Food web robustness depends on the network type and threshold for extinction

Ståhl, Patrik; Puntila-Dodd, Riikka; Zhang, Lai; Nordström, Marie Christine; Kortsch, Susanne

2025-05

Wiley Blackwell
http://hdl.handle.net/10138/593154
Ståhl, P, Puntila-Dodd, R, Zhang, L, Nordström, M C & Kortsch, S 2025, 'Food web robustness depends on the network type and threshold for extinction', Oikos, vol. 2025, no. 5. https://doi.org/10.1111/oik.11139

OIKOS

Check for updates

Research article

Food web robustness depends on the network type and threshold for extinction

Patrik P. G. Ståhl[1,2], **Riikka Puntila-Dodd**[1,2], **Lai Zhang**[3], **Marie C. Nordström**[2,4] and **Susanne Kortsch**[5]

[1]Marine and Freshwater Solutions, Finnish Environment Institute, Helsinki, Finland
[2]Environmental and Marine Biology, Åbo Akademi University, Turku, Finland
[3]School of Mathematical Science, Yangzhou University, Yangzhou, China
[4]Ecosystems and Environment Research Program, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland
[5]Tvärminne Zoological Station, Faculty of Biological and Environmental Sciences, University of Helsinki, Hanko, Finland

Correspondence: Patrik P. G. Ståhl (pastahl92@gmail.com)

Oikos
2025: e11139
doi: 10.1111/oik.11139

Subject Editor: Miguel Verdu
Editor-in-Chief:
Paulo R. Guimaraes
Accepted 12 December 2024

Species loss in ecological communities can trigger cascading extinctions, the extent of which likely depends on network type and extinction thresholds. Traditionally, network responses to node removal are analysed using unweighted food webs, ignoring interaction strengths and extinction thresholds. Here, we examine how food web robustness varies with network type (unweighted versus weighted), extinction thresholds, and species removal sequences, and explore how network properties – connectance and relative ascendency both unweighted and weighted – predict robustness. First, our results show that network robustness, measured by the R50 index, can be up to 40% lower in weighted networks compared to unweighted ones. Additionally, incorporating extinction thresholds reveals a consistent reduction in robustness when species deletions proceed from the highest to the lowest species degree or sum of link weights. This suggests that measures of robustness that do not include extinction thresholds overestimate of ecological network robustness. Furthermore, it highlights that species with high energy through-flow are crucial for maintaining energy pathways and network integrity in weighted food webs, emphasizing their importance in a conservation context. Second, relative ascendency emerged as the strongest predictor of food web robustness, providing the clearest temporal and ecological signals related to changes in energy fluxes. This metric reflects both link distribution (skewness) and pathway architecture (energy flux constraints), underscoring the importance of these network properties in assessing food web stability. Therefore, these properties should be considered in ecosystem management recommendations.

Keywords: Baltic Sea, ecosystem functioning, energy fluxes, secondary extinctions, Trophic interactions, weighted networks

NORDIC SOCIETY OIKOS

www.oikosjournal.org

Introduction

Ecosystems worldwide are being reshaped due to losses and gains of species, brought on by anthropogenic disturbances, non-indigenous species and climate change (Cardinale et al. 2006, Pimm et al. 2014, Young et al. 2016). Biodiversity loss does not only affect the species in question, but also the species that depend on them via ecological relationships. For example, prey items' disappearance can trigger secondary extinctions altering the whole food web (Pimm 1980, Dunne et al. 2002, Ebenman et al. 2004, Curtsdotter et al. 2011). Understanding how changes in species composition, and losses of species and their trophic interactions, affect ecosystem functioning and stability is of vital importance for guiding management efforts (Cardinale et al. 2012, Thompson et al. 2012, Antunes et al. 2024).

Food webs represent the flow of energy through a network of interacting species, where species are represented as nodes and the trophic interactions as links (Yletyinen et al. 2016, Olivier et al. 2019). In flux-weighted food webs, the interaction strength can be quantified using allometric scaling and metabolic theory, providing an estimate of energy flow from one taxon to another (Barnes et al. 2018, Gauzens et al. 2019). This type of mechanistic approach linking community composition and ecosystem functioning is central to enhancing our understanding of food web dynamics (Kortsch et al. 2021). One approach to studying stability in highly resolved food webs is network robustness – the effect of species removal on a food web's ability to resist secondary extinctions (Dunne et al. 2002, Landi et al. 2018), which occur when (non-basal) species lose all their prey items. In extinction simulations comparing unweighted and weighted networks, adding interaction weights has been found to trigger more abrupt collapses of network functioning, whereas qualitative networks were almost unaffected (Bellingeri et al. 2019). Yet, except for a few food web studies (Allesina et al. 2006, Curtsdotter et al. 2011), most secondary extinction simulations have been performed using unweighted, binary food webs (Dunne et al. 2002, Gilbert 2009).

In addition to a weighted network perspective on food web robustness, how species respond to reduced energy intake is fundamental for understanding overall food web responses to node loss. The idea that a species only goes extinct when it loses all its incoming energy could be seen as the best-case scenario in nature (Bodini et al. 2009), but a species is more likely pushed to functional extinction in a food web before all energy intake is completely lost (Bodini et al. 2009). Therefore, a more realistic assumption would be that a species goes extinct when it has lost a certain proportion of its energy intake. Using extinction thresholds may thus change the relationship between link architecture and robustness, especially for weighted networks. Studies that have included thresholds found a decrease in robustness when these were taken into account (Bodini et al. 2009, Thierry et al. 2011, Bellingeri and Bodini 2013). Empirical evidence about species-specific energetic requirements, or thresholds, remains largely unknown but has been suggested to be as important for understanding ecosystem robustness as the architecture of the ecological network (Thierry et al. 2011, Bellingeri and Bodini 2013). Overall, by ignoring energy thresholds for extinction, as well as energy flux variability in the network, we risk reaching biased conclusions regarding the functioning and stability of ecosystems.

Food web properties are often used as proxies to gain insight into how ecosystems function and how robust they are (Dunne et al. 2002, Curtsdotter et al. 2011, Canning and Death 2018). A property often used to express the complexity of unweighted networks is connectance – the proportion of potential links that are realized (Dunne et al. 2002, Van Altena et al. 2016). This property is also central in the long-standing and ongoing debate on the relationship between diversity, complexity and stability in food webs (MacArthur 1955, May 1972, Landi et al. 2018). Work on secondary extinctions in binary food webs has shown that robustness is positively linked to connectance (Dunne et al. 2002, Gilbert 2009, Bellingeri and Cassi 2018). However, the use of connectance as a reliable indicator of food web robustness and stability has been challenged in more recent studies finding no clear patterns between connectance and robustness (Canning and Death 2018, Van Altena et al. 2016). Instead, relative ascendency (A/C), an information-theoretic index (Ulanowicz 1986), was found better at predicting robustness (Canning and Death 2018). Relative ascendency takes the distribution of links (their skewness, connectivity and organisation) into account, whereas connectance does not reveal anything about how links are organised in the network. Consequently, networks with the same level of connectance can represent very different link distributions and food web topologies.

Food web properties can also be calculated for weighted networks. The weighted version of connectance – effective connectance – is based on Shannon's entropy index and describes the diversity of interaction strengths or energy fluxes (MacArthur 1955, Bersier et al. 2002). It is called effective connectance because it captures how some interactions (flows) are stronger than others, in other words, that a consumer derives most of its energy from a few of its resources. For example, the American mammalian predator *Puma concolor* feeds on eight resource species (it has eight in-going links in total), but approximately 74% of its diet comes from one single species of deer (Loxdale and Harvey 2016). Hence, the puma's effective number of prey is much lower than its topological node degree would suggest. Because of this, the puma is disproportionately dependent on its main prey item, making it more vulnerable to the loss of this single prey species. Such vulnerability, stemming from a skewed link weight distribution at the node level, could extend to the entire network, as the removal of strong links has been shown to reduce network functioning (Bellingeri et al. 2019).

The main objective of this study is to quantify how food web robustness may be influenced and predicted by network type (unweighted/weighted) and properties (complexity and skewness), as well as thresholds for species extinction. Both the inclusion of weights and extinction thresholds adds realism to the ecological networks and extinction simulations by acknowledging that organisms have varying preferences for prey and different tolerances for losing them – factors often overlooked in extinction studies (Bellingeri and Bodini 2013). To address our main objective, we used a quantitative marine food web time series of the Gulf of Riga (Kortsch et al. 2021). We asked the following questions: 1) how does robustness differ in unweighted and weighted networks, 2) how does the inclusion of extinction thresholds impact robustness outcomes, and 3) which network complexity metrics (connectance and relative ascendency) best predict robustness in these temporally resolved food webs? We focused on deletion sequences from highest to lowest degree or sum of link weights (also known as node strength or weighted degree) (Newman 2001, Barrat et al. 2004, Opsahl et al. 2010), for which we hypothesise:

H1) that unweighted networks are more robust than weighted networks (comparison between scenarios in Fig. 1a–b)

H2) that including thresholds decreases robustness (comparison between scenarios in Fig. 1a, c)

H3) that skewed weighted webs are less robust than more evenly distributed flux webs

Materials and methods

Study system

The Baltic Sea, including the Gulf of Riga, is well known to be subjected to multiple stressors ranging from over-harvesting to eutrophication (HELCOM 2023), and to have undergone regime shifts as a response to some of these stressors (Möllmann et al. 2006). This makes a Baltic Sea food web a good and relevant study system to investigate food web robustness in a temporal context. The Gulf of Riga is a relatively shallow and isolated sub-basin of the Baltic Sea. The gulf covers an area of about 16 330 km^2, has a mean depth of 27 m and an average salinity of about 5.0–6.5. There is no permanent halocline in the offshore area. The coastal parts of the gulf are heavily impacted by the inflow of rivers (Kotta et al. 2008). The water of the gulf gradually becomes more saline towards open water and the Irbe strait

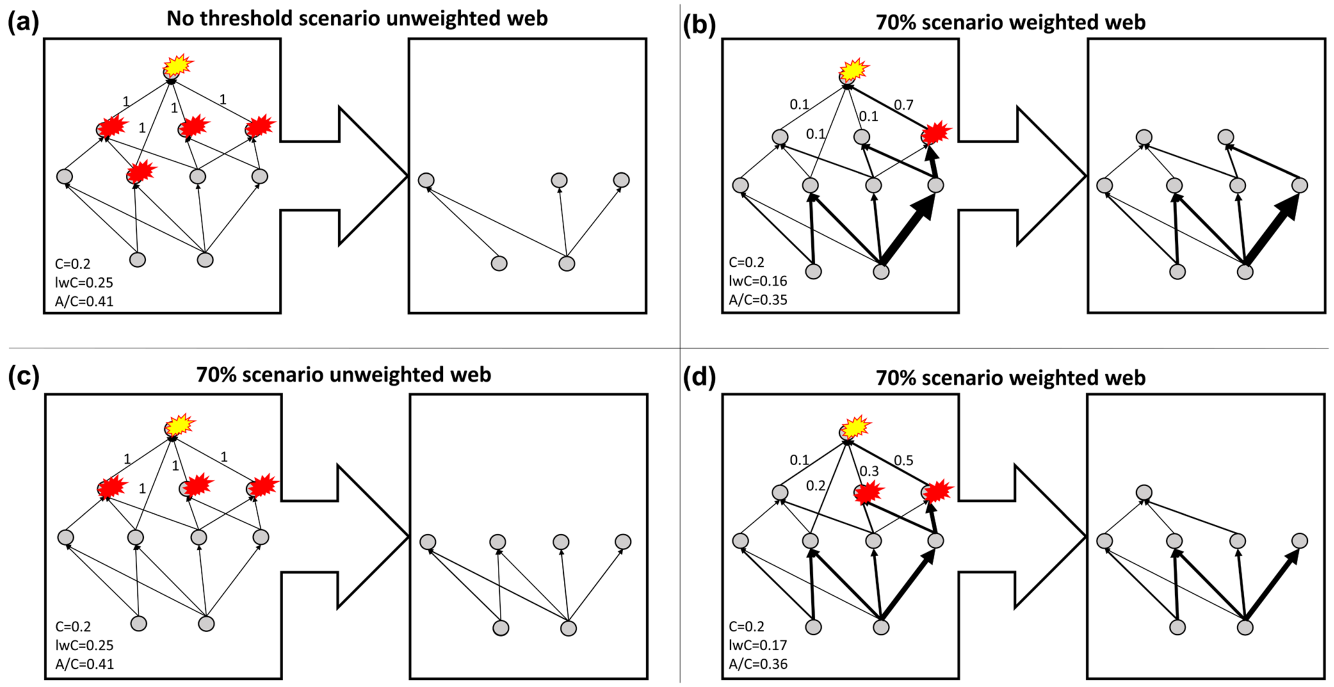

Figure 1. Conceptual model illustrating the value of analysing the robustness of food webs when taking link magnitude and distribution into account. Circles represent species, arrows represent trophic links and the direction of energy flow. The red explosion shapes represent primary species extinction events and the yellow explosion shapes represent secondary extinctions. The letters in the lower left of the panels are the metrics in the different scenarios: C = Connectance , lwC = link weighted connectance, A/C = relative ascendency. (a) shows the no-threshold scenario, where a species goes extinct when it loses all of its energy sources. In an unweighted web, all links are given equal strength. (b) illustrates the scenario with a 70% threshold for extinctions in a weighted web, where links have different weights representing the amount of energy flow of the interactions, i.e. losing 70% of incoming energy flow leads to a species extinction in the food web. Here, only one primary extinction is required to trigger the secondary extinction. (c) shows a scenario with a 70% threshold for secondary extinctions in an unweighted web. This time, three primary extinctions are required to trigger a secondary extinction. Finally, (d) illustrates a scenario with a 70% threshold for extinctions in a weighted web, in which link weights are more evenly distributed. Here, two primary extinctions are required to trigger a secondary extinction.

(Kotta et al. 2008). Overall, salinity in the gulf has fluctuated over time, increasing from the 1960s to the 1970s and then decreasing in the early 1990s (Skudra and Lips 2017) only to increase again slightly after 1993 (Jurgensone et al. 2011), similar to the Baltic Proper (Conley et al. 2009). Temperature-wise, the Gulf of Riga has been showing a gradual increase over the last decades (Jurgensone et al. 2011) with a rise in sea surface temperature of about 0.8–1.0°C per decade (The Bacc Ii Author Team 2015). The Gulf of Riga biota resembles similar brackish water basins in the Baltic and includes a mix of freshwater, marine and brackish species. Herring *Clupea harengus* and three-spined stickleback *Gasterosteus aculeatus* are prevalent fish species in the Gulf of Riga (Kotta et al. 2008) and the Baltic clam *Macoma balthica* is one of the dominating benthic species in large parts of the soft-sediment areas (Kotta et al. 2008). There has also been an arrival of invasive species to the Gulf of Riga, such as the the round goby *Neogobius melanostomus* (Kotta et al. 2008).

Gulf of Riga food web

In our study of food web robustness, we used an empirical food web time-series for the Gulf of Riga ecosystem (Kortsch et al. 2021). The time-series represents the offshore marine food web in spring/early summer (May and June) over 38 years from 1979 to 2016. The species biomass data were collected through national biomonitoring programs (Latvian Institute of Aquatic Ecology, Institute of Food Safety, Animal Health and Environment BIOR) targeting phytoplankton, zooplankton, benthos and fish. Because sampling effort varied considerably among the taxonomic groups and between years, a resampling procedure was used to standardize the number of samples per year over the sampling period (Kortsch et al. 2021). This was accomplished by randomly selecting a fixed number of stations for each taxonomic group within a five-year moving window within the sampling period to create a new food web time-series from 1981 to 2014. The resampling procedure was repeated 1000 times for each year resulting in 1000 food webs per year, 34 000 food webs in total. Weights (energy fluxes) were assigned to the trophic links using a bioenergetic food web modelling approach (Barnes et al. 2018, Gauzens et al. 2019), giving a corresponding set of 34 000 weighted networks. A more detailed description of the procedures and of the temporal changes in unweighted and weighted food web structure can be found in Kortsch et al. (2021).

Robustness

We tested food web robustness by exposing the Gulf of Riga food webs, both weighted and unweighted, to species extinction sequences, where species were removed from the networks one at a time. We applied three commonly used deletion sequences (highest to lowest, lowest to highest, and randomized order). For each food web, the order in which species were removed was determined by species degree in the unweighted version and by the sum of link weights in the weighted version, each ranked from highest to lowest, lowest to highest, and in randomized order (Supporting information). Basal species (autotrophs, heterotrophs and detritus) were exempt from deletion in all scenarios to constrain the deletion sequences as species in the networks cannot persist without the base of the food web. To measure the robustness of the food web, we calculated R50, which is a reliable measure of robustness frequently used in theoretical food web studies (Jonsson et al. 2015, Tejedor et al. 2017).

$$R_{50} = \frac{\text{Primary extinctions}}{\text{Species}} \tag{1}$$

R50 is defined as the proportion of primary species extinctions required before a food web is reduced to 50% of its initial size as a result of both primary and secondary extinctions. We assessed how R50 relates to unweighted and weighted network connectance and relative ascendency. R50 was calculated using the R package 'NetworkExtinction' (Avila-Thieme et al. 2023), ver. 1.0.3.

Thresholds

We also studied how different energy thresholds impact network robustness. We simulated extinctions as described above, applying ten different threshold scenarios for subsequent secondary extinctions to both unweighted and weighted networks, respectively, and followed the impact on robustness (R50). The first threshold (Fig. 1a), represents the no-threshold scenario, meaning that a species remains in the food web as long as it has an incoming link. The remaining nine threshold scenarios were percentage-based at 10% intervals, ranging from 90–10%, describing the minimum required proportion of energy inflow, and the level at which, species are lost from the community. For example, the 70% threshold means that a species would go extinct if it lost 70% or more of its incoming flow (Fig. 1b). Thresholds were applied to both unweighted and weighted food webs. In the weighted food webs, the link weights were defined as the amount of energy flux among species. In the unweighted food webs, all links were treated as having a weight of one 1) for the purpose of triggering extinctions. As such, the computed loss of energy for calculating extinction thresholds is based on the number of links. For example, if a species has four incoming links, each link is considered to contribute 25% of the species' incoming energy. If three of these links are removed due to primary or secondary extinction, the species would lose 75% of its initial resources but still remain in the network. However, if the extinction threshold is set at 70%, the species would itself be removed as a result of secondary extinction (Fig. 1c).

Metrics and indicators

We calculated several food web metrics and indicators for both weighted and unweighted networks. Connectance, C, is a food web property that is calculated from the number of species and the number of feeding links (Eq. 2). It describes the proportion of realised links out of all possible in a web, and is often used as a measure of food web complexity (May 1972, Dunne et al. 2002, 2004).

$$C = \frac{\text{Links}}{\text{Species}^2} \tag{2}$$

Connectance is an unweighted metric, meaning all links are equally important in the food web. However, in real-world food webs, it is common that the fluxes associated with the links vary considerably in magnitude (Paine 1980). To account for differences in link weights, weighted food web descriptors have been introduced (Bersier et al. 2002, Banašek-Richter et al. 2009). These descriptors are often based on information theory and utilize Shannon's entropy index H (Eq. 3):

$$H = -\sum_{n} \frac{t_{ij}}{T_{(t+)}} \log \frac{t_{ij}}{T_{(t+)}} \tag{3}$$

where n represents each link within a food web, t_{ij} represents the flow from species j to species i, and $T_{(i+)}$ represents the total flow entering species i. Weighted metrics take the unequal distribution of link weights in the food web into account and assign more importance to strong links than to weak links. Link-weighted connectance, lwC, is calculated by dividing qualitative weighted link density, qLDw (Eq. 4) with the number of species (Eq. 5) (Bersier et al. 2002, Banašek-Richter et al. 2009).

$$\text{qLDw} = \frac{1}{2T}\left(\sum_{i=1}^{S} T_{(i+)} \exp(H_i) + \sum_{j=1}^{S} T_{(+j)} \exp(H_j)\right) \tag{4}$$

$$\text{lwC} = \frac{\text{qLDw}}{S} \tag{5}$$

where = exp(H_i) and exp(H_j) are the effective number of resources and of consumers, and H_i and H_j are the taxon-specific Shannon indices of inflows and outflows. T is the total sum of the matrix, $T_{(i+)}$ the sum of row i and $T_{(+j)}$ the sum of column j , and finally S is the number of species.

Relative ascendency (A/C) is an information-theoretic index (Ulanowicz 1986) which is derived from average mutual information (AMI). AMI is a measure of constraint in a network: a maximally connected system, where all nodes are connected to all others and with links of equal weight (such as an maximally connected unweighted network), has the minimum AMI – i.e. there is no constraint since biomass can flow everywhere; conversely, a simple chain of energy flow, connecting all nodes will have maximum AMI – i.e. biomass transfer or energy flow is constrained to follow this route (Rutledge et al. 1976).

$$\text{AMI} = k\sum_{i=1}^{S}\sum_{j=1}^{S} \frac{t_{ij}}{T} \log\left(\frac{t_{ij}T}{T_{(i+)}T_{(+j)}}\right) \tag{6}$$

where k is a scalar constant, and is set to $k = 1$, S is the number of species, t_{ij} is the flow leaving species i and entering another species j, T is the sum of all flows within the network (total system throughput), $T_{(i+)}$ is the sum of all flows leaving species i, and $T_{(+j)}$ is the sum of all flows entering species j. As AMI increases, energy flow becomes more constrained and the number of potential energy flow pathways between species usually (but not always) reduces; therefore, webs with low AMI are more web-like (have greater flow diversity) than webs with high AMI. An unweighted web has lower AMI since there is less constraint (or more uncertainty) where energy is going because all links are considered as equal. In a weighted web, we have information on which links transport more energy, providing more constraints in the system and reducing uncertainty about where the energy will go (Fig. 2a–b). As a result, AMI increases.

One way to scale this information is to multiply AMI with total system throughput (T, the sum of all flows), replacing k with T. This yields a metric called ascendency (A), which measures both the degree to which energy flows are confined to specialist pathways, as well as the energetic size of food web. The theoretical maximum of ascendency is defined as development capacity (C) (Ulanowicz 2004). By looking at ascendency as a proportion of the developmental capacity, we get a quantity called relative ascendency (A/C), which allows for comparisons between food webs (varies between 0 and 1).

$$\text{A/C} = \frac{\text{AMI} \times T}{-\sum_{(i,j)} t_{ij} \log\left(\frac{t_{ij}}{T}\right)} \tag{7}$$

To calculate relative ascendency (A/C) we used the R package 'NetIndices' ver. 1.4.4.1, https://cran.r-project.org/package=NetIndices Kones et al. (2009). For link-weighted connectance, we used custom-written code (available in the companion tutorial to the paper by Kortsch et al. 2021 which can be accessed here: https://rfrelat.github.io/BalticFoodWeb.html). All data and scripts used in this study are available through GitHub (https://github.com/skortsch/GoR-Food-Web-Robustness) and via Zenodo (https://doi.org/10.5281/zenodo.14505584).

Simulations and statistical analyses

For each combination of network type and threshold (10–90%), we ran secondary extinction simulations on 1000 food webs per year (1981–2014). To examine the trends in the relationship between robustness (R50), threshold, and our selected measures of food web complexity (connectance, weighted connectance and relative ascendency), we applied spearman rank correlation since regression analysis is unsuitable for simulation studies with large data sets (White et al.

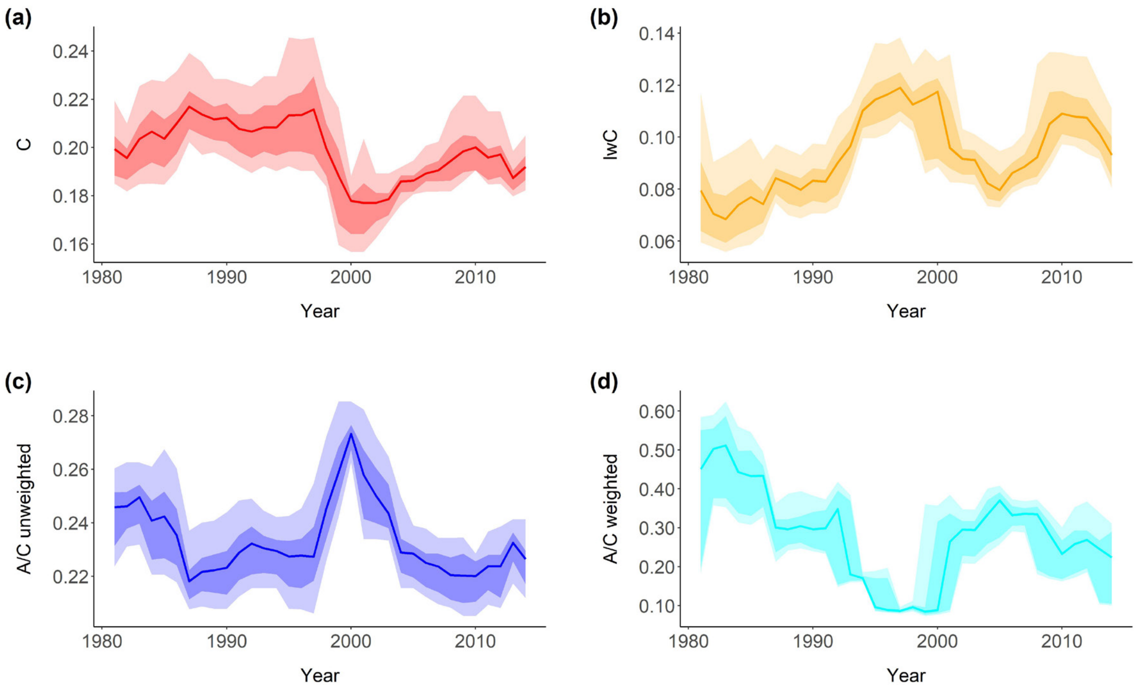

Figure 2. Time-series of C (connectance), lwC (weighted connectance) and A/C (relative ascendency) in the unweighted and weighted webs in the Gulf of Riga. The line represents the median value, shaded areas show 50 and 95% confidence intervals. Note that the y-axis scale differs between metrics.

2014). These trends were analyzed for both unweighted and weighted webs, with a total of 34 000 webs for each combination of network type and threshold.

Results

Metrics and indicators time series

The food web time series showed marked variability in unweighted and weighted food web metrics over time (Fig. 2). Unweighted connectance (*C*), and link-weighted connectance (lwC) displayed distinct temporal variability (Fig. 2a–b). Unweighted connectance (*C*) was highest in the 1980s until the end of 1990s when there was an abrupt drop (early 2000s), followed by a slight increase until the 2010s. In contrast, weighted connectance was lower in the 1980s but increased steadily in the 1990s. In the 2000s, weighted connectance droped again to around the same level as in the early 1990s, before peaking again in the 2010s (Table 1).

Unweighted and weighted relative ascendency (A/C) also displayed distinct temporal patters and variability (Fig. 2c–d). In the unweighted webs (Fig. 2c), relative ascendency was relatively high in the early 1980s but droped abruptly in the late 1980s and remained low until spiking in 2000, followed by an equally sharp decrease, after which, it remained

Table 1. Metric and indicators.

Metric/indicator	Relevance	Definition	Reference
Connectance (directed connectance, C)	Connectance is often used to express the complexity of unweighted networks, and to assess network robustness to perturbations (e.g. secondary extinctions)	The fraction of all possible realized links in a network. Ranges from 0 to 1	Dunne et al. 2002
Weighted connectance (link-weighted connectance, lwC)	Weighted connectance expresses complexity of a network while accounting for link weights (energy fluxes or feeding rates). Measures the effective number of links	The number of realised links in the whole web relative to the total number of links, in which each link is weighed on the basis of the flux rate associated with the trophic link. Ranges from 0 to 1	Bersier et al. 2002, Banašek-Richter et al. 2009
Relative ascendency (A/C)	Measures both the degree to which energy flows are confined to specialist pathways and the energetic size of a web. Allows for the comparison of specialisation and redundancy (multiple energy pathways supporting species)	Dimensionless index of ascendency – index of organization of the food web. Ranges from 0 to 1	Ulanowicz 1986

Table 2. Median percentage change (± SD) in robustness going from no threshold scenario to the different threshold scenarios.

Thresholds	Unweighted webs	Weighted webs
90%	0 ± 0	44.19 ± 4.77
80%	2.13 ± 2.37	53.33 ± 5.98
70%	6.98 ± 5.18542	56.73 ± 7.31
60%	15.56 ± 6.12	59.55 ± 7.44
50%	21.98 ± 5.04	62.63 ± 7.34
40%	35.22 ± 6.15	66.67 ± 6.34
30%	47.73 ± 5.03	68.97 ± 6.04
20%	55.44 ± 5.56	69.99 ± 6.011
10%	65.93 ± 4.44	71.95 ± 5.61

relatively low. In the weighted webs (Fig. 2d), relative ascendency decreased throughout the time series with lowest values in the late 1990s. In the early 2000s, relative ascendency in the weighted webs first increased but then declined slightly from around 2005 until the end of the time series. The time series trajectories of relative ascendency and connectance in both types of webs are close to inverted (Fig. 2a versus c, b versus d) and relating the two shows a strong negative correlation (Supporting information, Table 2).

Robustness in unweighted and unweighted food webs

To understand how unweighted and weighted metrics of network complexity, such as connectance and relative ascendency are related to food web robustness, we triggered secondary extinctions in unweighted and weighted food webs with and without extinction thresholds. Here we mainly focus on the results from deletions from the highest to lowest node degree and node sum of link weights. Detailed results of other deletion sequences (lowest to highest and randomized) are primarily presented in the Supporting information but used in the discussion. Our results show that unweighted food webs are more robust to node deletions compared to weighted food webs, but only when targeting nodes with high degree or highest through-flow first (Fig. 3a–b). When targeting the lowest to highest degree or sum of links weights, weighted food webs are more robust (Supporting information). This is also the case for random deletions sequence, but to a lesser extent (Supporting information).

Extinction thresholds and food web robustness

Generally, extinction thresholds decrease food web robustness (R50) (Fig. 3a–b, Supporting information), except for the low-to-high deletion sequences in the weighted webs regardless thresholds (Supporting information). In unweighted food webs, the decrease in robustness is gradual with decreasing thresholds – smaller and smaller losses of incoming energy are able to trigger an extinction – regardless of the deletion sequence (Fig. 3a, Supporting information). In the weighted food webs, there was a substantial drop in robustness from the no threshold scenario to the highest, 90%, threshold (Fig. 3b). Note that a 90% threshold means that 90% of the incoming energy needs to be lost before an extinction is triggered. Similar to the unweighted webs, robustness continued to decrease steadily in the weighted food webs with decreasing thresholds for extinction (Fig. 3b). When using the low-to-high deletion sequence, the weighted webs' robustness remained high for all thresholds (Supporting information). For the random deletion sequence in the unweighted webs, the drop in robustness with decreasing thresholds was gradual (Supporting information). The decrease in robustness using random deletions was also gradual for the weighted webs, however, the median robustness remained higher (≥ 0.2) compared to the unweighted networks (Supporting information).

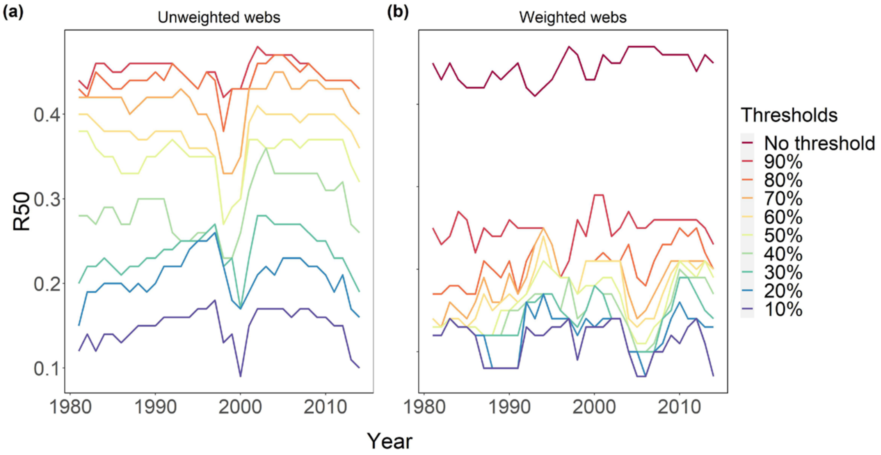

Figure 3. Median robustness (R50) over time in the (a) unweighted and (b) weighted food webs for different thresholds (line colors). Lines represent the median R50 values of the 1000 food webs per year. The extinctions were triggered in the order from highest to lowest species degree (i.e. its number of interactions) in the unweighted webs, and highest to lowest sum of link weights for the weighted webs. The no threshold-scenario represent the scenario where all food sources needs to be lost before a species goes extinct. The thresholds represent scenarios where species go extinct when they lose a certain percentage of incoming energy. For example, 90% threshold means that a 90% loss of incoming energy leads to secondary extinction(s) for species.

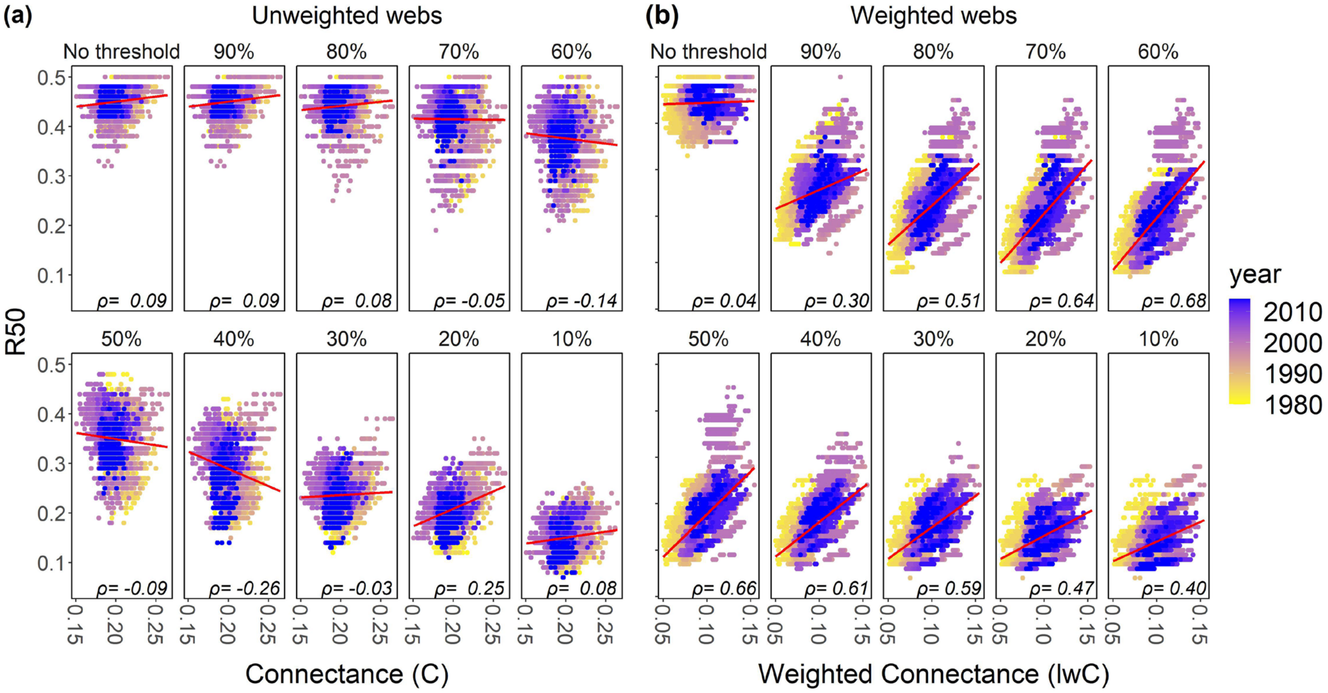

Figure 4. (a) Connectance and (b) weighted connectance plotted against R50 for the unweighted and weighted webs (34 000) at different thresholds. The points are the connectance and R50 values and the red line is the linear correlation between connectance and R50 at the different thresholds. ρ is the Spearman rank-order correlation coefficient for each scenario. The coloring gradient of the points correspond to the years (1981–2014) in the food web time series.

Relationship between food web metrics and robustness

There was little to no positive correlation between unweighted connectance (*C*) and robustness in the unweighted version of the Gulf of Riga food web for the high-to-low deletion sequence (Fig. 4a) and no discernible overall trend among the thresholds. In the case of the weighted food webs, there was a positive correlation between weighted connectance (lwC) and robustness (R50) for all thresholds, especially for the 80–30% threshold scenarios for the high-to-low deletion sequence (Fig. 4b). Interestingly, inclusion of thresholds are needed for this positive relationship to materialise, since there was no relationship between weighted connectance and robustness for the links or no links scenario (Fig. 4b). There was no strong temporal trend with regards to the correlation between weighted connectance and robustness. When the low-to-high deletion sequence was used, there was no clear pattern in correlation between unweighted connectance (*C*) and robustness in the unweighted webs (Supporting information). In the case of weighted connectance, there was little to no correlation regardless of the thresholds (Supporting information). Finally, when examining the random deletion sequence we found limited correlation, regardless of which connectance measure and thresholds used (Supporting information).

There was a negative correlation between relative ascendency (A/C) and robustness (R50) for both the weighted and unweighted food webs and for all thresholds with the high-to-low deletion sequence (Fig. 5a–b), except for the links or no links scenario in the weighted webs, which showed close to no correlation (Fig. 5b). Yet, the correlation between relative ascendency (A/C) and robustness (R50) was stronger in the weighted webs. Furthermore, there was no clear temporal trend between relative ascendency (A/C) and robustness (R50) in the unweighted food webs (Fig. 5a). The clearest temporal signal emerged between robustness (R50) and relative ascendency (A/C) in the weighted food webs (Fig. 5b), where the 1980s food webs had a relatively higher relative ascendancy and lower robustness, whereas the 2000–2010s had higher robustness and lower relative ascendency (Fig. 5b). Again, we found no or limited correlation between robustness and relative ascendency (A/C) when using the low-to-high as well as the random deletion sequence with no clear overall trend for the thresholds (Supporting information).

Discussion

How networks respond to node loss is a central question in network science, including ecology, since node failure can compromise the integrity of a network and negatively impact system functioning (Bellingeri and Cassi 2018). Here, we show that food web responses to node losses in a marine ecosystem depend on network type (unweighted/weighted), extinction thresholds, and deletion sequence. We show that

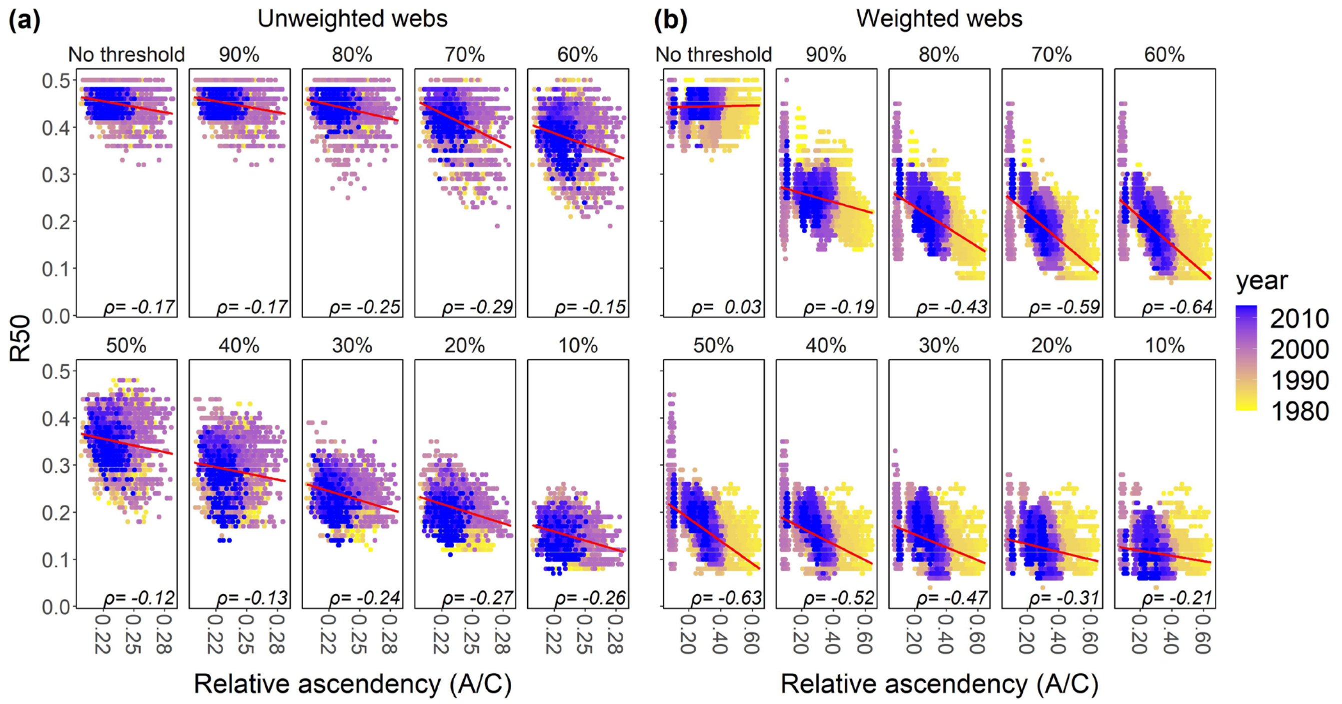

Figure 5. Relative ascendency plotted against R50 for the a) unweighted and b) weighted webs (34 000). The points are the relative ascendency and R50 values and the red line shows the linear correlation between relative ascendency and R50 at the different thresholds. ρ is the Spearman rank-order correlation coefficient for each scenario. The coloring gradient of the points correspond to the years (1981–2014) in the food web time series.

weighted food webs are less robust to node deletions compared to unweighted webs, when targeting nodes with high degree or highest through-flow first. Interestingly, when using the lowest-to-highest deletion sequences, weighted food webs are more robust than unweighted webs across extinction thresholds, which implies that flux-weighted food webs are vulnerable to losing species with high energy in-flow and out-flow, and robust to losing species which contribute little to the main energy pathways in the food web. Depending on the deletion sequence, the results also suggest that food web robustness is either over- or under-estimated in extinction simulations using binary food webs, which assume that all interactions are equally important for system functioning. Our results based on weighted webs show that when node interaction weights are taken into account, robustness either decreases or increases, depending on whether the species going extinct is important for maintaining the energy flow in the food web.

Differences in robustness in weighted and unweighted food webs

When comparing how robustness differs between weighted and unweighted food webs, we first see that there is no remarkable disparity between network types in the no-threshold scenario (Fig. 3a–b, Supporting information). This is likely because in this scenario, losing links becomes relatively unimportant as any remaining links simply act as insurance for energy provision. We are essentially simulating extinctions in a purely topological network in both cases. Since no thresholds are set, it means that link weights do not come into play, and that any link, no matter how strong or weak, is enough to sustain species persistence in the web. The small differences in robustness (R50) fluctuations over time (Fig. 3a–b) are probably due to differences in the order of nodes in the deletion sequences, since we in target nodes based on their degree (e.g. highest to lowest) in the unweighted webs and the sum of link weights in the weighted webs. From a classical topological perspective, it would therefore seem that the Gulf of Riga system is fairly robust, since no matter what deletion sequence is used, R50 remains close to max (Fig. 3a–b, Supporting information).

It is only with the inclusion of thresholds that greater differences in robustness emerge, depending on network type (Fig. 3a–b). The difference in the magnitude of robustness change between weighted and unweighted food webs can be explained by the differences in link weight distribution. It is well known that the degree distribution, or how skewed the links are towards a few nodes, can impact the robustness of food webs to species loss in unweighted webs (Estrada 2007). It is therefore reasonable to assume that the skewness of energy flow also is important, especially in weighted webs, which has indeed been shown in several studies (Neutel et al. 2002). For example, previous findings by Bellingeri et al. (2019) show that link weight heterogeneity reduces robustness in real world networks. Our results show that weighted food web structure reduces robustness when targeting nodes with high degree or high sum of link weights.

In our case, we see an increased risk of secondary extinctions when introducing energy thresholds in both weighted and unweighted webs. In the weighted webs, this is further enhanced by the skewness in consumer inflows. This again demonstrates the risk of over-estimating the robustness of a system when only looking at the topology and ignoring energy fluxes, how they are distributed, and how this translates into vulnerability to species loss. This disparity is due to the fact that in the unweighted webs, energy flow is uniformly distributed among the links, and contributes equally to the consumers' needs. When flows of links are allowed to vary in the weighted webs in combination with energy thresholds, the amount of links that remain after a node is removed may not be sufficient to guarantee species persistence in the food web. It is, however, worth noting that while Bellingeri et al. (2019) used real-world weighted networks, they did not include any thresholds in their analysis and did not use R50 as a measure of robustness. However, a commonality among our studies is that link weight heterogeneity seems to be closely tied to how food webs respond to species loss. In our case, this relationship only becomes truly clear when including extinction thresholds.

Influence of extinction thresholds on food web robustness

The idea that a species only goes extinct when it loses all its incoming energy is probably the best case scenario and does likely not always apply in nature. For this reason, species response to loss of energy intake is fundamental for understanding food web vulnerability (Thierry et al. 2011, Bellingeri and Bodini 2013). Early work on extinction simulations also faced criticism for their lack of realism and the assumption that a species only suffers an extinction (primary or secondary) once it loses all its resources (Thierry et al. 2011), when a species could be pushed to functional extinction in a food web before total energy intake is lost (Bodini et al. 2009).

A more realistic assumption would be that a species goes extinct when it loses a certain percentage of its energy intake at a given threshold. As we expected, this is indeed reflected in our results. The inclusion of thresholds lead to consistent decrease in robustness. This decline in robustness essentially means that introducing even a minor increase in species susceptibility to resource loss leads to a large increase in secondary extinctions compared to the no-threshold scenario. This result agrees with previous findings by Thierry et al. (2011), who used model food webs to show that secondary extinctions increase with the level of energy intake necessary for a species survival.

Thierry et al. (2011) also used food web rewiring (allowing species to switch to new prey upon loss of resources), and concluded that this mechanism has a stabilising effect on robustness. Yet, rewiring was less effective when thresholds became more severe (Thierry et al 2011). In our study, we did not consider rewiring. If included, this could potentially have impacted our results by increasing robustness of the food webs. For example, in our weighted webs we found a large decrease in robustness in the 10% threshold scenario. If we had included rewiring, this decrease could have been significantly less prominent since prey switching likely decreases secondary extinctions at lower thresholds (Thierry et al. 2011). At some point, rewiring stops being able to compensate for the severity of the energy thresholds, but without simulating this, it is hard to say at which point this would happen in our food webs.

Our results are more comparable to the findings by Bellingeri and Bodini (2013). Using empirical food webs, for which links were quantified as energy flows, they also concluded that secondary extinctions increase with the inclusion of thresholds. Similar to our finding for the weighted webs (Fig. 3b), Bellingeri and Bodini (2013) observed an abrupt decrease in robustness in ecological webs when moving from no threshold to including a threshold, and they hypothesized that this pattern is general for food webs when crucial nodes for energy transfer are targeted. Our results support this hypothesis, as targeting nodes with a high sum of link weights in the weighted webs leads to greater decreases in robustness.

It is worth highlighting that the species removal sequences in both Bellingeri and Bodini (2013) and Thierry et al. (2011) were different from ours. Thierry et al. (2011) removed nodes at random, and Bellingeri and Bodini (2013) removed nodes by highest to lowest node degree and highest to lowest out-degree. What deletion sequence is used plays an important role in our results, noticeably decreasing or increasing robustness depending on which one is used. We see this most clearly in our results for the weighted webs. For the high-to-low sequence, we get an abrupt decrease in robustness. This makes sense since we are targeting the nodes with the highest flow first, thus also removing the links that carry the most energy resulting in more secondary extinctions by more quickly bringing species below the energy threshold needed for survival. Especially species that are sustained by a few strong links and several weaker ones, are vulnerable to the loss of their stronger links since they make up most of their energy intake. When thresholds are included, the loss of major links therefore more easily triggers extinction cascades, regardless of the threshold level.

Skewness in link weights would also explain our results showing that when targeting the lowest to highest sum of link weights, and to a lesser extent with random deletions, weighted food webs are indeed more robust (Supporting information). In that case, robustness remains high since we are essentially targeting the least important food items from an energy flux perspective that only make up a minority of the energy intake while preserving all the major food items until last, ensuring that species keep above the energy threshold require for survival.

In the case of the random removal sequence, it essentially comes down to whether the species randomly going extinct is important for maintaining the energy flow in the food web. If the node is important, then the web destabilizes more, if not, the damage is minimal. This is more noticeable in the weighted webs due to the disparity in link weights, unlike in the unweighted webs where the link weights are all the same. This results in the weighted webs being more robust than the unweighted ones for random removal sequence of species, since food webs tend to skew towards many nodes with weak links and a few with strong (McCann et al. 1998, Emmerson and Yearsley 2004). This results in nodes with low throughflow (weak links) being more often targeted at random during random deletion sequences, increasing robustness.

How the different deletion sequences affect our webs fits well with previous observations that networks are more sensitive to targeted attacks, such as the selective removal of highly connected nodes (Dunne et al. 2002, Bellingeri and Bodini 2013), and that random removals cause less damage (Bellengeri and Bodini 2013). Despite methodological differences, our results are comparable to Thierry et al. (2011) and Bellingeri and Bodini (2013), and therefore we may assume that the pattern of extinction thresholds decreasing robustness is fairly consistent in food webs. This suggest that using weighted webs in conjunction with thresholds could be more appropriate when trying to ascertain how different food webs would react to species removal.

Relationship between food web metrics and robustness

Corroborating previous results (Bellingeri and Bodini 2013, Canning and Death 2018), we find no clear relationship between unweighted connectance and robustness (Fig. 4a) even across thresholds. Interestingly this differs from early findings by Dunne et al. (2002, 2004), who showed that food webs display increasing robustness to loss of highly connected species with increasing connectance. Our results suggest that connectance is not a reliable metric for predicting food web robustness. This is likely because unweighted connectance does not consider the relative distribution of links but only the proportion of realised interactions. Therefore, two networks with the same level of connectance can represent very different link distributions and network topologies. As discussed in Canning and Death (2018), Dunne et al. (2002) likely found a higher robustness in more connected unweighted webs because of a relatively uniform degree distribution in the investigated food webs.

In contrast to unweighted connectance, there is consistent negative correlation between relative ascendency and robustness across all thresholds in the unweighted web (Fig. 5a), though the correlation is low. Robustness generally decreased with increasing relative ascendency (Fig. 5a). Unlike unweighted connectance, relative ascendency accounts for the link distribution and connectivity of the network. Hence, relative ascendency may be better predictor of food web robustness in unweighted web, consistent with conclusions by Canning and Death (2018).

Robustness was best predicted by connectance and relative ascendency in the weighted webs compared to their unweighted counterparts, but only in conjunction with thresholds (Fig. 4a–b, 5a–b). The ability of connectance and relative ascendency to better reflect food web robustness in the weighted webs can be explained by the distribution of link weights. When the distribution is skewed towards a few strong links, the system is more constrained, making it more brittle and inflexible to cope with disturbances (Holling 1985), although this type of food web may be efficient in moving energy through a few strong pathways from the bottom to the top. The idea that the amount of ‘choice’ for the energy flow plays a part in how systems react to disturbances was already proposed in the 1950s by Odum (1954). We see evidence for this in our results. For example, in the 1980s, the weighted webs were less robust, with both relative ascendency being low and weighted connectance being high, indicating a few dominant flows (Fig. 5b). The most robust webs are found around the 2000s (Fig. 5b), which is when both relative ascendency and weighted connectance indicate more evenly distributed flow regimes (Fig. 2b, d). When energy flows are more evenly distributed, there is more ‘choice’, or more equal parallel paths for the energy to flow, making the webs more robust, and as the links are more even, there is less of a chance of losing any one link of sufficient magnitude to fall under the energy threshold triggering extinctions.

Although relative ascendency and weighted connectance both capture the skewness (or evenness) of energy flow in the network, relative ascendency more clearly reveals a temporal signal in the weighted food web time series with regard to robustness (Fig. 5b). This may be due to differences in what aspects of the network these metrics capture. Weighted connectance emphasizes the role of species (Bersier et al. 2002); its total incoming and outgoing energy, whereas relative ascendency emphasizes the role of links and their skewness (Ulanowicz 1986). Ecologically, weighted connectance may fail to capture subtle changes in the strength of link fluxes if these are too small to significantly alter the total in- and outgoing energy. However, such changes may be captured by relative ascendency, because it quantifies the energy pathways and their constraints at the network level. Relative ascendency may, thus, be better at picking up ecological signals related to changes in energy flow regimes in food webs, as reflected in the strong temporal signal in robustness (Fig. 5b).

The noticeable temporal signal in robustness as predicted by relative ascendency (Fig. 5b) reflects documented ecological changes in the Gulf of Riga. At the end of the 1980s, the gulf underwent a major multi-trophic reorganisation in species community structure and trait composition (Casini et al. 2012, Pecuchet et al. 2020) related to decreases in salinity and increases in temperature (Pecuchet et al. 2020). In a food web study using the same time series as in the present study, Kortsch et al. (2021) associated the shift in network properties (weighted and unweighted) and functions during the late 1980s to the early 1990s with a transition period from high benthic and detritivorous flows to high phyto-and zooplanktivorous flows. In the 1980s the food webs were dominated by species with strong flows (especially benthic and detritivorous) compared to the 1990s and 2000s, when flows were distributed more evenly across the trophic groups within the food web. Here, we see that relative ascendency in the weighted webs reflect these changes, relative ascendency in the weighted webs is highest in the early 1980s and lowest in the later years (Fig. 2d). The skewed link weight distribution in the 1980s coincides with the lowest robustness in our webs (Fig. 5b). In the 1990s, the link weights became more evenly distributed, corresponding to low relative ascendency at the time (Fig. 2d), again reflected in the robustness of the webs, with the 1990s having some of the most robust food webs (Fig. 5b). Thus our simulations show that food webs dominated by few strong pathways may make the network more susceptible to disturbances (Fig. 5b).

Caveats and future directions

In our modeling framework, we made some simplifying assumptions, which may be addressed in future extensions of the current model. First, we assume that species are equally affected by loss of energy intake, which likely is not the case in nature. This assumption could be addressed by introducing variability in species responses to reductions of energy intake through in silico simulations or by empirically testing species-specific responses to prey loss in controlled feeding experiments. Second, we assume that link weights stay constant in our webs throughout the deletion process. This caveat could be overcome by recalculating energy fluxes after each node deletion (Zhang et al. unpubl.), mimicking shifts in feeding preferences upon prey loss. Third, we do not allow for predators switching to new prey items that were not previously consumed and documented in our predefined metaweb forming the basis for our temporal food web topologies. Fourth, our food web is spatially isolated to the Gulf of Riga, and therefore does not consider any potential rescue effects through meta-population dispersal from neighboring Baltic Sea food web areas (Brown and Kodric-Brown 1977, Van De Leemput et al. 2024). Spatial coupling of food webs likely increases the robustness of local food webs (Rollin et al. 2024), as populations of species going locally extinct may persist through immigration of individuals from neighbouring food webs. Such rescue effects could be analysed with existing spatially-explicit, dynamic food web models, such as Ecopath with Ecosim or Atlantis (Pauly 2000, Audzijonyte et al. 2019). Lastly, it remains uncertain how general our findings are across ecosystems (i.e. marine, freshwater, terrestrial), as consistent differences in the trophic structures of aquatic and terrestrial food webs have been documented (Shurin et al. 2006). To address this, future extensions of this study should include cross-ecosystem comparisons to test the broader applicability of our results.

Conclusions

Our secondary extinction simulations in both unweighted and weighted food webs show that ignoring energy flux variability and extinction thresholds can lead to biased conclusions about food web functioning and robustness. We find that connectance, a common measure of complexity in unweighted food webs, is an unreliable predictor of robustness. Therefore, we recommend moving away from this metric in favor of information-theory-based indicators, particularly relative ascendency. This metric effectively captures subtle changes in link distributions and network skewness, which are crucial for understanding ecosystem functioning and stability.

Acknowledgements – We would like to thank everyone who contributed to the development and construction of the Gulf of Riga food webs, especially the Latvian Institute of Aquatic Ecology, Institute of Food Safety, Animal Health and Environment BIOR.
Funding – PS and RPD were funded by GES4SEAS (HORIZON-CL6-2021-BIODIV-01-04, grant agreement no. 101059877). RPD was also funded by a research grant from the Research Council of Finland (grant no. 349616) SK acknowledges the support from the Walter and Andrée de Nottbeck Foundation and the Centre for Coastal Ecosystem and Climate Change Research (www.coastclim.org), and the Research Council of Finland for the Academy research fellowship (grant no. 361049). MCN was funded by MARBEFES (MARine Biodiversity and Ecosystem Functioning leading to Ecosystem Services) through the European Union under the Horizon Europe Program (HORIZON-CL6-2021-BIODIV-01; grant agreement no. 101060937), and through Research Council of Finland University Profiling funding InterEarth (grant no. 353218) . LZ acknowledges the financial support by the State Key Laboratory of Lake Science and Environment (2022SKL009), the Natural Science Foundation of Jiangsu Province (BK20231328).

Author contributions

Patrik P. G. Ståhl: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Riikka Puntila-Dodd**: Conceptualization (equal); Formal analysis (supporting); Methodology (supporting); Supervision (equal); Writing – original draft (supporting). **Lai Zhang**: Formal analysis (supporting). **Marie C. Nordström**: Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Susanne Kortsch**: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Software (supporting); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data and scripts are available from GitHub (https://github.com/skortsch/GoR-Food-Web-Robustness) and the Zenodo Repository: https://doi.org/10.5281/zenodo.14505584 (Ståhl et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Allesina, S., Bodini, A. and Bondavalli, C. 2006. Secondary extinctions in ecological networks: bottlenecks unveiled. – Ecol. Modell. 194: 150–161.

Antunes, A. C., Berti, E., Brose, U., Hirt, M. R., Karger, D. N., O'Connor, L. M., Pollock, L. J., Thuiller, W. and Gauzens, B. 2024. Linking biodiversity, ecosystem function, and Nature's contributions to people: a macroecological energy flux perspective. – Trends Ecol. Evol. 39: 427–434.

Audzijonyte, A., Pethybridge, H., Porobic, J., Gorton, R., Kaplan, I. and Fulton, E. A. 2019. Atlantis: a spatially explicit end-to-end marine ecosystem model with dynamically integrated physics, ecology and socio-economic modules. – Methods Ecol. Evol. 10: 1814–1819.

Avila-Thieme, M. I., Kusch, E., Corcoran, D., Castillo, S. P., Valdovinos, F. S., Navarrete, S. A. and Marquet, P. A. 2023. NetworkExtinction: an R package to simulate extinction propagation and rewiring potential in ecological networks. – Methods Ecol. Evol. 14: 1952–1966.

Banašek-Richter, C., Bersier, L.-F., Cattin, M.-F., Baltensperger, R., Gabriel, J.-P., Merz, Y., Ulanowicz, R. E., Tavares, A. F., Williams, D. D., Ruiter, P. C., Winemiller, K. O. and Naisbit, R. E. 2009. Complexity in quantitative food webs. – Ecology 90: 1470–1477.

Barnes, A. D., Jochum, M., Lefcheck, J. S., Eisenhauer, N., Scherber, C., O'Connor, M. I., De Ruiter, P. and Brose, U. 2018. Energy flux: the link between multitrophic biodiversity and ecosystem functioning. – Trends Ecol. Evol. 33: 186–197.

Barrat, A., Barthélemy, M., Pastor-Satorras, R. and Vespignani, A. 2004. The architecture of complex weighted networks. – Proc. Natl Acad. Sci. USA 101: 3747–3752.

Bellingeri, M. and Bodini, A. 2013. Threshold extinction in food webs. – Theor. Ecol. 6: 143–152.

Bellingeri, M. and Cassi, D. 2018. Robustness of weighted networks. – Phys. A 489: 47–55.

Bellingeri, M., Bevacqua, D., Scotognella, F. and Cassi, D. 2019. The heterogeneity in link weights may decrease the robustness of real-world complex weighted networks. – Sci. Rep. 9: 10692.

Bersier, L.-F., Banašek-Richter, C. and Cattin, M.-F. 2002. Quantitative descriptors of food-web matrices. – Ecology 83: 2394–2407.

Bodini, A., Bellingeri, M., Allesina, S. and Bondavalli, C. 2009. Using food web dominator trees to catch secondary extinctions in action. – Philos. Trans. R. Soc. B 364: 1725–1731.

Brown, J. H. and Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. – Ecology 58: 445–449.

Canning, A. D. and Death, R. G. 2018. Relative ascendency predicts food web robustness. – Ecol. Res. 33: 873–878.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S. and Naeem, S. 2012. Biodiversity loss and its impact on humanity. – Nature 486: 59–67.

Cardinale, B. J., Srivastava, D. S., Duffy, J. E., Wright, J. P., Downing, A. L., Sankaran, M. and Jouseau, C. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. – Nature 443: 989–992.

Casini, M., Blenckner, T., Möllmann, C., Gårdmark, A., Lindegren, M., Llope, M., Kornilovs, G., Plikshs, M. and Stenseth, N. C. 2012. Predator transitory spillover induces trophic cascades in ecological sinks. – Proc. Natl Acad. Sci. USA 109: 8185–8189.

Conley, D. J. et al. 2009. Hypoxia-related processes in the Baltic Sea. – Environ. Sci. Technol. 43: 3412–3420.

Curtsdotter, A., Binzer, A., Brose, U., De Castro, F., Ebenman, B., Eklöf, A., Riede, J. O., Thierry, A. and Rall, B. C. 2011. Robustness to secondary extinctions: comparing trait-based sequential deletions in static and dynamic food webs. – Basic Appl. Ecol. 12: 571–580.

Dunne, J. A., Williams, R. J. and Martinez, N. D. 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. – Ecol. Lett. 5: 558–567.

Dunne, J., Williams, R. and Martinez, N. 2004. Network structure and robustness of marine food webs. – Mar. Ecol. Prog. Ser. 273: 291–302.

Ebenman, B., Law, R. and Borrvall, C. 2004. Community viability analysis: the response of ecological communities to species loss. – Ecology 85: 2591–2600.

Emmerson, M. and Yearsley, J. M. 2004. Weak interactions, omnivory and emergent food-web properties. – Proc. R. Soc. B 271: 397–405.

Estrada, E. 2007. Food webs robustness to biodiversity loss: the roles of connectance, expansibility and degree distribution. – J. Theor. Biol. 244: 296–307.

Gauzens, B., Barnes, A., Giling, D. P., Hines, J., Jochum, M., Lefcheck, J. S., Rosenbaum, B., Wang, S. and Brose, U. 2019. fluxweb: an R package to easily estimate energy fluxes in food webs. – Methods Ecol. Evol. 10: 270–279.

Gilbert, A. J. 2009. Connectance indicates the robustness of food webs when subjected to species loss. – Ecol. Indic. 9: 72–80.

HELCOM 2023. State of the Baltic Sea 2023 – third HELCOM holistic assessment 2016–2021. – Baltic Sea Environ. Proc. 194, pp. 6.

Holling, C. 1985. Resilience of ecosystems: local surprise and global change. – Cambridge Univ. Press, pp. 228–269.

Jonsson, T., Berg, S., Pimenov, A., Palmer, C. and Emmerson, M. 2015. The reliability of R50 as a measure of vulnerability of food webs to sequential species deletions. – Oikos 124: 446–457.

Jurgensone, I., Carstensen, J., Ikauniece, A. and Kalveka, B. 2011. Long-term changes and controlling factors of phytoplankton community in the Gulf of Riga (Baltic Sea). – Estuaries Coasts 34: 1205–1219.

Kones, J. K., Soetaert, K., Van Oevelen, D. and Owino, J. O. 2009. Are network indices robust indicators of food web functioning? A Monte Carlo approach. – Ecol. Modell. 220: 370–382.

Kortsch, S., Frelat, R., Pecuchet, L., Olivier, P., Putnis, I., Bonsdorff, E., Ojaveer, H., Jurgensone, I., Strāķe, S., Rubene, G., Krūze, E. and Nordström, M. C. 2021. Disentangling temporal food web dynamics facilitates understanding of ecosystem functioning. – J. Anim. Ecol. 90: 1205–1216.

Kotta, J., Lauringson, V., Martin, G., Simm, M., Kotta, I., Herkül, K. and Ojaveer, H. 2008. Gulf of Riga and Pärnu Bay. – In: Caldwell, M. M., Heldmaier, G., Jackson, R. B., Lange, O. L., Mooney, H. A., Schulze, E. D., Sommer, U. and Schiewer, U. (eds), Ecology of Baltic coastal waters, vol. 197. Springer, pp. 217–243.

Landi, P., Minoarivelo, H. O., Brännström, Å., Hui, C. and Dieckmann, U. 2018. Complexity and stability of ecological networks: a review of the theory. – Popul. Ecol. 60: 319–345.

Loxdale, H. D. and Harvey, J. A. 2016. The 'generalism' debate: misinterpreting the term in the empirical literature focusing on dietary breadth in insects. – Biol. J. Linn. Soc. 119: 265–282.

MacArthur, R. 1955. Fluctuations of animal populations and a measure of community stability. – Ecology 36: 533–536.

May, R. M. 1972. Will a large complex system be stable? – Nature 238: 413–414.

McCann, K., Hastings, A. and Huxel, G. R. 1998. Weak trophic interactions and the balance of nature. – Nature 395: 794–798.

Möllmann, C., Müller-Karulis, B., Diekmann, R., Flinkman, J., Kornilovs, G., Pastuszak, E. L., Modin, J., Plikshs, M., Walther, Y. and Wasmund, N. 2006. An integrated ecosystem assessment of the central Baltic Sea and the Gulf of Riga. – International Council for the Exploration of the Sea (ICES) archives. A workshop report from a conference (2006 Annual Science Conference, Maastricht, Netherlands). https://doi.org/10.17895/ices.pub.25259194.

Neutel, A.-M., Heesterbeek, J. A. P. and De Ruiter, P. C. 2002. Stability in real food webs: weak links in long loops. – Science 296: 1120–1123.

Newman, M. E. J. 2001. Scientific collaboration networks. II. Shortest paths, weighted networks, and centrality. – Phys. Rev. E 64: 016132.

Odum, E. 1954. Fundamentals of ecology. Philadelphia: W. B. Saunders Company, 1953 P. – Sci. Educ. 38: 314–314.

Olivier, P., Frelat, R., Bonsdorff, E., Kortsch, S., Kröncke, I., Möllmann, C., Neumann, H., Sell, A. F. and Nordström, M. C. 2019. Exploring the temporal variability of a food web using long-term biomonitoring data. – Ecography 42: 2107–2121.

Opsahl, T., Agneessens, F. and Skvoretz, J. 2010. Node centrality in weighted networks: generalizing degree and shortest paths. – Soc. Netw. 32: 245–251.

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. – J. Anim. Ecol. 49: 666.

Pauly, D. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. – ICES J. Mar. Sci. 57: 697–706.

Pecuchet, L., Lindegren, M., Kortsch, S., Całkiewicz, J., Jurgensone, I., Margonski, P., Otto, S. A., Putnis, I., Strāķe, S. and Nordström, M. C. 2020. Spatio-temporal dynamics of multitrophic communities reveal ecosystem-wide functional reorganization. – Ecography 43: 197–208.

Pimm, S. L. 1980. Properties of food webs. – Ecology 61: 219–225.

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M. and Sexton, J. O. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. – Science 344: 1246752.

Rollin, G., Kortsch, S., Lages, J. and Gauzens, B. 2024. Identifying important species in meta-communities. – Methods Ecol. Evol. 15: 1691–1703.

Rutledge, R. W., Basore, B. L. and Mulholland, R. J. 1976. Ecological stability: an information theory viewpoint. – J. Theor. Biol. 57: 355–371.

Shurin, J. B., Gruner, D. S. and Hillebrand, H. 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. – Proc. R. Soc. B 273: 20053377.

Skudra, M. and Lips, U. 2017. Characteristics and inter-annual changes in temperature, salinity and density distribution in the Gulf of Riga. – Oceanologia 59: 37–48.

Ståhl, P. P. G., Puntila-Dodd, R., Zhang, L., Nordström, M. C. and Kortsch, S. 2024. Data from: Food web robustness depends on the network type and threshold for extinction. – Zenodo Repository, https://doi.org/10.5281/zenodo.14505584.

Tejedor, A., Longjas, A., Zaliapin, I., Ambroj, S. and Foufoula-Georgiou, E. 2017. Network robustness assessed within a dual connectivity framework: joint dynamics of the active and idle networks. – Sci. Rep. 7: 8567.

The Bacc Ii Author Team (ed.). 2015. Second assessment of climate change for the Baltic Sea basin. Regional climate studies. – Springer Int. Publ.

Thierry, A., Beckerman, A. P., Warren, P. H., Williams, R. J., Cole, A. J. and Petchey, O. L. 2011. Adaptive foraging and the rewiring of size-structured food webs following extinctions. – Basic Appl. Ecol. 12: 562–570.

Thompson, R. M., Brose, U., Dunne, J. A., Hall, R. O., Hladyz, S., Kitching, R. L., Martinez, N. D., Rantala, H., Romanuk, T. N., Stouffer, D. B. and Tylianakis, J. M. 2012. Food webs: reconciling the structure and function of biodiversity. – Trends Ecol. Evol. 27: 689–697.

Ulanowicz, R. E. 1986. Growth and development. – Springer.

Ulanowicz, R. E. 2004. Quantitative methods for ecological network analysis. – Comp. Biol. Chem. 28: 321–339.

Van Altena, C., Hemerik, L. and De Ruiter, P. C. 2016. Food web stability and weighted connectance: the complexity–stability debate revisited. – Theor. Ecol. 9: 49–58.

Van De Leemput, I. A., Bascompte, J., Buddendorf, W. B., Dakos, V., Lever, J. J., Scheffer, M. and Van Nes, E. H. 2024. Transformation starts at the periphery of networks where pushback is less. – Sci. Rep. 14: 11344.

White, J. W., Rassweiler, A., Samhouri, J. F., Stier, A. C. and White, C. 2014. Ecologists should not use statistical significance tests to interpret simulation model results. – Oikos 123: 385-388. https://doi.org/10.1111/j.1600-0706.2013.01073.x

Yletyinen, J., Bodin, O., Weigel, B., Nordström, M. C., Bonsdorff, E. and Blenckner, T. 2016. Regime shifts in marine communities: a complex systems perspective on food web dynamics. – Proc. R. Soc. B 283: 20152569.

Young, H. S., McCauley, D. J., Galetti, M. and Dirzo, R. 2016. Patterns, causes and consequences of Anthropocene defaunation. – Annu. Rev. Ecol. Evol. Syst. 47: 333–358.