



Topology of additive pairwise effects in food webs

Ágnes Mór  h^a, Anett Endr  di^a, S  ndor Imre Piross^b, Ferenc Jord  n^{a,b,c,*}

^a Evolutionary Systems Research Group, Centre for Ecological Research, Budapest, Hungary

^b Balaton Limnological Institute, Centre for Ecological Research, Tihany, Hungary

^c Stazione Zoologica, Napoli, Italy

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ABSTRACT

Contrasting reductionistic versus holistic views, it is a general question whether adding the parts equals the sum. In the time of multiple drivers of anthropogenic change, it is a crucial issue, and better understanding additivity is critical for strategy and management. More particular research questions ask what are the community effects of the extinction of a single species and whether multiple local effects on different species will generate additive community responses. Here we perform food web simulations and study the community response to perturbing each species, one by one, and perturbing each possible pairwise combination of species. By comparing the two, we quantify additivity and analyze how does it depend on the topological positions of perturbed species pairs. Results increase the predictability of food web research, supporting systems-based conservation management and, possibly, multi-species maximum sustainable yield assessment in fisheries.

1. Introduction

In natural ecosystems, various species are interconnected by a multiplicity of inter-specific interactions. In multi-species ecological communities, the perturbation of any species has direct and indirect effects on all of the others. Some species are better connected and indirect chain effects can spread in more directions, while others are peripheric: their perturbations cascade less easily across the food web. It is an old question how to better understand dynamical effects based on simple topological information, i.e. how to link structure to dynamics (see Pimm, 1980; Jord  n et al., 2002, 2008; Endr  di et al., 2018; Hansen et al., 2019). To establish this link is not straightforward, yet, perturbing a single species is a major simplification. During either climate change or fisheries, several species are perturbed and a new question emerges: are these effects additive? Determining the community responses of perturbing species *i* and *j* separately may not help to predict the community response of their pairwise perturbation. Beyond theoretical investigations, also experimental results suggest high selectivity of effects, the poor predictability of community response and the mutual dependence of effects on various species and interactions (Breitburg et al., 1997). Indirect effects spreading in food webs and their effects on dynamical behavior are key issues to study in a network context (Brose et al., 2005; Borrett 2013; Lau et al., 2017; Cirtwill et al., 2018).

This issue was raised in a surprisingly few papers, for several reasons.

The difference and the relationship between short-term and long-term effects is hard to understand, so community response itself is not easy to quantify and predict (Yodzis, 1988). This is true for single-species effects and even harder for multi-species scenarios (see Yodzis, 2000). As an example, for maximum sustainable yield estimations in multi-species context, the complications have been richly discussed (May et al., 1979; Legovic and Gecek, 2010; Legovic et al., 2010, 2012).

Following a simple pilot study on this issue (focusing on a single network, M  r  h et al., 2018), here we scale up that previous analysis by dramatically increasing the number of food webs and enriching the analysis. In this paper, we study a large number of model food webs: (1) we quantify the topological importance of particular species and their pairs, (2) we define community dynamics and perform food web simulations, (3) we quantify community response for single-species and pairwise perturbations, (4) we quantify the level of additivity and (5) we analyze which topological combinations of perturbed species pairs lead to additive or non-additive community responses. The main question to understand if central network position generates larger dynamical effects and if network position has an effect on the additivity of pairwise perturbations.

* Corresponding author at: Balaton Limnological Institute, Centre for Ecological Research, Klebelsberg Kuno 3, 8237, Tihany, Hungary, +36204285162.
E-mail address: jordan.ferenc@ecolres.hu (F. Jord  n).

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2. Methods

2.1. Networks, dynamical simulations and perturbations

The whole process of the preparatory work (generating proper networks), simulating their dynamics and the systematic perturbations of consumers and their pairs is summarized in Fig. 1.

2.1.1. Random networks

The investigated networks were created randomly by fixing the total number of species nodes ($S = 15$) and the number of basal species ($S_b = 3$). The links between the nodes were drawn randomly taking some restrictions into account: i) consumers can consume only from lower levels (cannibalism and loops are excluded); ii) we defined the maximum number of trophic levels ($\max_{TL} = 4$) and top predators ($\max_{top} = 3$); iii) the number of trophic links was constant ($NL = 36$, thus connectance $C = NL/S^2 = 0.16$) and iv) the graph was connected (i.e. composed of a single component). If a randomly created network did not meet these requirements, it was rejected. The suitable ones were used in dynamical simulations. These topological features are based on observations in a real food web (Lin et al., 2004; Jord  n et al., 2009) and are used in an earlier pilot study (M  r   et al., 2018) making the results comparable with those ones.

2.1.2. Dynamical simulations

The dynamical behavior of the webs followed an earlier model (M  r   et al., 2018). A system of ODEs describes the dynamics of each species in the webs as follows:

$$\frac{dB_i}{dt} = r_i B_i \left(1 - \frac{B_i}{K_i}\right) + \sum_{p \in res.} \frac{B_i B_p^h \omega_{ip}}{B_0^h + \sum \omega_{ip} B_p^h} - \sum_{c \in cons.} \frac{B_c B_i^h \omega_{ci}}{B_0^h + \sum \omega_{ci} B_i^h} - d_i B_i$$

where B_i refers to the biomass of species i . The basal ($i \leq 3$) species' increase is described by the logistic growth model, where K_i and r_i are the carrying capacity and the intrinsic growth rate, respectively. The consumption of the consumers is characterized by a Holling type-III functional response, where B_0 refers to the half-saturation density. The relative consumption rates (ω_{ip}) are set to be inversely proportional to the number of resources ($\omega_{ip} = 1/n_i$, where n refers to the number of prey species of i). The increase and decrease of the biomass of the consumer species ($i > 3$) depend only on the strength of their own and their predators' consumption ($r_i = 0$), and the external mortality rate (d_i).

Our aim was to focus on the impact of network topology on dynamics, thus, we did not model explicitly the conversion and consumption rates, but the strength of a predator-prey link (ϵ) was assumed inversely proportional to the number of its prey ($\epsilon_{ci} = \epsilon_{pi} = 1/n_i$). For the sake of the same cause, the parameters were fixed ($h = 2$; $B_0 = 0.5$; r_{basals}

$= K_{basals} = 1$; $d_{consumers} = 0.1$), only the different distributions of the links between the nodes determine the topology as well as the system's dynamics.

In the course of network-composition not only the structural features mentioned above, but also the dynamical stability was an important criterion. It is meant by the coexistence of all the 15 species on the one hand, but, on the other hand we had required the network's robustness against perturbations affecting single species or their pairs (see below). Thus, we integrated the system (Hindmarsh et al., 2005) until it settled to a fixed point; if any of the species were extinct, the integration was terminated and the network (adjacency-matrix) was neglected. All initial biomass-values were set to 1 and the system was integrated over $T = 20,000$ time steps. If the abundance of any species decreased below the threshold of 10^{-6} , we considered it to be extinct and the integration was terminated. If all species reached a fixed point and coexisted, we made a preliminary stability analysis by arbitrary changing the biomass-values of all species (pulse perturbation).

2.1.3. Perturbation

After the system returned to the original equilibrium after this pulse perturbation event (meaning local stability), we made a systematic perturbation process on all consumers (the producers were part of the dynamical system but their community effects were not evaluated). In practice, we simulated the external perturbations by changing the mortality rate (d_i) of the species in question increasing it by 10%. This analysis can be considered as a press perturbation experiment (sensu Bender et al., 1984). Following the single-species perturbations (12 per web), we perturbed the mortality rates of the consumers in all possible pairwise combinations ($(12 \times 11)/2 = 66$ per web) as well. In that case the perturbations of species i and j were parallel in time and were of equal strength (10% increase of d_i and d_j).

If the system is robust against all perturbation events (no extinction happens), we use the adjacency-matrix of the network and also the biomass-values before and after perturbation (see Fig. 1). We run this process until collecting 1000 proper networks, fulfilling all structural and dynamical criteria. Using the adjacency-matrices of the networks we i) calculated several structural indices of the consumers; ii) categorised all species-pairs based on the interspecific interactions between them. With the help of the biomass-values of each species registered before and after perturbation, we calculated the i) community response-values caused by the species(-pairs), and ii) the measure of additivity of the single-species perturbations (see details below).

2.2. Structural network indices

In order to quantify the position of individual species in food webs, we calculated several structural network indices. The calculated indices

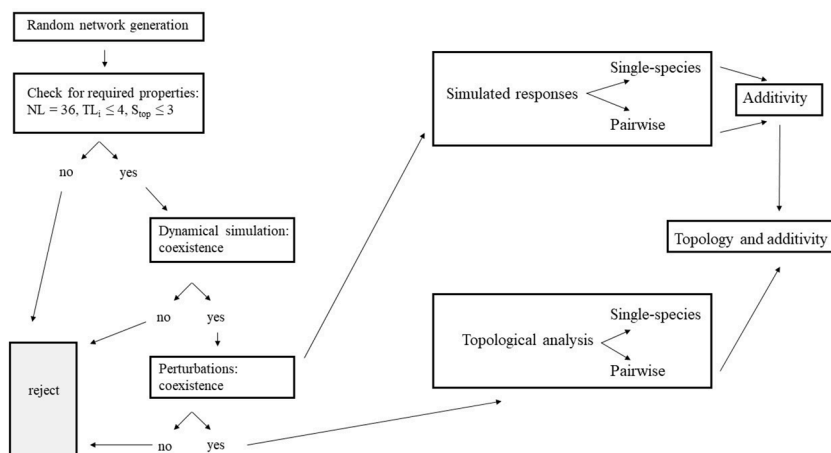


Fig. 1. Flow diagram of the preparatory work of collecting 1000 proper networks meeting structural ($S_b = 3$, $S_c = 12$, $NL = 36$, $\max_{TL} = 4$, $\max_{top} = 3$) and dynamical requirements. The latter means that the networks are supposed to be robust against not only all single-species perturbations (the 12 consumers were disturbed systematically), but also all possible pairwise perturbations (66 consumer-pairs), thus, there is no extinction. The adjacency-matrices and the registered biomass-values of the proper networks were utilized in the further study of the relationships between the structural features of the species and the measure of effects caused by perturbing them.

are collected in Table 1. Here, we give a short summary of their most important features, for more detailed descriptions see references in Table 1.

2.2.1. Centrality indices (D , wD , BC , CC)

The degree (D_i) of a species is the number of other nodes connected directly to it, thus, in other words, the sum of its predators and preys. If a network is weighted, the weighted degree (wD_i) is the sum of the weights of the links adjacent to the species in question. These are the most local network index, not considering indirect effects spreading in the web. Betweenness centrality (BC_i) is a measure of positional importance. It quantifies how frequently is a node (i) on the shortest path between every other node-pairs (j and k). This index measures the centrality of a node in the sense of being an element of many shortest paths in the web. If it is large for a group, it means that if we delete this group, it will more affect many rapidly spreading effects in the network. The other centrality index we used (closeness centrality, CC_i) quantifies how short are the minimal paths from a given node to all others, or, in other words, how close a node is to others. Larger CC_i -values means that deleting node i will affect the majority of other nodes more directly.

2.2.2. Positional importance based on indirect chain effects (TI^t , WT^t)

Trophic effects can spread in a network assumed with undirected links in many directions without bias. Indirect effects do spread in both top-down and bottom-up directions and, as a result, horizontally, too. Considering either binary or weighted networks, indirect chain effects up to a t threshold (maximum indirect chain length) can be expressed by TI^t and WT^t , respectively (see Jord  n et al., 2003). We considered various interaction ranges ($t = 1, 3, 5$).

2.2.3. Status indices and its components (s , s' , Δs)

These indices have been introduced in sociometry (Harary, 1959) and applied soon to ecological problems, too (Harary, 1961). The status (s) of node i is the sum of its d_{ij} distance values to all other j nodes in the web. The contra-status (s') is the same calculated after reversing the sign of all links in the graph. The net status (Δs) is the difference of the two former indices.

2.2.4. Keystone-index and its components (K , K_{bu} , K_{td} , K_{dir} , K_{indir})

While the degree (D) of a node gives only the number of its connected

nodes (thus, its neighbours), the keystone index gives information also on how these neighbours are connected to their neighbours. Since it separates indirect from direct ($K = K_{indir} + K_{dir}$) as well as top-down from bottom-up ($K = K_{td} + K_{bu}$) effects in food webs, it quantifies only vertical interactions (like trophic cascades), without considering horizontal ones (apparent competition).

2.3. Classification of node-pairs

While centrality indices quantify the position of single nodes in a network, the position of node pairs can be characterized in two ways: first, the ecological relationship between species belongs to five categories: (1) predator-prey interaction; (2) intra-guild predation; (3) trophic cascade interaction; (4) exploitative competition; (5) none of the above (Fig. 2). Second, the combinations of single-node topological indices (their average and difference) characterize the positional importance of the species pair. For example, if there are two poorly connected nodes i and j , their pair is characterized by the combination of low average and small difference of degree values.

2.4. Community response (CR) and the measure of (non-)additivity (NA)

The effects of species extinctions may be highly selective (Ives and Cardinale, 2004), so we decided to perturb each consumer (non-producer) species in the dynamical model, one by one, then each pair of consumer species, one by one. We are interested in the effect of these perturbations on the whole ecosystem. Perturbation effects cascade in the interaction network, provoking answers in the remaining $n-1$ (single-species) or $n-2$ (pairwise) species of the community. The community response (CR) to the perturbation of species i or the ij pair of species (CR_i or CR_{ij}) can be determined as the sum of these answers. Pairwise perturbations were performed in parallel, so we did not consider studying the effect of synchrony (Vasseur and Fox, 2007).

For determining the response of a community to any kind of perturbations, more different approaches (i.e. formulas) exist and are used in parallel (Paine, 1992; Power et al., 1996; Hurlbert, 1997; Okey, 2004; Livi et al., 2011). Based on M  r   and Jord  n (2019), where the different formulas are collected and compared, we decided to take neither the sign of changes, nor self-loops into account (we use the absolute value of the differences between the species' biomass values from 1).

All in all, the community response to the single-species perturbation on species i is

$$CR_i = \sum_{k=1}^n \left| \frac{B_k^{aff}}{B_k^{bef}} - 1 \right| (k \neq i)$$

while in the pairwise case, the parallel perturbation of species i and j frames this formula into the following:

$$CR_{ij} = \sum_{k=1}^n \left| \frac{B_k^{aff}}{B_k^{bef}} - 1 \right| (k \neq i \neq j)$$

where $n = 15$ (we do not perturb basal species but also these respond to the perturbations of consumer species); B_k^{bef} and B_k^{aff} are the biomass-values of the species in the equilibrium states before and after the perturbation events, respectively. Note that we do not take into account the self-effect (the change of biomass of the perturbed species itself). By comparing the effects of single-species and pairwise perturbations by the formula

$$NA_{ij} = |CR_i + CR_j - CR_{ij}|$$

we can quantify the measure of non-additivity of the perturbing species i and j in parallel. The smaller the values of NA_{ij} , the larger the measure of additivity. We consider the effects non-additive, if the small effects of

Table 1
Summary of structural network indices.

Index name	Notation	Reference
Centrality indices		
degree	D	Wassermann and Faust (1994)
weighted degree	wD	
betweenness centrality	BC	
closeness centrality	CC	
Positional importance		Jord��n et al. (2003)
topological importance, $t = 1$	TI^1	
topological importance, $t = 3$	TI^3	
topological importance, $t = 5$	TI^5	
weighted topological importance, $t = 1$	WT^1	
weighted topological importance, $t = 3$	WT^3	
weighted topological importance, $t = 5$	WT^5	
Status index and its components		Harary (1959)
Status	s	
contra-status	s'	
net status	Δs	
Keystone index and its components		Jord��n et al. (1999)
keystone index	K	
bottom-up effects	K_{bu}	
top-down effects	K_{td}	
direct effects	K_{dir}	
indirect effects	K_{indir}	

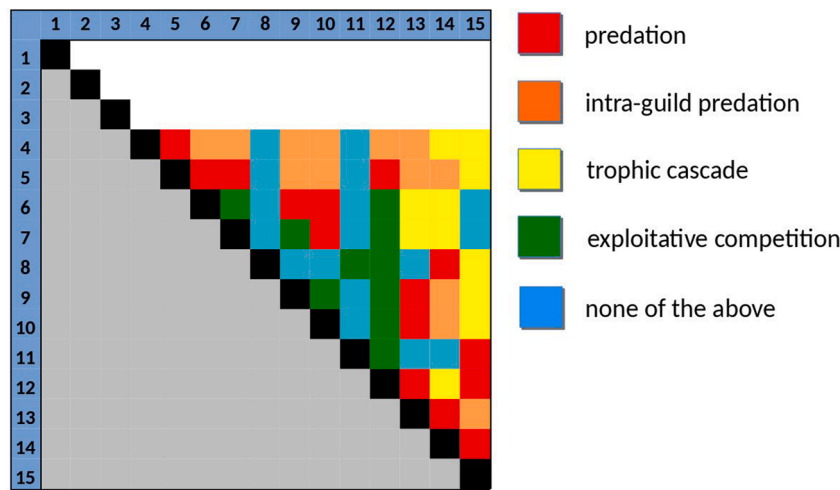


Fig. 2. Five categories of species pairs based on the interspecific interactions between two consumers. Note that the fifth category (“none of the others”) includes a variety of indirect effects, e.g. apparent competition. The half-matrix represents the non-ordered pairs of species and the empty lines show the producers not perturbed in the simulations.

the single-species perturbations are escalated, or, the large effects are dampened in the pairwise cases. For making the results more interpretable, we expressed NA in percentages:

$$NA_{ij}\% = \frac{NA_{ij}}{\sum_{m=1}^{66} NA_{ij}} \times 100 \quad (i \neq j \text{ and } j > i)$$

where m refers to the 66 consumer-pairs in each network (i and $j > 3$, $i \neq j$ and $j > i$).

3. Results

3.1. Correlations of network indices and single-species community response

The correlation coefficients (Spearman’s ρ) between community importance quantified by the various network indices and community importance quantified by the effects of single-species perturbations are given in Table 2. We were interested in only the strength of correlations

($|\rho|$), we did not take the sign of the correlations into account. We considered a connection stronger if $|\rho| > 0.5$.

The wD and WT^t -indices, the status-indices and the K_{bu} and K_{td} indices of the perturbed species correlate strongly ($|\rho| > 0.5$) with community response. This is in agreement with earlier results (Jord  n et al., 2008), suggesting that indices sensitive to indirect effects should be calculated in weighted networks in order to maximize predictability between structure and dynamics. We considered as much as 18 centrality indices but there exist many more: for example, also throughflow centrality (Borrett, 2013) would probably give results similar to wD .

3.2. The measure of non-additivity

The frequency-distribution of the NA%-values (Fig. 3b) is unimodal, strongly right-skewed distribution. The most frequent value of the deviation of NA%-values from zero is about 1%. This means, that highly non-additive pairwise effects are rare. This is understandable if we take into account the small original value of the perturbed d_i , the small intensity of perturbations (10% of d_i). Small changes result in mainly additive results.

The summed community responses to perturbing species i and j do not necessarily predict the community response to ij perturbations. These are the less additive cases. In Fig. 3a, we can see how pairwise effects and single effects are related to each other. On the y axis, we denote the pairwise community response values (CR_{ij}), while on the x axis we can see the sum of the single-species community response values ($CR_i + CR_j$). It can be seen that the dots are either on the $x = y$ line (additive effects), or below it (dampening effects), it is quite exceptional to see dots above the line (escalating effects). Note that taking the sign of each biomass-changes into account in the course of calculating the CR -values, the frequencies of non-additive dampening and escalating effects are similar (for more details see M  r   and Jord  n, 2019). Nevertheless, we used the formula without the sign of changes, because its correlation is higher with some the structural indices than the formulas taking the sign into account (M  r   and Jord  n, 2019). Thus, in this study we did not deal with the escalating or dampening effects separately, we investigated only the possible relationships between the measure of (non-) additivity and the topological features of species(-pairs).

3.3. The topological background of non-additivity

Fig. 3b shows that the frequency-distribution of NA-values is strongly right-skewed, meaning that results with smaller non-additivity are more

Table 2

The strength of correlations ($|\rho|$) between structural network indices and community responses generated by single-species perturbations. Indices are ranked: the higher ones better indicate species of large dynamical effects.

Index	$ \rho $
wD	0.69
WT^5	0.675
WT^3	0.662
K_{bu}	0.641
WT^1	0.6
K_{td}	0.596
Δs	0.588
s	0.58
s'	0.56
K_{indir}	0.345
K	0.282
K_{dir}	0.161
BC	0.14
TT^1	0.137
TT^3	0.102
TT^5	0.093
D	0.063
CC	0.037

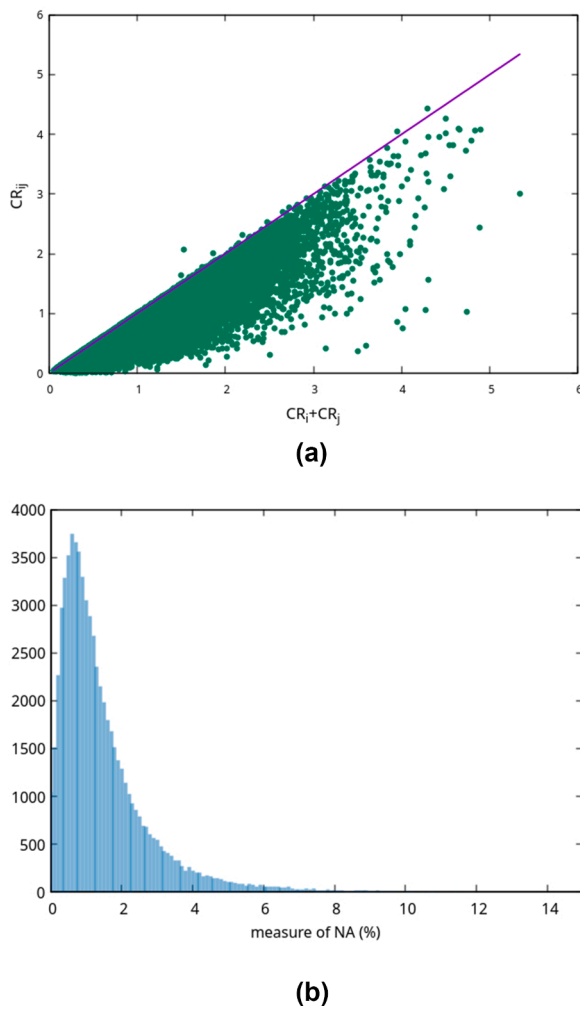


Fig. 3. A plot in (a) shows the relationship between the community responses of pairwise perturbations (CR_{ij}) and the sum of single i and j perturbations ($CR_i + CR_j$). Almost all of the dots are on or below the $x = y$ line, which means that the effects of single-species perturbations are mostly additive or dampening. The frequency-distribution of the NA%-values (b): the most frequent value of the deviation of NA%-values from zero is about 1%.

frequent. To investigate the proportions of non-additive effects in different node pair categories (Fig. 2), we created smaller ranges according to the NA%-values. The definition of range borders considered the frequency-distribution of NA% values: ranges are more narrow for more frequent NA% values, in order to increase the resolution of the plot. We show the proportions of the five node pair categories in the total of 66,000 results (Fig. 4a) and related to only each other (Fig. 4b). Curves in Figs. 3b and 4a suggest that non-additivity distributions largely follow the pattern for the whole set of node pairs but the relative frequency of node pair categories changes *within* the ranges (Fig. 4b): the proportions of the prey-predator relationship (PP) and exploitative competition (EXC) are increasing, while it is decreasing for trophic cascade (TRC) and no effect (NO). For intra-guild predation (IGP) it is low and slowly increases. This means that perturbing a prey and a predator or two competitors will probably result in less additive effects.

Considering topological positions of species pairs, we used the average and the difference of their centrality indices (for the 66,000 simulated species pairs). After finding the minimum and maximum of average and difference values, we created 50 categories between them, thus, we got an 50×50 matrix with 2500 possible categories for each index. We calculated in all these categories the median of NA%-values, because it is less sensitive to the extreme values than the mean (of

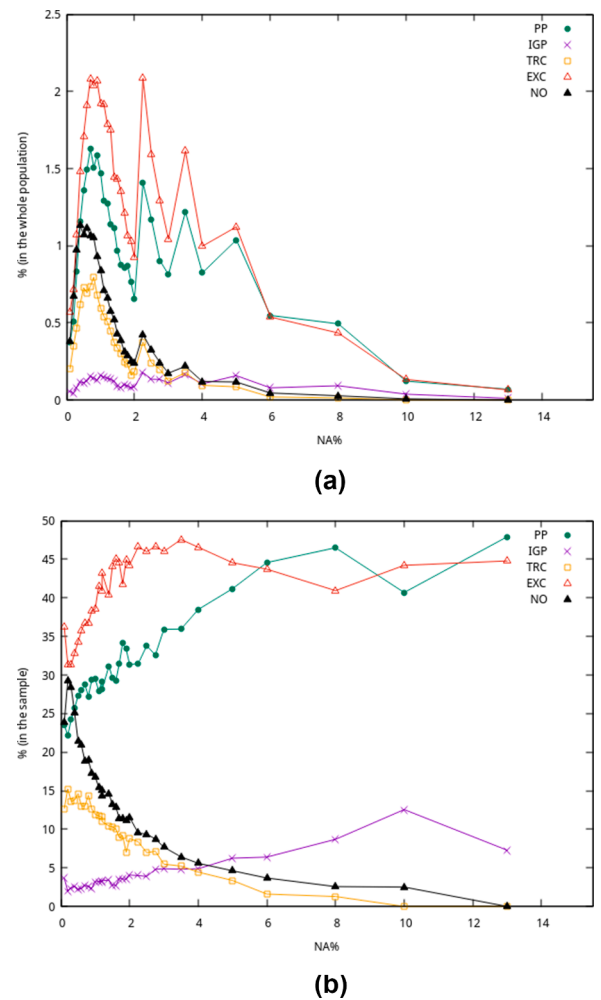


Fig. 4. Frequencies of the different types of ecological interactions according to the increasing measure of NA% in case of all networks (a) and within the NA %-ranges investigated separately (b). The types are PP (prey-predator relationship), IGP (intra-guild predation), TRC (trophic cascade), EXC (exploitative competition) and NO (none of the others, including apparent competition).

course, there were “empty” categories). The results are demonstrated in heat maps corresponding the certain indices (Fig. 5). There are visible trends in case of wD , the keystone-, the status- and WT -indices (note, that these indices have stronger correlation in the pairwise case). For the wD , K_{bw} , s , Δs and WT^t indices, community responses are less additive if both the average and the difference are small (small and similar index-values). For the K_{td} , K_{dir} , K_{indir} , K and s' indices, the CR s of single-species indices are less additive, if the averages of these indices are higher. In these case the differences of the indices less matter.

4. Conclusions

Our results reinforce earlier findings suggesting that weighting trophic interactions is crucial for higher correlations between structure and dynamics (Jordán et al., 2008; Zhao et al., 2016). As Table 2 shows, the highest correlations are all found for weighted structural indices (wD , WT^t), while the lowest correlations characterize binary ones (D , CC , TT^t , BC). Interestingly, the strongest correlation among the weighted indices is seen for the direct wD index, but for the indirect indices the longer the better one (compare WT^5 , WT^3 and WT^1).

Based on pairwise combinations of perturbed species, Fig. 4 shows that their topological position clearly influences whether their combined effect is additive. This might have implications for fisheries management

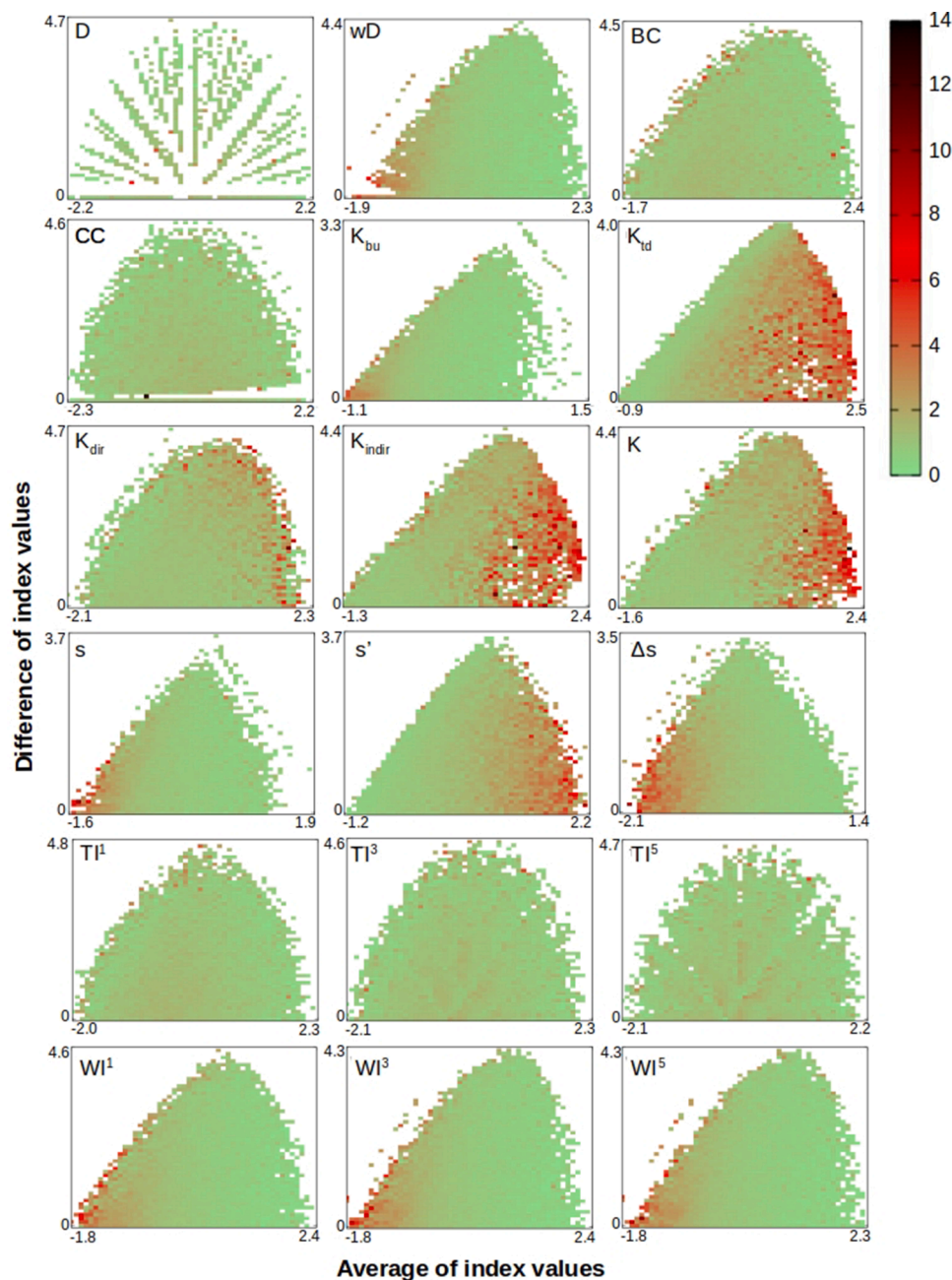


Fig. 5. The median of NA% (the measure is shown in the colored box) for different indices, as a function of the average and the difference of index values for the two species. Red values indicate less additive results (higher median of NA%).

or systems-based conservation management. Perturbing species at different trophic level has been suggested to result in non-additive effects, both dampening and escalation (Hansen et al., 2019).

Since various centrality indices show different and typically not very strong correlations between structure and dynamics, there is need to combine a small but efficiently –chosen set of centrality indices in order to maximize the predictability (Gouveia et al., 2020, submitted).

Better understanding the limits of predictability will contribute to more applicable food web research. In case of conflicting single-species conservation programs or multi-species fishing efforts, food web analysis can help to assess the chance for additive, predictable management. In an optimal case, wisely selected pairs of species can be chosen for management. If their food web topology supports additivity, the higher predictability is advantageous for strategic planning. If non-additive effects are expected, either dampening or escalating outcomes can be

used strategically. For example, dampening may mean that two overfished stocks can partly balancing each other's negative effects and escalation may mean the mutually higher success of two parallel, single-species conservation efforts.

The philosophical implications are clear: calculating community response with using absolute values means that we prefer small effects (even if negative), thus, we do not want to make an impact on nature. Instead, focusing on the signed effect means that we prefer positive effects (even if small), thus, we want to help nature. Accordingly, the preferred response function can be used.

Credit author statement

FJ designed the research, evaluated the results and wrote the paper. AM performed the simulations and wrote the paper. AE contributed to

network analysis. SIP contributed to the statistical analyses.

Declaration of Competing Interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2020.109414](https://doi.org/10.1016/j.ecolmodel.2020.109414).

References

- Bender, E.A., Case, T.J., Gilpin, M.E., 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* 65, 1–13.
- Borrett, S.R., 2013. Throughflow centrality is a global indicator of the functional importance of species in ecosystems. *Ecol. Indicators* 32, 182–196.
- Breitbart, D.L., Lohr, T., Pacey, C.A., Gerstein, A., 1997. Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. *Ecology* 67, 489–507.
- Brose, U., Berlow, E.L., Martinez, N.D., 2005. Scaling up keystone effects from simple to complex ecological networks. *Ecol. Lett.* 8, 1317–1325.
- Cirtwill, A.R., Dalla Riva, G.V., Gaiarsa, M.P., Bimler, M.D., Cagua, E.F., Coux, C., Dehling, D.M., 2018. A review of species role concepts in food webs. *Food Webs* 16. <https://doi.org/10.1016/j.fooweb.2018.e00093>.
- Endr  di, A., Sen  nszky, V., Libralato, S., Jord  n, F., 2018. Food web dynamics in trophic hierarchies. *Ecol. Model.* 368, 94–103.
- Gouveia, C., M  r  ,   ., Jord  n, F., 2020. Finding the most predictive cocktails of centrality indices. Submitted.
- Hansen, C., Drinkwater, K.F., J  hkel, A., Fulton, E.A., Gorton, R., Skern-Mauritzen, M., 2019. Sensitivity of the Norwegian and Barents Sea Atlantis end-to-end ecosystem model to parameter perturbations of key species. *PLoS ONE* 14 (2), e0210419.
- Harary, F., 1959. Status and contrastatus. *Sociometry* 22 (1), 23.
- Harary, F., 1961. Who eats whom? *Gen. Syst.* 6, 41–44.
- Hindmarsh, A.C., Brown, P.N., Grant, K.E., Lee, S.L., Serban, R., Shumaker, D.E., Woodward, C.S., 2005. SUNDIALS: suite of nonlinear and differential/algebraic equation solvers. *ACM Trans. Math. Softw.* 31, 363–396.
- Hurlbert, S.H., 1997. Functional importance vs. keystone: reformulating some questions in theoretical biocenology. *Austral Ecol* 22 (4), 369–382.
- Ives, A.R., Cardinale, B.J., 2004. Food-web interactions govern the resistance of communities after non-random extinctions. *Nature* 429, 174–177.
- Jord  n, F., Tak  cs-S  nta, A., Moln  r, I., 1999. A reliability theoretical quest for keystones. *Oikos* 86 (3), 453–462.
- Jord  n, F., Scheuring, I., Vida, G., 2002. Species positions and extinction dynamics in simple food webs. *J. Theor. Biol.* 215, 441–448.
- Jord  n, F., Liu, W.C., van Veen, F., 2003. Quantifying the importance of species and their interactions in a host-parasitoid community. *Commun. Ecol.* 4 (5), 79–88.
- Jord  n, F., Okey, T.A., Bauer, B., Libralato, S., 2008. Identifying important species: linking structure and function in ecological networks. *Ecol. Model.* 216, 75–80.
- Jord  n, F., Liu, W., Mike,   ., 2009. Trophic field overlap: a new approach to quantify keystone species. *Ecol. Model.* 220 (21), 2899–2907.
- Lau, M.K., Borrett, S.R., Baiser, B., Gotelli, N.J., Ellison, A.M., 2017. Ecological network metrics: opportunities for synthesis. *Ecosphere* 8, e01900.
- Legovic, T., Gecek, S., 2010. Impact of maximum sustainable yield on independent populations. *Ecol. Model.* 221, 2108–2111.
- Legovic, T., Klanjscek, J., Gecek, S., 2010. Maximum sustainable yield and species extinction in ecosystems. *Ecol. Model.* 221, 1569–1574.
- Legovic, T., Gecek, S., 2012. Impact of maximum sustainable yield on independent populations. *Ecol. Model.* 230, 63–72.
- Lin, H.-J., Shao, K.-T., Hwang, J.-S., Lo, W.-T., Cheng, I.-J., Lee, L.-H., 2004. A trophic model for kuosheng bay in Northern Taiwan. *J. Mar. Sci. Techn.* 12 (5), 424–432.
- Livi, C.M., Jord  n, F., Lecca, P., Okey, T.A., 2011. Identifying key species in ecosystems with stochastic sensitivity analysis. *Ecol. Model.* 222 (14), 2542–2551.
- May, R.M., Beddington, R.J., Clark, C.W., Holt, S.J., Laws, R.M., 1979. Management of multispecies fisheries. *Science* 205, 267–277.
- M  r  ,   ., Jord  n, F., 2019. Comparing community response indices in aquatic food web models. *Adv. Oceanol. Limnol.* 10, 94–101.
- M  r  ,   ., Endr  di, A., Jord  n, F., 2018. Additivity of pairwise perturbations in food webs: topological effects. *J. Theor. Biol.* 448, 112–121.
- Okey, T.A., 2004. Shifted Community States in Four Marine ecosystems: Some Potential mechanisms. PhD Thesis. University of British Columbia, Vancouver.
- Paine, R.T., 1992. Food-web analysis through field measurement of per capita interaction strength. *Nature* 355, 73–75.
- Pimm, S.L., 1980. Food web design and the effect of species deletion. *Oikos* 35, 139–149.
- Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R.T., 1996. Challenges in the Quest for Keystones. *Bioscience* 46 (8), 609–620.
- Vasseur, D.A., Fox, J.W., 2007. Environmental fluctuations can stabilize food web dynamics by increasing synchrony. *Ecol. Lett.* 10, 1066–1074.
- Wassermann, S., Faust, K., 1994. Social Network analysis: Methods and Applications. Cambridge University Press, New York.
- Yodzis, P., 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* 69, 508–515.
- Yodzis, P., 2000. Diffuse effects in food webs. *Ecology* 81, 261–266.
- Zhao, L., Zhang, H., O’Gorman, E.J., Tian, W., Ma, A., Moore, J.C., Borrett, S.R., Woodward, G., 2016. Weighting and indirect effects identify keystone species in food webs. *Ecol. Lett.* 19, 1032–1040.