



Robustness of temperate versus tropical food webs: comparing species trait-based sequential deletions

Vanessa Mendonça^{1,2}, Carolina Madeira^{3,4}, Marta Dias², Augusto A. V. Flores⁵,
Catarina Vinagre^{1,2,*}

¹CCMAR—Centre of Marine Sciences, University of Algarve, 8005-139 Faro, Portugal

²MARE—Centro de Ciências do Mar e do Ambiente, Universidade de Lisboa, Faculdade de Ciências, Campo Grande, 1749-016 Lisboa, Portugal

³Associate Laboratory i4HB - Institute for Health and Bioeconomy, NOVA School of Science and Technology, NOVA University of Lisbon, 2829-516 Caparica, Portugal

⁴UCIBIO—Applied Molecular Biosciences Unit, Department of LifeSciences, NOVA School of Science and Technology, NOVA University Lisbon, 2819-516 Caparica, Portugal

⁵Centro de Biologia Marinha, Universidade de São Paulo, Rod. Manoel Hipólito do Rego, km 131.5, São Sebastião, SP 11600-000, Brazil

ABSTRACT: Loss of species can unleash a cascade of secondary extinctions that cause dramatic changes in the structure and dynamics of food webs. The consequences for the food web depend on the traits of the species that are lost; thus, it is crucial to identify species' traits associated with secondary extinction risk. Another important issue is to determine where the most vulnerable ecosystems are located. In this study, we aimed to compare the robustness of temperate versus tropical ecosystems to species loss. A total of 34 intertidal rock pools were analysed from a temperate and a tropical region (17 pools in each). Binary food web networks were assembled for each pool depicting who eats whom. Eighteen topological network properties were estimated to compare temperate and tropical webs. Robustness, a measure of network tolerance to species extinction, was assessed. Species loss was simulated *in silico* using sequential deletion protocols aimed at species that were (1) most connected, (2) least connected, (3) most abundant, and had the largest (4) body mass (mean weight) and (5) size (mean length). Tropical food webs exhibited higher robustness than temperate food webs. Both temperate and tropical food webs were less robust when the removal was directed at the most-connected species, confirming that highly connected species are particularly important in food webs. This study revealed, for the first time, that the positive relationship previously found between robustness and connectance is only confirmed for temperate webs, highlighting the need for more tropical case-studies in general data sets.

KEY WORDS: Intertidal · Rock pools · Food web complexity · Food web topology · Ecological robustness · Secondary extinctions

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1. INTRODUCTION

Comparisons between temperate and tropical environments are important, given that conservation actions need to be prioritized in a world undergoing global change (Ghalambor et al. 2006, Tewksbury et al. 2008). The tropics are considered the cradle of biodiversity and are also home to vastly understudied ecosystems. The temperate zone is better studied and where most of the human population is concentrated. Together, they make up most of all inhabited

areas of the globe. How robust temperate and tropical ecosystems are to species loss is a crucial question in the 21st century (Duarte et al. 2012, Vinagre et al. 2018, 2019a,b, Gauzens et al. 2020).

Robustness is the capacity to maintain functioning after a disturbance without fundamental changes (Dunne et al. 2002, 2004, Memmott et al. 2004). Food web robustness has been studied *in silico* by subjecting the webs to different species deletion sequences. Species are eliminated sequentially from food web networks; each deletion is called a 'primary extinc-

*Corresponding author: cmvinagre@ualg.pt

tion', and the extinctions resulting from such deletions are called 'secondary extinctions'. These occur when a consumer loses all its resources (Dunne et al. 2002). Secondary extinctions may be an outcome of cascading effects which follow single direct extinctions caused by one or multiple stress events (Pimm 1980, Greenwood 1987, Borrvall et al. 2000, Dunne et al. 2002, Ebenman et al. 2004, Montoya et al. 2006, Dunne 2009, Fowler 2010). A robust system is characterized by a low number of secondary extinctions (Dunne et al. 2002). In other words, the higher the proportion of species that need to be deleted to collapse the food web, the more robust the web is.

The risk of cascading extinctions depends on the order of species' removals, the number and function of the species removed as well as on the trophic structure of the affected ecosystem (Solé & Montoya 2001, Dunne et al. 2002, Dunne & Williams 2009, Staniczenko et al. 2010). Thus, the robustness of a food web to species loss is non-random with respect to species identity but depends on the traits of the species that are lost from the community. Deletion sequences aimed at the most-connected species cause substantially more secondary extinctions than random removals (Solé & Montoya 2001, Dunne et al. 2002, 2004). Dunne et al. (2002) found that robustness increases with food web connectance but appears to be independent of species richness and the proportion of omnivory within the web. Dunne et al. (2004) concluded that marine food webs are fairly robust to species loss and attributed that robustness to their high connectance. Previous studies have suffered from low replication because the assemblage of highly resolved food web networks is labour-intensive and time-consuming. Here, intertidal rock pools were used as independent microcosms, allowing high replication of food web networks and therefore increasing the chances of detecting relevant patterns, bringing new insights into food web network analysis and the robustness of intertidal food webs.

In a large-scale sampling effort covering 116 intertidal rock pools encompassing 6 ecoregions, Mendonça et al. (2018) revealed that highly resolved food web networks of intertidal rock pools are just as topologically complex as those of larger, open ecosystems and that these microcosm food webs fit the theoretical niche model put forward by Williams & Martinez (2000). This means that these rock pools share a general structural organization with previously reported webs and can thus be used as proxies for larger ecosystems—the study of which is very costly. This finding opened the way for the use of intertidal rock pools as models for the study of uni-

versal processes regulating the complex network organization of food webs (e.g. Brose et al. 2019, Gauzens et al. 2020).

The present work uses a subset of the data used by Mendonça et al. (2018) to investigate food web network robustness to species loss and, in particular, if there are differences between temperate and tropical food webs. This subset comprises a temperate (Portugal) and a tropical (Brazil) area, using tide pools of standardized size (surface area and depth) and location (lower intertidal). In this work, we compared the robustness (i.e. the fraction of species that would have to be removed for $\geq 50\%$ total species loss) of temperate and tropical intertidal rock pool food webs, using sequential deletion protocols aimed at species that are (1) most connected, (2) least connected, (3) most abundant, and that that have the largest (4) body mass and (5) size. The effect of species removal was analysed for 18 network properties. The relationship between robustness and connectance was also investigated.

Deletion sequences aimed at the 'most-connected' or 'least-connected' species have been widely explored in previous studies (Dunne et al. 2002, 2004, Srinivasan et al. 2007, Dunne & Williams 2009), which have shown that the removal of highly connected species can have catastrophic consequences for the food web (Solé & Montoya 2001, Dunne et al. 2002). The least-connected scenario is conceptually similar to finding a 'weak interactor' with strong effects on the abundances of species in a community from a population dynamics perspective (e.g. Berlow 1999). Here, we aimed to detect that effect from a topological perspective by targeting least-connected species.

Deletion sequences based on the 'most abundant', the 'largest body mass' or the 'largest size' have seldom been used in previous robustness studies. However, such criteria are relevant for fisheries, as this industry typically targets abundant and/or large animals (Jackson et al. 2001) and should thus be included in exercises using marine data sets.

2. MATERIALS AND METHODS

2.1. Study area

A data set composed of highly resolved food webs from 116 intertidal rock pools assembled by Mendonça et al. (2018) was used in this study. Of these, a subset of 34 pools was selected from a temperate (average sea surface temperature [SST]: 17°C) and a tropical (average SST: 25°C) region. Seventeen tidal

pools were selected from the Portuguese West Coast (Site A: Cabo Raso—38° 42' 38" N, 9° 29' 9" W; Site B: Raio Verde—39° 17' 11" N, 9° 20' 23" W) and 17 tidal pools were selected from Southeastern Brazil, in São Paulo State (Site A: São Sebastião—23° 49' 26" S, 45° 25' 38" W; Site B: Ubatuba—23° 28' 1" S, 45° 3' 36" W). All selected intertidal rock pools were located in the lower intertidal and had similar sizes and depths (surface area: 0.15–33.00 m²; depth: 0.05–0.80 m; for more details see Mendonça et al. 2018 and Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m691p019_supp.pdf).

Sampling took place in summer, when biodiversity is highest in tide pools, for standardization purposes. All macroscopical organisms were collected and identified *in situ* (when possible), quadrats were scraped for later identification of encrusting and inconspicuous organisms, and sediment samples were collected for species identification in the laboratory. All individuals were counted, weighed and measured (length). The mean number of individuals per pool, mean weight and mean length were estimated for all pools, for each species in each region. Zooplankton and phytoplankton were assumed to always be present and were added as groups due to the low resolution of their predators' diets. Detritus was also assumed to always be present and was added as a single node to all food webs.

Highly resolved binary food webs, depicting who eats whom, were assembled for each pool based on

published information for each species' diet (see supplementary information in Mendonça et al. 2018). Non-consumptive links were not included. Static webs were constructed purely from presence–absence of species. Data on species lists for temperate and tropical regions can be found in Table S1, while data on the food web networks is available at the iDiv Data Repository (see *Data availability*). Mendonça et al. (2018) explored potential correlations between food web properties and pool area, depth and height. Such size-related correlations were not observed for the subset of data used in the present work.

2.2. Food web topology

The assembly of networks was based on trophic species. Trophic species are groups of taxa with 100% similarity in predators and prey (Briand & Cohen 1984). We aggregated nodes or taxa into trophic species (hereafter referred to as 'species') by a standard method used in structural food web studies in order to reduce methodological biases of uneven resolution of taxa within and among food webs (Briand & Cohen 1984, Williams & Martinez 2000).

For each food web, 18 structural properties were calculated to compare temperate and tropical networks (Table 1). A measure of biodiversity was included: the number of trophic species (S). Two standard measures of food web trophic interaction

Table 1. Definition of the food web network properties calculated (adapted from Vinagre & Costa 2014)

Properties		Description
Number of trophic species	S	Number of species in the food web after being converted into a trophic web
Links per species	L/S	Number of predator/prey links per species
Connectance	C	Proportion of actual trophic links to all possible links (L/S ²)
Top species	T	Species with prey and no predators or parasites
Intermediate species	I	Species with both predators and prey
Basal species	B	Species with predators and no prey
Herbivores plus detritivores	H	Species that prey on primary producers
Cannibals	Can	Species that prey on their own species
Omnivores	Omn	Species with food chains of different lengths, where a food chain is a linked path from a nonbasal to a basal species
Resource count		Count of all species that serve as resources in the food web
Consumer count		Count of all species that serve as consumers in the food web
Trophic level	TL	Trophic level averaged across taxa
Mean food chain length	Chain	Mean number of links in every possible food chain or sequence of links connecting top species to basal species
Mean shortest path length	Path	The mean shortest set of links between species pairs
Generality standard deviation	GenSD	Resources per taxon, how many prey items a species has
Vulnerability standard deviation	VulSD	Consumers per taxon, how many predators a species has
Normalized standard deviation of links	LinkSD	Links per taxon
Clustering coefficient	Clust	The mean shortest set of links between species pairs

richness are reported (Table 1): links per species (L/S) and connectance (C). Six properties give percentages of types of species in a food web (Table 1): top (T), intermediate (I) and basal species (B), cannibals (Can), omnivores (Omn) and herbivores plus detritivores (H). Resource and consumer counts were also estimated for each trophic species. Seven overall properties of trophic web structures were also quantified (Table 1): mean short-weighted trophic level (TL), mean number of links connecting top species to basal species (Chain), characteristic path length (Path), standard deviation of mean generality (GenSD), vulnerability (VulSD), normalized standard deviation of links (LinkSD) and a clustering coefficient (Clust).

2.3. Extinction analyses

The structural robustness (R_{50}) of food webs to species removal was calculated as the fraction of species that had to be removed to collapse the food webs to 50% or more (primary species removals and secondary extinctions) of their original size, as defined by Dunne et al. (2002). Because species are discrete entities, in some cases exact R_{50} can be surpassed. In those cases, the value of the fraction of species removed up to that point was registered as it was, with no additional procedure. A secondary extinction occurs when a consumer species loses all of its prey items or when a cannibalistic species loses all of its prey items except itself. When the first primary extinction leads to the loss of 50% of the species there is minimum robustness (1/S), and when 50% of the species have been deleted and no secondary extinctions have occurred there is maximum robustness (0.50) (Dunne et al. 2002). The exact R_{50} is often overshoot because species are discrete units. Lower values of R_{50} mean more secondary extinctions and, thus, lower robustness.

Species were removed using sequential deletion protocols aimed at species that were (1) most connected, (2) least connected, (3) most abundant, and had the largest (4) body mass (sequence followed an order from the highest to the lowest mean weight of the species recorded) and (5) size (sequence followed an order from the largest to the lowest mean length of the species recorded). For criteria 3, 4 and 5, regional mean values were estimated and used to establish a general ranking to be used in all sequential deletions in each region.

R_{50} was calculated as the average value for all webs analysed for each criterion and region. The

relationship between robustness and connectance was investigated separately for temperate and tropical webs using a logarithmic regression. All robustness values were truncated at 0.5 for this analysis. This allowed a direct comparison with Dunne et al. (2002, 2004), who also explored the correlation between robustness and connectance, and in both studies truncated robustness at 0.5.

2.4. Statistical analysis

To ensure that the temperate and tropical intertidal rock pools selected had similar areas and depths, *t*-tests were performed. For the calculations of network properties and extinction analysis, the software Network3D was used (Yoon et al. 2004, Williams 2010). Differences in the food web networks' properties between tropical and temperate food webs were analysed using *t*-tests. Prior to these tests, normality and homoscedasticity were confirmed. A significance level of 0.05 was used in all test procedures. All statistical analyses were carried out using Statistica software version 12.0 (StatSoft).

3. RESULTS

Temperate webs had more taxa and L/S than tropical webs (Table 2). They also presented a higher proportion of I, H and Can species than tropical webs as well as higher GenSD, TL, Chain and Clust (Table 2). Temperate and tropical webs showed similar C, VulSD and Path (Table 2). Tropical webs presented a higher proportion of T, B and Omn species (Table 2).

Tropical webs were more robust to removals than temperate webs based on the 'most-connected' criterion ($t = -3.31$, $p < 0.001$; Fig. 1, Table 3). Tropical webs also presented lower values of extinctions per removal than temperate webs ($t = 2.68$, $p = 0.01$; Table 3). However, the proportion of secondary extinctions that occurred was similar between the 2 regions (Table 3).

Following 'least-connected' species deletions, tropical food webs had similar robustness ($t = 1.34$, $p = 0.19$; Fig. 1), greater extinction rates per removal ($t = -2.08$, $p = 0.04$) and a greater proportion of secondary extinctions ($t = -2.17$, $p = 0.04$). All were relative to their temperate counterparts (Table 3).

Tropical webs were more robust to removals based on the 'most-abundant' criterion than temperate webs ($t = -2.30$, $p = 0.02$; Fig. 1), presented lower val-

ues of extinctions per removal than temperate webs ($t = 2.51$, $p = 0.01$) and had a lower proportion of secondary extinctions ($t = 2.92$, $p < 0.001$) relative temperate webs (Table 3).

Temperate and tropical webs presented similar robustness to species removal ($t = -1.48$, $p = 0.15$),

values of extinction per removal and proportion of secondary extinctions, according to the 'largest body mass' criterion (Table 3). Following the 'largest size' sequence deletions, tropical webs were more robust to removals ($t = -3.74$, $p = 0.001$), had lower values of extinction per removal ($t = 3.57$, $p = 0.001$) and a lower proportion of secondary extinctions ($t = 3.62$, $p = 0.001$) than their tropical counterparts (Table 3).

A positive logarithmic relation was found between robustness and C , for the deletion exercises based on most-connected, largest-size and largest body mass species, but only for the temperate webs (Fig. 2). No significant relationships were found for the tropical webs in any of the deletion exercises (Fig. 2).

Table 2. Structural food web network properties (mean \pm SD). See Table 1 for definitions. Significant ($p \leq 0.05$) differences between regions are in **bold**

Property	Temperate	Tropical	t	p
S	35.88 \pm 9.54	14.71 \pm 3.46	8.605	<0.001
L/S	5.32 \pm 0.93	2.45 \pm 0.38	11.748	<0.001
C	0.16 \pm 0.04	0.17 \pm 0.03	-1.214	0.234
T	0.09 \pm 0.04	0.26 \pm 0.1	-5.389	<0.001
I	0.80 \pm 0.05	0.52 \pm 0.16	6.839	<0.001
B	0.12 \pm 0.04	0.21 \pm 0.04	-7.070	<0.001
H	0.25 \pm 0.05	0.10 \pm 0.05	9.042	<0.001
Omn	0.64 \pm 0.06	0.69 \pm 0.06	-2.313	0.027
Can	0.28 \pm 0.03	0.22 \pm 0.05	3.888	0.001
GenSD	1.12 \pm 0.10	0.66 \pm 0.07	14.943	<0.001
VulSD	1.12 \pm 0.18	1.17 \pm 0.19	-0.887	0.382
LinkSD	0.68 \pm 0.10	0.52 \pm 0.08	5.360	<0.001
TL	2.23 \pm 0.08	2.11 \pm 0.14	3.185	0.003
Chain	1.89 \pm 0.04	1.82 \pm 0.09	2.712	0.011
Path	1.78 \pm 0.09	1.79 \pm 0.08	-0.354	0.726
Clust	0.30 \pm 0.03	0.24 \pm 0.04	4.761	<0.001
ResourceCount	32.76 \pm 8.92	11.06 \pm 3.91	9.188	<0.001
ConsumerCount	32.00 \pm 9.37	11.65 \pm 3.26	8.461	<0.001

4. DISCUSSION

This work showed, for the first time, that tropical food web networks are generally more robust to species loss than temperate food webs. In recent years, the debate on the relative vul-

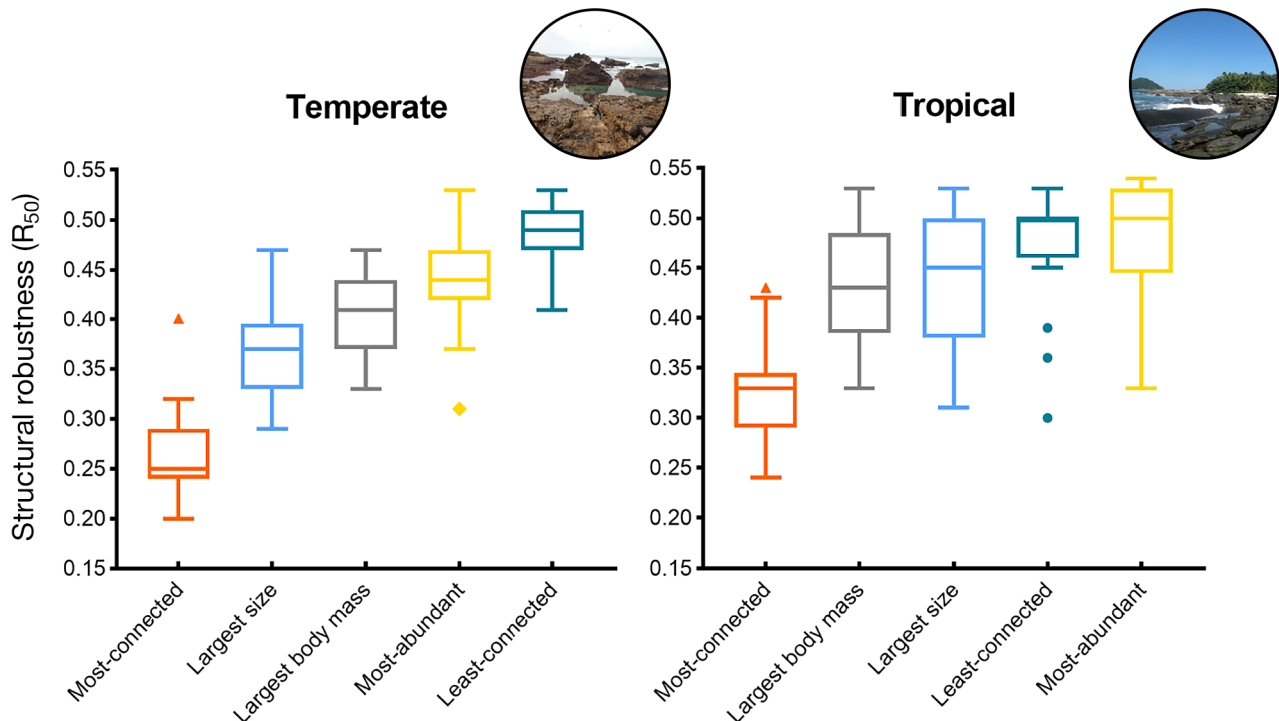


Fig. 1. Structural robustness (R_{50}) is the fraction of species that have to be removed to collapse the food webs to 50% of their original size. On the x-axis are the deletion sequence types, ordered by increasing robustness; on the y-axis is robustness measured as R_{50} . Box defines 25th percentile and 75th percentile; midline represents the mean; whiskers represent outlier limits; the outlier coefficient used was 1.5

Table 3. Mean \pm SD (min–max) percentage of species removed and secondary extinctions in each criterion and region; **bold** indicates significant differences between regions. Structural robustness (R_{50}) is the fraction of species that had to be removed to collapse the food webs to 50% of their original size. S: number of total taxa

	Most connected		Least connected		Most abundant		Largest body mass		Largest size	
	Temperate	Tropical	Temperate	Tropical	Temperate	Tropical	Temperate	Tropical	Temperate	Tropical
R_{50}	26.79 \pm 4.5 (20.0–40.0)	32.37 \pm 5.30 (23.53–42.86)	48.81 \pm 3.10 (40.38–53.33)	46.57 \pm 6.19 (30.0–52.94)	43.43 \pm 4.77 (30.77–53.33)	47.75 \pm 6.10 (33.33–53.33)	40.56 \pm 4.56 (32.69–47.37)	43.20 \pm 5.79 (33.33–53.33)	36.66 \pm 4.28 (29.84–46.67)	43.69 \pm 6.45 (31.25–53.33)
Extinctions per removal	1.02 \pm 0.30 (0.33–1.63)	0.73 \pm 0.33 (0.20–1.75)	0.04 \pm 0.06 (0.0–0.24)	0.15 \pm 0.19 (0.0–0.67)	0.20 \pm 0.15 (0.0–0.63)	0.08 \pm 0.12 (0.0–0.40)	0.30 \pm 0.13 (0.14–0.53)	0.24 \pm 0.18 (0.0–0.6)	0.44 \pm 0.15 (0.27–0.80)	0.23 \pm 0.18 (0.0–0.60)
% secondary extinctions from initial S	26.11 \pm 4.71 (13.33–33.33)	22.44 \pm 7.09 (8.33–41.18)	2.0 \pm 2.53 (0.0–9.62)	5.74 \pm 6.63 (0.0–20.0)	8.10 \pm 5.01 (0.0–19.23)	3.30 \pm 4.54 (0.0–14.29)	11.86 \pm 3.85 (6.25–17.5)	9.32 \pm 6.10 (0.0–20.0)	15.55 \pm 3.58 (10.00–23.07)	9.27 \pm 6.20 (0.0–18.75)
% S final over S initial	47.11 \pm 2.28 (42.11–50.00)	45.18 \pm 6.10 (30.77–50.0)	49.19 \pm 1.03 (46.67–50.0)	47.69 \pm 2.83 (40.0–50.0)	48.47 \pm 2.37 (41.03–51.06)	48.94 \pm 2.96 (45.45–58.33)	47.58 \pm 3.52 (36.84–50.0)	47.48 \pm 3.28 (40.0–50.0)	47.79 \pm 3.15 (40.00–53.33)	47.04 \pm 4.07 (36.36–50.0)

nerability of tropical versus temperate ecosystems has been centred on global warming and how these 2 ecosystem types will respond, with most studies concluding that tropical ecosystems are more vulnerable and will probably lose more species in the future than temperate ecosystems (e.g. Ghalambor et al. 2006, Tewksbury et al. 2008, Duarte et al. 2012, Vinaigre et al. 2016, 2018, 2019a). Such studies were based on experimental research on thermal tolerances, acclimation response and/or thermal safety margins of tropical and temperate species. The present study shows how important it is to move to the next scale of biological organization and investigate species interactions. Our robustness exercise indicates that even though previous studies suggest that tropical ecosystems will lose more species (in the context of climate warming), their food web networks seem to be more robust to species loss than temperate webs. These results should, nevertheless, be taken with caution given that only the bottom-up perspective for presence/absence of links was considered in these deletion scenarios. Conclusions about robustness could be different if top-down processes, energetics, interaction strength and thermal vulnerability of individual species are considered, as it is well-known that the binary topological approach followed here overestimates robustness (Curtsdotter et al. 2011).

Various previous works have reported that food web networks are particularly vulnerable to the loss of highly connected species (e.g. Solé & Montoya 2001, Dunne et al. 2002, 2004, Memmott et al. 2004, Montoya et al. 2006, Curtsdotter et al. 2011); this concept was confirmed in the present study, both for temperate and tropical webs. The robustness of tropical webs to the removal of species directed at the 'most-connected' species was 32%. This is within the interval previously reported by Dunne et al. (2002), which was between 30 and 60% for webs with a similar S, C, L S⁻¹ and Omn percentage (Chesapeake, Bridge Bay, Coachella and Skipwith; in Dunne et al. 2002). Temperate webs, with a robustness of only 27%, revealed not only a lower level of robustness than tropical webs but were also lower than previously determined by Dunne et al. (2002) for the 4 comparable webs mentioned above. Dunne et al. (2004) reported higher robustness (on a most-connected deletion exercise) for Caribbean reef webs and a northeastern USA shelf web (>45%) than that found in the present study, for both tropical and temperate webs. However, for the Benguela marine web, robustness was 30% (Dunne et al. 2004), which is similar to that found in the present work.

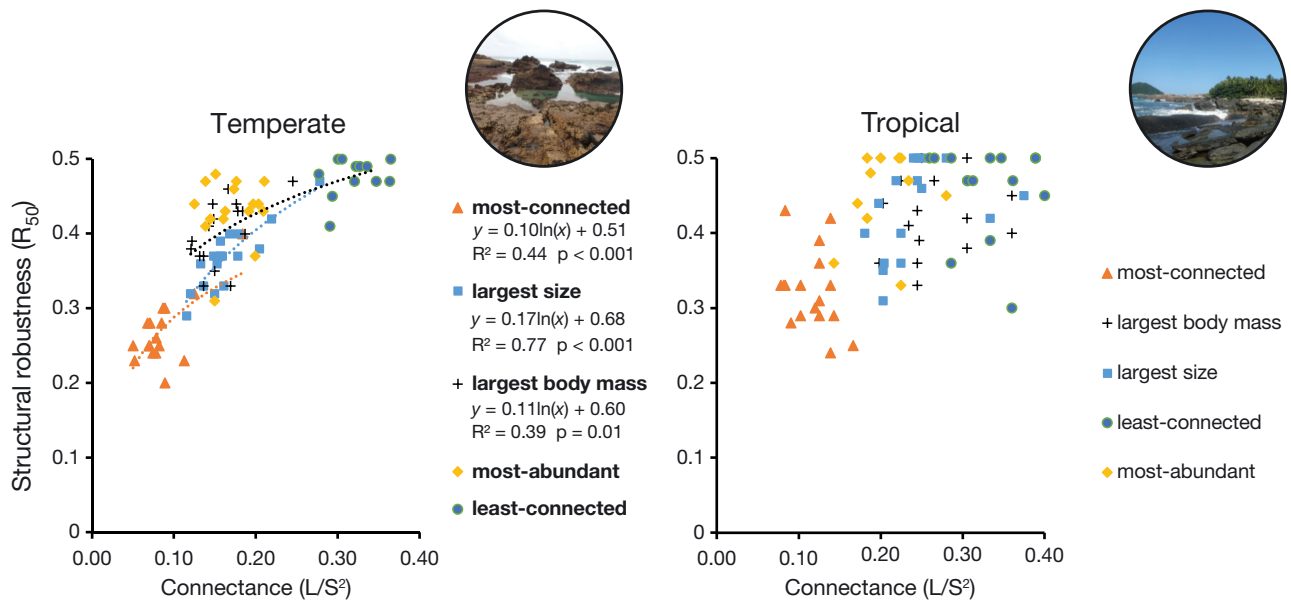


Fig. 2. Structural robustness as a function of connectance (L/S^2) in the temperate and tropical food webs for each deletion criterion. Maximum robustness value = 0.50 (i.e. no secondary extinctions). Lines represent the logarithmic regressions between robustness and connectance; whenever significant, their equation, R^2 and associated p-value are presented

Dunne et al. (2002, 2004) found that robustness and connectance are logarithmically related (positively). The data for tropical and temperate webs fall out of this curve, having lower robustness than expected for their connectance level, similar to the Benguela marine web analysed by Dunne et al. (2004). Most importantly, this study showed for the first time that while a positive logarithmic relationship exists for temperate webs, it does not exist for tropical webs. This suggests that general patterns uncovered in temperate systems or with data sets where tropical systems are underrepresented should be taken with caution. Robustness increases with connectance (Dunne et al. 2002, 2004), but apparently not in tropical food webs. Further investigations using tropical food webs from other habitats are needed to resolve this concept.

Albouy et al. (2019) found no detectable difference in robustness from the tropics to the poles. They did find differences in robustness between open-sea and coastal areas, with coastal areas (0–200 m depth) presenting considerably higher robustness. The results of Albouy et al. (2019) are, however, not directly comparable to the present study because they were based exclusively on fish-to-fish interaction networks, and the criteria used for the removal sequences are not equivalent to the ones used here.

The temperate food webs tested in the present study presented more than double the number of taxa and links per species than that of tropical webs

but similar connectance to tropical webs. Thus, the temperate webs observed here have the same level of complexity as tropical webs but involve considerably more species, which may be a factor determining their lower robustness. The differences found in robustness confirm findings by Dunne et al. (2002), who concluded that robustness is independent of species richness. The higher number of taxa identified in the temperate webs may seem counterintuitive considering common assumptions on global biodiversity gradients. This is probably the case because the Portuguese coast is a region rich in biodiversity, where cold, temperate and subtropical species have overlapping ranges, which is common in mid-latitude regions (Cabral et al. 2001, Vinagre et al. 2011, 2019a). Another important factor that probably influences species richness is that tide pools are thermally harsher environments in the tropics than in temperate zones, with a higher proportion of tropical pool dwellers having thermal limits below the maximum habitat temperature (Vinagre et al. 2018, 2019a).

The higher robustness of tropical webs can be related to a number of aspects of the network topology prior to removals, such as the higher proportion of top, basal and omnivorous species. The higher proportion of top species has already been related to higher robustness in previous studies (Carscadden et al. 2012). Also, basal species are of great importance in food webs, as any food web is supported by the presence of primary producers. Dunne et al. (2002)

showed that protecting basal species in removal exercises confers additional robustness to food webs at any connectance level. Omnivorous species are also stabilizing elements in food webs and reduce the likelihood of secondary extinctions, as previously reported (Fagan 1997, McCann & Hastings 1997, Borrvall et al. 2000, Bascompte et al. 2005). Tropical webs also displayed lower TL, lower clustering of the network and lower GenSD but similar variation in vulnerability (VulSD) compared to their temperate counterparts. The role these properties may have in determining the robustness of food webs has not been discussed so far in previous works; however, since they are important in defining the topology of the food webs, they too may be contributing to the results observed.

Modelling cascading extinctions has demonstrated that the impacts of non-random species extinctions are markedly different from scenarios that assume that species extinction is random (Solé & Montoya 2001, Dunne et al. 2002). Although other studies have tested the effect of random species removal, this criterion was not used in the present study since the extinction of species in the marine environment does not appear to be random (Dunne et al. 2002)—particularly with respect to anthropogenic effects, which tend to impact high trophic levels (e.g. fishing, which tends to select top and larger species; Jackson et al. 2001, Coll et al. 2007). For this reason, the present study tested removals directed at the 'largest body mass', 'largest size' and 'most-abundant' criteria, which are relevant for fisheries but have seldom been tested in previous studies. It was concluded that robustness was considerably high (37–48%) for these criteria, both for temperate and tropical webs.

Curtsdotter et al. (2011) compared robustness in purely topological and dynamical food web models (allometrically scaled, taking into account abundance and interaction strength) and revealed that the topological approach (followed in the present work) overestimates robustness. In the topological approach, secondary extinctions occur only when a species loses all of its prey, deeming all secondary extinctions the product of bottom-up cascades. However, empirical observations have long shown that species loss can result in top-down cascades (e.g. Paine 1966, Elmhagen & Rushton 2007). There are numerous examples in nature of mesopredator control release caused by the loss of a top predator, resulting in the loss of lower-level prey (e.g. Estes & Palmisano 1974, Johnson et al. 2007, Elmhagen & Rushton 2007). Similar effects can occur when top-down control ceases over strongly competitive species, resulting in com-

petitive exclusion (Paine 1966, van Veen et al. 2005). Field exclusion experiments in rock pools have shown the important role of primary consumers, such as limpets, in macroalgal cover and richness (Benedetti-Cecchi & Cinelli 1992, O'Connor & Crowe 2005, Mrowicki et al. 2015). Donohue et al. (2017) showed that the loss of a single predator species can trigger rapid secondary extinction cascades in rocky shores. Donohue et al. (2017) also assembled a dynamic food web network model and concluded that it only reproduced these results when non-trophic interactions, based on competition for space and predator-avoidance, were included. More recently, White et al. (2020), using rock pool communities, showed that individual species can simultaneously stabilize and destabilize ecosystems along different dimensions of stability. Sahasrabudhe & Motter (2011) reported an example of such extensive secondary extinction cascades identified in dynamical food web models. Thus, the present work, as with all purely topological exercises, is a best-case scenario that only accounts for a minimum number of secondary extinctions, failing to identify top-down cascades. This is particularly important in a warming world. Given that the metabolism of ectotherms increases with increasing temperature, stronger feeding pressure by predators could lead to the depletion of prey. Likewise, a predator could go extinct because it cannot catch enough prey to match its metabolic demands (e.g. Binzer et al. 2012).

Dynamic approaches that model abundance and interaction strength, therefore, may be more appropriate for the study of robustness than purely topological approaches. However, in most ecosystems, abundance and interaction strength are unknown for the vast majority of species. This is especially true for highly resolved, complex food webs, such as the ones used in the present work. Here, a topological approach is often the only possible approach.

At a time when some policymakers (e.g. the European Union) are promoting ecosystem-based approaches to achieve sustainability goals, such as the maintenance of marine biodiversity, it is important to understand that such a commitment requires, first and foremost, a deeper understanding of biotic interactions. Topological studies, like the one presented here, are often the only option, given data scarcity. Hence, important efforts should be directed at better understanding food web dynamics all over the world.

The present study brings important new insights into food web structure and robustness for temperate and tropical ecosystems and is also one of the rare exercises in food web topology that uses a high num-

ber of replicate webs. Our finding that tropical food web networks do not present any relationship between robustness and connectance—apparently contradicting the accepted correlation of robustness increasing with connectance—highlights just how much more data needs to be collected from the tropics.

Future studies should use removal criteria based on realistic rankings of species vulnerability towards stressors (e.g. high temperature, acidification, hypoxia, oil contamination) so that their impact on food webs can be simulated. Such vulnerabilities must be tested, and their rankings made available for food web research. This will require a joint effort from field and experimental biologists, as well as from food-web modellers, to gather information for the most common species within a study ecosystem.

Data availability. Data is available at <https://doi.org/10.25829/iDiv.283-3-756>.

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