similarity. After each species extinction, we examined the impact on food web stability and fragmentation. We did not analyze secondary extinctions after the removal of a species.

To estimate stability, we calculated the average of the real part of the maximum eigenvalue of the community matrix (i.e., the Jacobian) with randomly varying magnitudes of the matrix elements while preserving the predator-prey sign structure (Allesina & Pascual, 2008; Grilli et al., 2016; Saravia et al., 2022). The maximum eigenvalue describes the rate at which a small perturbation decays or amplifies over time near an equilibrium point. A more negative index indicates a more stable food web with a reduced probability of perturbation amplification. In predator-prey networks, system stability can be achieved by reducing network size, connectivity, or increasing self-regulation (Allesina & Tang, 2012). In our analysis, in the Jacobian the self-regulation terms are zero (the diagonal), this implies that the maximum eigenvalue values obtainable are mostly positive, indicating system instability.

This could be interpreted as the degree of self-regulation required for the food web to achieve stability (Grilli et al., 2016). Species whose removal results in a sharp decrease in the maximum eigenvalue and, consequently, an important increase in stability may be recognized as key species within the network. Their presence indicates a higher level of self-regulation necessary for network stability thus they may have an impact on the whole food web.

Food webs tend to naturally organize into modular patterns, where groups of species interact more strongly with each other than with species from other groups. Species can assume various roles within this modular organization based on the pattern of trophic links within their own module and/or across modules. Typically, a few key species, with high connectivity both between and within modules, play a crucial role in linking the entire food web. We measured the cohesion of the food web by calculating the number of connected components after the removal of a species. These connected components represent species or subgroups unconnected to others and can be considered an extreme form of modules. The number of components in ecological networks is important for the overall structure and resilience of the ecosystem. When an ecological network becomes separated into smaller components, it represents distinct channels of energy flow and species interactions. This characteristic could confer an advantage in scenarios where the network is subjected to perturbations, as it prevents the effects of perturbations from propagating to other components (Gilarranz et al., 2017; Stouffer & Bascompte, 2011). However, a higher number of components can be detrimental to the network. It can lead to fragmented energy pathways, reduced energy transfer, and limited species interactions. We considered the food web fragmented when there was more than one component, with the species responsible for the fragmentation considered a key species contributing to maintaining a cohesive food web structure.

We conducted 1000 simulations for the removal of each species, calculating the maximum eigenvalue for the food web in each case. We plotted the sequential species' extinction results, according to the different species properties, and their effect on food web stability and fragmentation.

VI. Data analysis and availability

All analyses, simulations and graphs were performed in R version 4.3.1 (R Core Team, 2023) using the R packages 'igraph' (Csardi & Nepusz, 2005), cheddar (Hudson et al., 2013) and the 'multiweb' R package to calculate all network metrics and food web simulations (Saravia, 2024).

Results

I. Interaction strength distribution

The interaction strength distribution analysis of the Potter Cove food web showed that the gamma model was the best fit, according to the AIC analysis, with a high proportion of weak interactions, and only a few strong interactions (Figure 2, Supporting Information Table S1).

II. Species interaction strength and topological properties

We found that species' total interaction strength was positively associated with both degree and trophic similarity in all three quantile regressions (Figure 3.b and d, Supporting Information Table S2). The species trophic level and omnivory showed a negative relationship with the total interaction strength for the quantile 75 regression (Figure 3.a and c, Supporting Information Table S2). However, no significant relationship was observed for regressions at quantiles 25 and 50 for both unweighted species properties (Supporting Information Table S2).

This suggests that species exhibiting the highest interaction strength tend to exhibit a higher degree and higher dietary and predator overlap, occupy lower trophic positions and display lower levels of omnivory. The identity of species that exert the most substantial influence on Potter Cove food web are basal species (detritus and some species of macroalgae) and grazers (mostly amphipods) (Supporting Information Table S2.a).

III. Species impact on food web stability and fragmentation

The extinction analyses revealed that removal performed by different species properties has distinct effects on food web stability (Figure 4). While no clear pattern emerged in stability when removing species by decreasing trophic level and omnivory (Figure 4.b and d), we observed that network stability increased after the removal of species with higher interaction strength, degree, and trophic similarity (Figure 4.a, c and e).

When extinctions were performed by decreasing interaction strength, we found that the removal of the amphipods *Prostebbingia sp.* and *P. gracilis*, the 3rd and 4th species with higher interaction strength, substantially increased food web stability (Figure 4.a, Supporting Information Table S2.a). In sequential removals of high-degree species, the amphipods *Gondogenia antarctica* and *Prostebbingia gracilis* caused a major increase in food web stability (Figure 4.c, Supporting Information Table S2.c).

Regarding food web fragmentation, we observed that the removal of the fish *Notothenia coriiceps*, in extinctions by trophic level, degree, and omnivory (Figure 4.b-d, Supporting Information Table S2.b-d), was responsible for the fragmentation of the food web into 9 compartments. For extinctions performed by interaction strength, the amphipod *Paradexamine fissicauda* caused the fragmentation of the food web into 2 compartments, which remained unchanged until *N. coriiceps* was removed, dividing the food web into 14 compartments (Figure 4.a, Supporting Information Table S2.a). In the simulations run by decreasing trophic similarity *N. coriiceps* did not contribute to the fragmentation of the food web. Instead, *Nacella concinna* was responsible for the fragmentation of the network (Figure 4.e, Supporting Information Table S2.e). Notably, network fragmentation does not seem related to stability as fragmentation points do not align with significant stability changes.

Discussion

The estimation of the species interaction strength for the Potter Cove food web allowed us a better understanding of species' role in food web stability. We found that the distribution of interaction strength was skewed toward a few strong and many weak links, as observed in extensive theoretical and empirical studies (Drossel et al., 2004; Kortsch et al., 2021; Marina et al., 2024; J. T. Wootton & Emmerson, 2005). This asymmetrical pattern has been proposed to promote ecosystem persistence and stability (Bascompte et al., 2005; Drossel et al., 2004; Emmerson & Yearsley, 2004; McCann et al., 1998).

We employed a range of descriptors, including unweighted and weighted metrics, to elucidate what makes a species important in the Potter Cove food web. Our findings revealed a positive correlation between a species' interaction strength and its degree, as well as trophic similarity. Conversely, trophic level and omnivory exhibited a negative correlation with the highest levels of interaction strength. The species that exert the most substantial influence on Potter Cove food web are basal species (detritus and some species of macroalgae) and grazers (mostly amphipods), with a high number of interactions and trophic redundancy. This theoretical framework aligns with empirical evidence that the large biomass macroalgae dominating shallow benthic communities, along with the detritus derived from them, play a fundamental role as the energetic base of the Potter Cove food web (Gómez & Huovinen, 2020) and support a high-density assemblage of invertebrates, especially amphipods (Huang et al., 2007). While macroalgae have a great influence in shaping the structure of the Potter Cove food web, their direct impact on its stability appears to be less important. Local losses of macroalgae species do not immediately destabilize the food web; rather, they exhibit relative robustness until a high critical stress threshold is surpassed. Beyond this point, negative effects propagate rapidly throughout the entire food web, leading to its collapse (Cordone et al., 2018, 2020).

The Potter Cove food web tends to be more stable and less connected upon the removal of species, as expected. Our study underscores that species exhibiting high total interaction strength, degree, and trophic similarity need to be considered with particular attention when trying to predict the effects of perturbations on the Potter Cove ecosystem. The extinction simulations reveal a threshold behavior in stability—meaning it does not increase gradually—when species are removed by interaction strength, degree, and to a lesser extent by trophic similarity. This is significant as it suggests non-linear effects and confirms the existence of key species that produce these thresholds. This pattern is not observed with omnivory or trophic level. Contrary to expectations, species with the highest degree or interaction strength are not necessarily the most important. Instead, our analysis suggests that interaction strength and degree predominantly shape network structure, influencing the stability of the Potter Cove food web.

Stability appears to be unrelated to the fragmentation of the network, as extinctions causing fragmentation do not correspond to shifts in stability. Fragmentation is linked to modularity as species causing fragmentation are responsible for connecting different modules (Melián & Bascompte, 2004). If these connecting species go extinct, the modules become disconnected. Previous studies, such as Grilli et al. (2016), have demonstrated that the modular structure in food webs can yield varied effects, including no effect, contingent on the distribution of interaction strengths and the degree of self-regulation. Therefore, our observed results align with these expectations.

Our findings show some discrepancies with those of Marina et al. (2024), who applied the same method to calculate interaction strength for the Weddell Sea (Antarctica) food web, without incorporating empirical density/biomass values. They found a positive relationship between species interaction strength, trophic level, and degree. They identified that species that possess key positions in terms of food web stability are characterized by high interaction strength, a middle to high trophic level, a high number of interactions, and middle to low trophic similarity. The discrepancies between their results and those of our study underscore the intricate nature of the relationship between topological unweighted indices and interaction strength. This highlights the inadequacy of relying solely on unweighted indices as reliable indicators of interaction strength. Conversely, utilizing interaction strength estimations applied to the study of food web stability appears to be a valuable tool for identifying key species within ecosystems, considering the unique characteristics and structure of individual food webs.

Our findings revealed that the black rockcod, *Notothenia coriiceps*, a generalist, omnivorous, top predator fish with the highest degree, consistently contributes to the fragmentation of the Potter Cove food web in most extinction simulations (by decreasing interaction strength, trophic level, degree and omnivory). This further supports its potential status as a keystone species in this ecosystem. Previous research examining topological characteristics of the Potter Cove food web has highlighted the central role of *N. coriiceps* in enhancing overall network connectivity (Marina, Salinas, et al., 2018; Rodriguez et al., 2022). Salinas et al. (2024) observed that the removal of *N. coriiceps* resulted in cascading effects on metrics such as connectance, modularity, and stability.

Furthermore, our different analysis consistently points at grazers, like the limpet *Nacella conncina* and the amphipods *Paradexamine fissicauda, Gondogenia antarctica* and species of the genus *Prostebbingia,* as another group of key species influencing the structure and stability of the Potter Cove food web. Amphipods constitute an important and abundant component of antarctic benthic communities and, alongside macroalgae, represent the primary food sources for antarctic fish, such as *N. coriiceps* (Barrera-Oro et al., 2019).

Climate change-induced warming in Potter Cove is substantially changing the community composition, species distribution, and abundance. This warming has led to glacier retreat, creating new habitats for macroalgal colonization, and increased glacier sediment runoff, impacting the photosynthetic rates of primary producers and intensifying competition among species (Deregibus et al., 2016). Simultaneously, Barrera-Oro et al. (2019) observed changes in the feeding selectivity of *N. coriiceps* on amphipods, correlating with shifts in the macroalgae-associated amphipod community. These shifts are linked to alterations in salinity and changes in water column mixing processes, which regulate phytoplankton biomass accumulation (Schloss et al., 2002, 2012). However, the net effects of climate change on macroalgae and other key species, such as amphipods and fish, remain uncertain and represent a challenge to elucidate.

The methodology applied in this study shows great potential for guiding monitoring and conservation strategies, focused on key species, aimed at protecting the integrity of Antarctic marine ecosystems in times of rapid climate changes. Through the incorporation of species interaction strength into our analysis of the Potter Cove food web, we have identified characteristics and potential key species that exert significant influence over both the structure and stability of the ecosystem. The non-linear effects observed in the stability analysis stress the importance of protecting these key species to maintain ecosystem resilience.

Data availability statement

All source code and data that support the findings of this study are openly available in GitHub at https://github.com/123iamela/pottercove-IS and Zenodo at https://doi.org/10.5281/zenodo.10790590.

Conflict of interest statement

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Figures

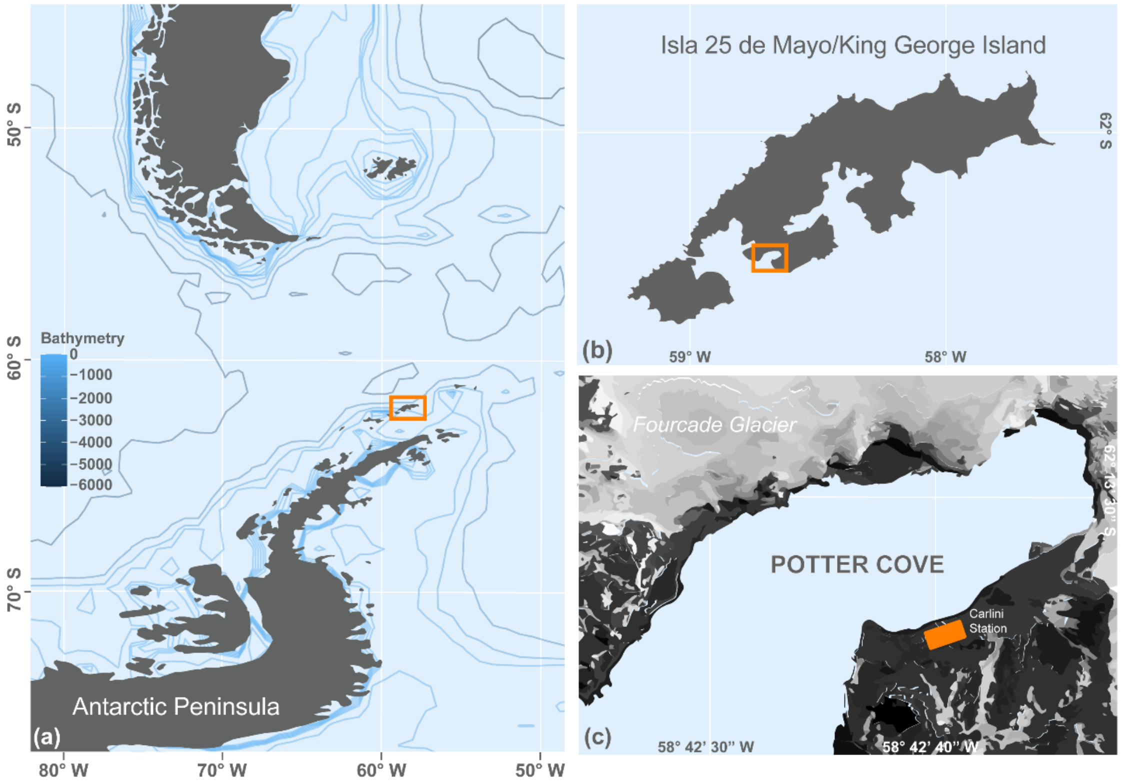

Figure 1. Map of Potter Cove and its location at Isla 25 de Mayo/King George Island (South Shetland Islands, Antarctic Peninsula). The bicontinental map (a) was drawn using the 'marmap' R package (Pante et al., 2023). Contour shape file for Isla 25 de Mayo/King George Island (b) was obtained from www.ign.gob.ar, and Potter Cove's (c) from (Neder et al., 2022).

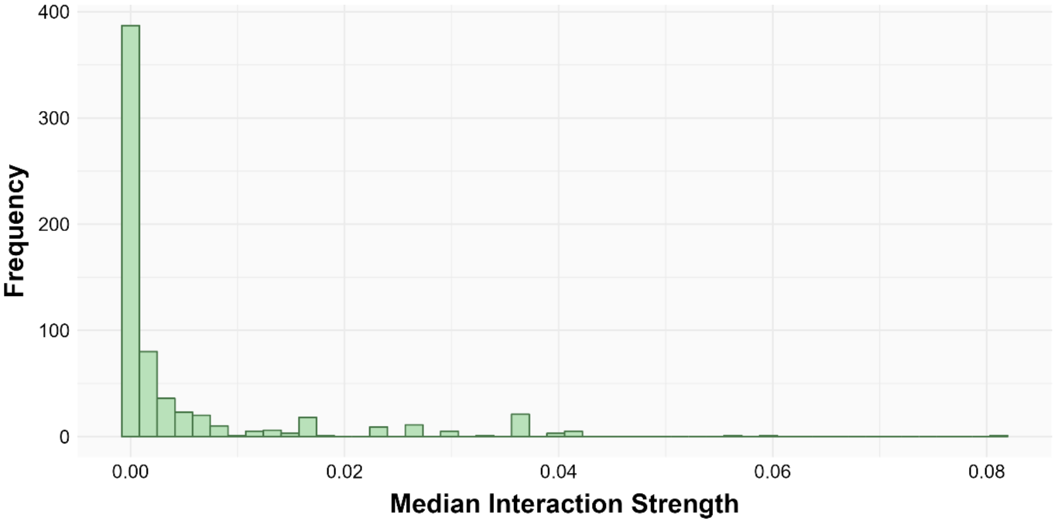

Figure 2. Frequency distribution of the median interaction strengths for the Potter Cove food web. Total number of interactions = 649. The distribution was best fitted to a gamma model.

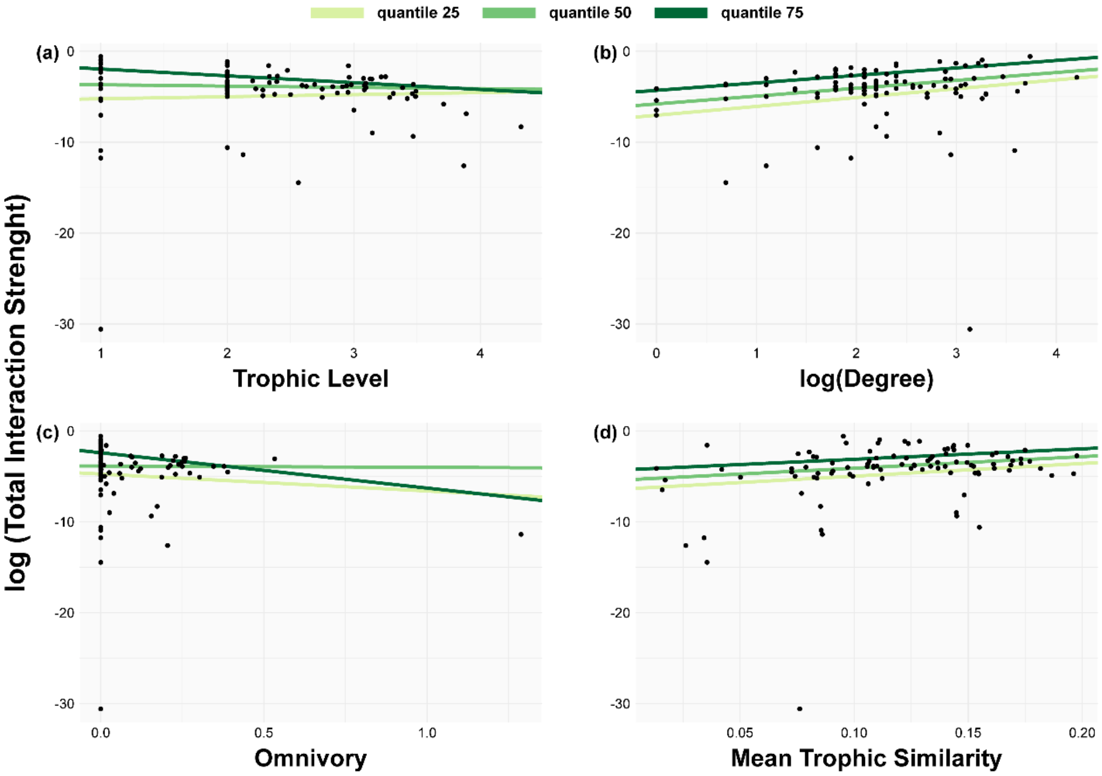

Figure 3. Relationships between weighted (total interaction strength) and unweighted food web properties. We fitted quantile regressions (light green line = quantile 25, medium green

line = quantile 50, dark green line = quantile 75) to show the tendency between log total interaction strength and (a) trophic level, (b) degree, (c) omnivory, and (d) trophic similarity.

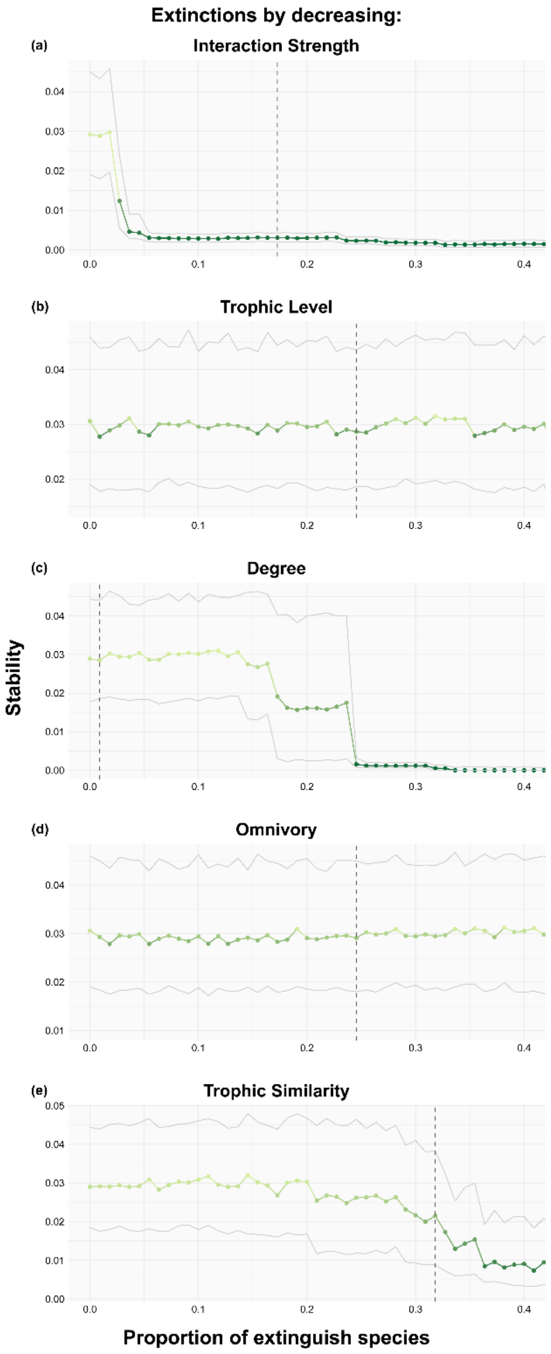

Figure 4. Effects on stability (median maximum eigenvalue) when removing species sequentially based on decreasing weighted and unweighted network properties: (a)

interaction strength, (b) trophic level, (c) degree, (d) omnivory, and (e) trophic similarity. Gray continuous lines represent interquartile stability values. Dark gray dotted vertical line represents the species whose extinction results in the fragmentation of the food web into more than one compartment.