Additivity of pairwise perturbations in food webs: topological constraints and multi-species MSY assessment

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Abstract

Food webs dynamically react to perturbations and it is an open question how additive are the effects of single-species perturbations. Network structure may have topological constraints on additivity and this influences community response. Better understanding the relationships between single-species and multi-species perturbations can be useful for systems-based conservation management. One example is the potential improvement of maximum sustainable yield (MSY) assessment, by putting it in a multi-species context. Here we study a single model food web by (1) characterizing the positional importance of its nodes, (2) building a dynamical network simulation model and performing sensitivity analysis on it, (3) determining community response to each possible single-species perturbation, (4) determining community response to each possible pairwise species perturbation and (5) quantifying the additivity of effects for particular types of species pairs. We found that perturbing pairs of species that are either competitors or have high net status values in the network is less additive: their combined effect is dampened.

Highlights:

- Perturbing species in different food web positions cause different community effects
- Comparing single-species and pairwise perturbations helps to quantify additivity
- Non-additive effects can be caused by particular topologies of perturbed species pairs
- Topological constraints on additivity have consequences on multi-species MSY assessment

Keywords: food web, topology, multi-species models, MSY

Introduction

The complexity of ecosystems makes it very hard to predict the effects of various perturbations, in terms of both sign and size (Yodzis 1988; Eklöf and Ebenman 2006). It is even more difficult in case of multiple perturbations. In the context of a dynamical food web, it is a basic question how individual single-species perturbations are related, how additive are their effects in terms of community response.

One practical challenge here is how to use single-species maximum sustainable yield (MSY) assessment for multi-species fisheries. Approaches focusing on single-species stocks are routinely used worldwide as if different species would live independently (Schaefer 1991; Chakraborty et al. 1997). Actual MSY values may depend also on fishing technique (e.g. longline vs floating object: Maunder 2002), the trophic height of the species (Pauly 1979) and body length ratios of the catch (Pauly 1979). Single-species MSY assessment models are being criticized frequently, although they are suggested to work quite well for short-term predictions on top predators (Hollowed et al. 2000; Legović et al. 2010].

From a community ecology perspective, it is quite clear that fish stocks are inter-dependent in a food web and should be considered simultaneously. The need for multi-species approaches was addressed a long time ago (May et al. 1979), but not too many successful attempts have been made so far. For some examples, the non-additive nature of single-species evaluations was demonstrated (Beddington and May 1980; Mueter and Megrey 2006). Clear and general results are needed, especially if multi-species MSY assessment is to be used also as a better policy instrument (see MEY: Guillen et al. 2013), following earlier attempts for economical applications (Hannesson 1983). Comparing the performance of single-species versus multi-species MSY assessments is not yet conclusive but efforts are being made (Hollowed et al. 2000; Walters et al. 2005).

Legović and Geček (2010, 2012) and Geček and Legović (2012) suggested that the topological positions of several fish species fished simultaneously may also matter. They found in a dynamical model that fishing on independent stocks leads to higher robustness than multi-species fisheries on a multi-level system. Thus, predatory and competitive interactions among simultaneously harvested species decrease robustness. Better understanding the relationships between preys and predators as well as between different predators has a robust theoretical background (Yodzis 1994) and this line of thinking raises the need to include the network position of species in modern MSY indicators. This is especially desirable since the major advantage of multispecies MSY models over single-species MSY models seems to be the capability to explicitly consider indirect effects (Hollowed et al. 2000).

It is an old problem to understand the effects of species deletions (perturbations) in food webs (Pimm 1980; Allesina and Bodini 2004; Quince et al. 2005; Allesina et al. 2006). Recent developments in network ecology generated a wide interest in the link between population dynamics and network position of nodes. Several topological characteristics have been proposed to be a useful proxy for understanding and predicting dynamics (Jordán et al. 2003; Estrada 2007; Jordán 2009; Pocock et al. 2011) with the help of dynamical models. Following Pimm (1980), a number of studies focused on better understanding this aspect of the pattern to process issue in both toy models (Jordán et al. 2002; 2003; Móréh et al. 2009) and realistically parameterized system models (Jordán et al. 2008; Livi et al. 2011). Importantly, network analysis cannot directly solve the problems of multi-species fisheries but it can quantify the mathematical (topological) constraints on ecosystem dynamics. In order to separately analyse topological effects on the additivity of single-species perturbations in food webs, simple models should be used with the minimal number of factors complicating the evaluation of the structure to dynamics link.

In this paper, we present a dynamical sensitivity analysis of a model food web. Our goals are (1) to perform a topological analysis of the food web and determine key nodes (central trophic groups), (2) to build and run a simulation model for the same system, in order to perform sensitivity analysis, (3) to determine the community response generated by single-species perturbations, (4) to perform pairwise perturbations with the same conditions and (5) to compare the results of single-species and multi-species perturbations and determine the level of additivity. The key aim is to determine the topological position of species *j* and *k* such that their parallel perturbation has dampened effects on the ecosystem.

Data

We analyse a single food web, containing three producers (species #1, #2 and #8), one top predator (species #15) and 11 intermediate species (Figure 1). The network is of intermediate size (N = 15 living trophic groups), so it is still manageable for dynamical simulations (using several population dynamical parameters) but already interesting enough for topological studies (focusing only on food web structure). The topology of the network is arbitrary but a similar study of 100 randomly generated, comparable networks is already in progress.

Methods

Network structure

In order to quantify the structural importance of network nodes, first, we consider the food web as an undirected network where effects can spread in any direction (from prey to predator and from predator to prey). These are clearly not only energy flows but trophic interactions in a broader sense. A range of network indices can be used for quantifying the positional importance of nodes in undirected networks (note that some of these indices have versions adapted to directed networks too). Since we still do not understand the structure to dynamics relationship, it makes sense to test several structural indices and clarifying their relationship with dynamics. The structural indices are clearly not independent of each other but we study relationships between structural versus simulated metrics and investigate which structural indices are correlating best with simulated non-additive effects.

Degree and weighted degree (D, wD)

The most local network centrality index is the *degree* of a node (*D*). This is the number of other nodes connected directly to it. In a food web, the degree of a node *i* (D_i) is the sum of its preys and predators. In the case of weighted networks, the weighted degree of node *i* (wD_i) equals the sum of weights on links adjacent to node *i* (Wassermann and Faust 1994). Degree and weighted degree can be calculated by the UCINET programme (Borgatti et al. 2002).

Betweenness centrality (BC)

This measure of positional importance quantifies how frequently a node *i* is on the shortest path between every pair of nodes *j* and *k*. This index is called ”betweenness centrality” (*BC*), used routinely in social network analysis (Wassermann and Faust 1994) and we calculated it using the UCINET programme (Borgatti et al. 2002). The standardised index for node *i* (BC_i) is:

$$BC_i = \frac{2\sum_{j<k}\frac{g_{jk}(i)}{g_{jk}}}{(N-1)(N-2)} \qquad (1)$$

where $i \neq j$ and k. g_{jk} is the number of equally shortest paths between nodes j and k, and $g_{jk}(i)$ is the number of these shortest paths to which node i is incident (of course, g_{jk} may equal one). The denominator is twice the number of pairs of nodes without node i. This index thus measures how central a node is, in the sense of being incident to many shortest paths in the network. If BC_i is large for trophic group i, it means that deleting this group will more affect many rapidly spreading effects in the web.

Closeness centrality (CC)

Closeness centrality (*CC*) is a measure quantifying how short are the minimal paths from a given node to all others (Wassermann and Faust 1994) and is again calculated using UCINET (Borgatti et al. 2002). The standardised index for a node i (CC_i) is:

$$CC_i = \frac{N-1}{\sum_{j=1}^{N} d_{ij}} \qquad (2)$$

where $i \neq j$ and d_{ij} is the length of the shortest path between nodes i and j in the network. This index thus measures how close a node is to others. The larger CC_i is for trophic group i, the more directly deleting this group will affect the majority of other groups.

Positional importance based on indirect chain effects (TI^n and WI^n)

We can assume a network with undirected links where trophic effects can spread in many directions without bias. Indirect effects do spread in both bottom-up and top-down directions through trophic links and, as a result, horizontally, too. We first consider an unweighted network. Here, we define $a_{n,ij}$ as the effect of j on i when i can be reached from j in n steps. The simplest mode of calculating $a_{n,ij}$ is when n=1 (*i.e.* the effect of j on i in 1 step): $a_{1,ij} = 1/D_i$, where D_i is the degree of node i (*i.e.* the number of its direct neighbours including both prey and predator species). We assume that indirect chain effects are multiplicative and additive. For instance, we wish to determine the effect of j on i in 2 steps, and there are two such 2-step pathways from j to i: one is through k and the other is through h. The effects of j on i through k is defined as the product of two direct effects (*i.e.* $a_{1,kj} \times a_{1,ik}$), this is why multiplicative. Similarly, the effect of j on i through h equals to $a_{1,hj,1} \times a_{1,ih}$. To determine the

2-step effect of *j* on *i* ($a_{2,ij}$), we simply sum up those two individual 2-step effects (*i.e.* $a_{2,ij}= a_{1,kj}\times a_{1,ik}+ a_{1,hj}\times a_{1,ih}$) in an additive way (Jordán et al. 2003).

When the effect of step *n* is considered, we define the effect received by species *i* from all species in the same network as:

$$\varphi_{n,i} = \sum_{j=1}^{N} a_{n,ji} \qquad (3)$$

which is equal to 1 (*i.e.* each species is affected by the same unit effect.). Furthermore, we define the *n*-step effect originated from a species *i* as:

$$\sigma_{n,i} = \sum_{j=1}^{N} a_{n,ji} \qquad (4)$$

which may vary among different species (*i.e.* effects originated from different species may be different). Here, we define the topological importance of species *i* when effects "up to" *n* step are considered as:

$$TI_i^n = \frac{\sum_{m=1}^{n} \sigma_{m,i}}{n} = \frac{\sum_{m=1}^{n}\sum_{j=1}^{N} a_{m,ji}}{n} \qquad (5)$$

which is simply the sum of effects originated from species *i* up to *n* steps (one plus two plus three…up to *n*) averaged over by the maximum number of steps considered (*i.e.* *n*). For the undirected network with weighted links, all effects are defined in the same way as above with the exception of 1-step effects, which is defined as:

$$a_{1,ij} = \frac{\varepsilon_{ij}}{\mu_i} \qquad (6)$$

where μ_i is the sum of the strength of the links connected to *i* and ε_{ij} is the strength of the link connecting *i* and *j*. The weighted approach of calculating 2-step effects (*i.e.* $a_{2,ij}$) was originally developed by Godfray and colleagues for assessing apparent competition in host-parasitoid communities (Müller and Godfray 1999; Müller et al. 1999; Rott and Godfray 2000). Furthermore, we define WI_i^n as the topological importance of species *i* for networks with weighted links when effects "up to" *n* steps are considered:

$$WI_i^n = \frac{\sum_{m=1}^{n} \sigma_{m,i}}{n} = \frac{\sum_{m=1}^{n} \sum_{j=1}^{N} a_{m,ji}}{n} \qquad (7)$$

We analysed indirect effects of different maximum length (n = 1, 3, 10); these indices can be calculated by the Cosbi Graph software (Valentini and Jordán 2010).

Status index and its components (s, s`, Δs)

We also consider the food web as a directed acyclic graph (DAG). In this case, we can apply different network indices for measuring the positional importance of nodes. The status of node i (s_i) in a hierarchy is the sum of its d_{ij} distance values to all other j nodes in the network. The contrastatus of this i node ($s`_i$) is the same calculated after reversing the sign of all links in the graph. The net status of this node i (Δs_i) equals the difference of the two former indices:

$$\Delta s_i = s_i - s\ _i \qquad (8)$$

These indices have been introduced in sociometry (Harary 1959) and applied subsequently to ecological problems (Harary 1961). We may note that this latter attempt to quantify the relative importance of species in ecological communities, based on their network position was a pioneering effort not followed by biologists for decades (see Mills et al. 1993; but even the qualitative discussion of species importance came only years later Paine 1966). These indices can be calculated by the Cosbi Graph software (Valentini and Jordán 2010).

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

The keystone index (K, Jordán et al. 1999) is derived from earlier works on DAGs (Harary 1959; 1961). The keystone index of a species i (K_i) is defined as:

$$K_i = K_{bu,i} + K_{td,i} = K_{dir,i} + K_{indir,i} = \sum_{c=1}^{n} \frac{1}{d_c}(1 + K_{bc}) + \sum_{e=1}^{m} \frac{1}{f_e}(1 + K_{te}) \qquad (9)$$

where n is the number of predators eating species i, d_c is the number of prey species of its c^{th} predator and K_{bc} is the bottom-up keystone index of the c^{th} predator. And symmetrically, m is the number of prey eaten by species i, f_e is the number of predators of its e^{th} prey and K_{te} is the top-down keystone index of the e^{th} prey. For node i, the first sum in the equation (*i.e.*

$\sum 1/d_c(1+K_{bc})$) quantifies the bottom-up effect ($K_{bu,i}$) while the second sum (*i.e.* $\sum 1/f_e(1+K_{te})$) quantifies the top-down effect ($K_{td,i}$). After rearranging the equation, terms including K_{bc} and K_{te} (*i.e.* $\sum K_{bc}/d_c + \sum K_{te}/f_e$) refer to indirect effects for node i ($K_{indir,i}$), while terms not containing K_{bc} and K_{te} (*i.e.* $\sum 1/d_c + \sum 1/f_e$) refer to direct ones ($K_{dir,i}$). Both $K_{bu,i} + K_{td,i}$ and $K_{indir,i} + K_{dir,i}$ equals K_i. The degree of a node in a network (D) characterises only the number of its connected (neighbour) points, while the keystone index gives information also on how these neighbours are connected to *their neighbours*. It quantifies only vertical interactions (like trophic cascades), without considering horizontal ones (like apparent competition), separating indirect from direct, as well as bottom-up from top-down effects in food webs. These indices can also be calculated by the Cosbi Graph software (Valentini and Jordán 2010).

We used 18 positional importance indices to quantify the relative importance of nodes in the food web (D, wD, BC, CC, TI^1, TI^3, TI^{10}, WI^1, WI^3, WI^{10}, s, $s`$, Δs, K, K_{bu}, K_{td}, K_{dir}, K_{indir}). Although all of these indices say something about the positional importance, also all of them are different. Some of them (e.g. D) are local, not considering indirect effects (i.e. the neighbours of neighbours) while others are non-local or mesoscale indices (e.g. BC, TI^{10}). Some of them consider binary interactions (e.g. TI^3), while others can quantify weighted networks (e.g. WI^3). Finally, some of them characterize undirected (e.g. D), while others do directed networks (e.g. s, K).

Clearly, there are several more indices, still quantifying node centrality in networks (e.g. information centrality, IC). Here we focus on some of the most used and probably more promising indices (McDonald-Madden et al. 2016). Apart from their *nature*, these particular indices differ also from the viewpoint of robustness, for example. Some of them are more, while others are less sensitive to incomplete data (sampling, see Fedor and Vasas 2009). Table 1 shows the values of all these indices for the nodes of the food web (for the results of statistical analyses, see Table 2 below).

Network dynamics

For modelling the dynamic behaviour of these trophic networks, we extended an earlier model of ours, focusing on overfishing in small model food webs (Móréh et al. 2009). The dynamics of each species can be described by the following differential equation:

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{N_i}{K_i}\right) + \sum\nolimits_{\rho=resources} N_i\, \varepsilon_{i\rho} \frac{N_\rho^h \omega_{i\rho}}{N_0^h + \omega_{i\rho} Q_{i\rho}} - \sum\nolimits_{c=consumers} N_c \varepsilon_{ci} \frac{N_i^h \omega_{ci}}{N_0^h + \omega_{ci} Q_{ci}} - d_i N_i \tag{10}$$

where N_i means the abundance of species *i*; r_i and K_i are the rate of increase and carrying capacity of the logistic model, respectively. These quantities characterise the *basal* species only ($i=1,2,8$, see Figure 1); d_i is the mortality rate of *consumer* species *i*. Holling type-III ($h=2$) functional response refers to the realized fraction of *i*'s maximum ingestion rate when consuming its prey species. $\omega_{i\rho}$ is species *i*'s relative consumption rate when consuming ρ, N_0 is the half-saturation density and $Q_{i\rho}$ is the sum of the abundances of the resources *i* can consume. The relative consumption rates are inversely proportional to the number of resources: $\omega_i = 1/n$.

In order to focus on how network topology influences dynamics, we did not model the consumption or conversion rates of species explicitly and assumed that the strength of a predator-prey link (ε) is solely proportional to the number of preys ($\varepsilon_i = 1/n$). Similarly, almost every parameter was fixed ($K_i = 1$, $r_i = 1$ for basal species, $\varepsilon_i = \omega_i = 1/n$) except mortality rates (d_i), which were chosen from a biologically plausible range to achieve a stable coexistence of all 15 species. We searched for different sets of d_i-combinations that lead to robust coexistence.

For the integration of the set of ODEs described in the previous equation, we used the CVODE code with adaptive backward differentiation scheme (Hindmarsh et al. 2005). For all simulations, all initial abundances were set to 1 and the system was integrated over T = 20.000 time steps (since one step is a unit change of population size of the fastest-growing organisms, say phytoplankton, this range roughly corresponds to a decadal time-scale, like 20-30 years). 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 the dynamics is settled to a fixed point during the integration and the solution was locally asymptotically stable, the systems were used for sensitivity analysis, see below. We note that we have found limit cycles in less than 1% of the simulations and we have not found chaotic solutions. The limit cycles were excluded from further investigations.

Sensitivity analysis

Having selected the robust webs in this manner, sensitivity analysis became possible. We perturbed only the 12 consumer species, so the producer species #1, #2 and #8 were part of the dynamical system but their community effects were not evaluated. We applied the following method in all cases. We selected a set of d_i parameters where the web was robustly present, and run the integration again. After the dynamical equilibrium was settled, we perturbed the mortality rate of the species in question by increasing it by 10%. Our in silico sensitivity analysis can be considered as press perturbation experiments (sensu Bender et al. 1984) and we trace also indirect, not only the direct consequences.

Following single-species perturbations, we perturbed species in all possible pairwise combinations as well. In the case of pairwise perturbations, the perturbations on species *i* and species *j* were parallel in time and they were of equal strength (10% increase of d_i *and* d_j).

Community response

We were interested in the effect of perturbing species *i* on all other species *j* in the system and we determined the community response to this perturbation (CR_i) as the sum of all these answers (without considering the feedback of perturbing species *i* on itself, i.e. self-effects).

So, if $N_{i(*)}^t$ is the population size of species *i* at time *t* in the reference simulation and $N_{i(j)}^t$ is the population size of species *i* at time *t* in a simulation where species *j* was disturbed, then the individual answer of a species *i* to perturbing species *j* is

$$R_j = \frac{N_{i(j)}^t}{N_i^t} \qquad (11)$$

and this can be larger or smaller than 1 (the former meaning increased population size as a response to perturbation and the latter meaning decreased population size as a response to perturbation). The community response to the single-species perturbation on species *j* is

$$CR_j = \sum_{i=1}^{n} \left| \frac{N_{i(j)}^t}{N_i^t} - 1 \right| / 14, (i \neq j) \qquad (12)$$

In case of pairwise perturbations, the community response to perturbing species *j* and *k* in parallel is

$$CR_{[jk]} = \sum_{i=1}^{n} \left| \frac{N_{i(j,k)}^{t}}{N_i^t} - 1 \right| / 13, (i \neq j \neq k) \qquad (13)$$

A question that is of both technical and philosophical nature is whether we prefer small effects (even if negative) or positive effects (even if large). In other words, we want to minimize our impact on nature (small negative better than large positive) or to help it (large positive better than small negative). Because we preferred the former scenario (small effect), we calculated the absolute values of the differences from 1 (meaning no change). A number of alternative response functions are used in community ecology (Livi et al. 2011; Hurlbert 1997; Okey 2004): our function is most similar to the interaction strength index (ISI).

Comparing the effects of single-species and pairwise perturbations by

$$NA_{[jk]} = \left| CR_j + CR_k - CR_{[jk]} \right| \qquad (14)$$

quantifies the non-additivity of the effects of perturbing species *j* and *k* in parallel. Smaller *NA* values mean large additivity. Non-additive effects can be realized in two ways. First, the small effects of the single-species [*j*] and [*k*] perturbations can be escalated in a [*j k*] pairwise perturbation. Second, the large effects of the single-species [*j*] and [*k*] perturbations can be dampened in a [*j k*] pairwise perturbation.

Classification of node pairs

Since the food web contains 15 nodes but we do not perturb the 3 producer species, we have 12 single-species perturbations and (12+11)/2 = 66 combinations for pairwise perturbations. These 66 combinations of two species can be characterized by several ways.

Centrality

We are interested in the pairwise perturbation of species combinations where each species belongs to the most central 5 nodes of the network, according to each of the 18 topological indices we used. The pairwise combinations of the 5 highest-centrality nodes provide 10 (unordered) species pairs. For an example, we have species #14, #4, #3, #13 and #12 on the top of the centrality rank based on TI^3, so we study if their pairwise combinations ([14 4], [14

3], [14 13], [14 12], [4 3], [4 13], [4 12], [3 13], [3 12] and [13 12]) have different community responses than other species pairs. Note that we have 15 species pairs for *D*, since there is a tie between species #10 and #12 in the *D*-rank (Table 1) and we decided to consider both as highest-centrality nodes in the network; 6 species provide 15 pairwise combinations. All of these categorizations, according to the 18 structural indices are seen in Table 3.

Regular equivalence

We used the regular equivalence measure (*REGE*, see Lorrain and White 1971; Everett and Borgatti 1991; Luczkovich et al. 2003) for defining network roles in the food web. This measure quantifies the similarity between the positions of network nodes *i* and *j*, based on their network position (this approach is a general version of the quite similar, classical concept of trophospecies, Yodzis and Winemiller 1999). Their composition is based on the *REGE* analysis. The dendrogram that expresses the similarity can be cut at any threshold level in order to define and create aggregated functional groups. We were interested in pairs of species of similar ($REGE^s$) and dissimilar ($REGE^d$) network position. In Figure 2, we show the dendrogram and we mark a group of similarly-positioned species ($REGE^s$) in blue, while the most distant branch of the dendrogram (species #15) as well as its highest-level branching point in red (this group provides the $REGE^d$ category when combined with any of the others). Producers (marked in green) are not considered in the analysis, otherwise, they would provide the highest branching point in the dendrogram. Both of these categorizations are seen in Table 3: node pairs in very similar ($REGE^s$; [9 10], [4 9], [4 10] and [5 6]) and very different ($REGE^d$; all of the 11 [15 i] pairs) network positions.

Modules

Based on the ecological characteristics of interspecific interactions, we categorize all species pairs in the food web as (1) being in predator-prey interaction, (2) being in intra-guild predation (IGP) interaction, (3) being in a trophic cascade interaction, (4) being exploitative competitors or (5) none of the above (including apparent competition). The colouring of the community matrix on Figure 3 shows this classification and group identities are shown in Table 3: we have 14 pairs in prey-predator relationship („pred”), 13 intra-giuld predations („IGP”), 11 trophic cascades („tr casc”), 11 exploitative competitions („expl comp”) and 17 relationships belonging to none of the above („none”).

Statistical analysis

In the case of single-species perturbations, we had numerical values (Table 1) and the relationship between structural importance and community response was evaluated by the Spearman correlation (rho and p-values given in Table 2). In the case of pairwise perturbations, we had categorical values (Table 3) and the relationship between structural importance and community response was evaluated by Mann-Whitney test (Table 4).

Results

Table 1 shows the topological characteristics of the 12 graph nodes that are of interest for the perturbation experiments (values for species #1, #2 and #8 are not shown). Based on local measures, species #3 and #4 are the most central ones in the binary ($D = 8$), while species #4 is the single most central one in the weighted ($wD = 2{,}06$) network. Classical non-local centrality measures suggest the key position of either species #14 ($BC = 25{,}05$) or species #4 and #13 ($CC = 66{,}67$). Topological importance identifies species #14 for shorter ($TI^{1} = 2{,}38$, $TI^{3} = 1{,}81$) and species #4 for longer ($TI^{10} = 1{,}6$) pathways. Based on weighted importance, the same species dominate but species #4 gets dominance earlier as pathway length increases ($WI^{3} = 1{,}88$, $WI^{10} = 2{,}06$), preceding species #14 that is still the most central one for the most local interactions ($WI^{1} = 2{,}47$).

Hierarchical indices suggest different key nodes for the directed version of the food web. Species #3 has the highest status ($s = 11$) and species #15 has the highest contra-status ($s` = 26$), and the net status index identifies these two species with the most extreme values (Δs). Based on net status, species #11 and #12 are the most balanced ones ($\Delta s = 0$). The keystone index suggests species #3 based on bottom-up ($K_{bu} = 6{,}48$) and species #15 based on top-down ($K_{td} = 14$) effects, while species #14 based on direct ($K_{dir} = 3{,}89$) and species #15 based on indirect ($K_{indir} = 11$) effects. The overall key species is suggested to be species #15 ($K = 14$).

Based on these 18 topological indices of positional importance, we can identify 5 species that are of critical importance in this trophic network (species #3, #4, #13, #14 and #15). Note that species #3 is more important in unweighted (binary) networks, species #4 is more important in undirected (symmetrical) ones, species #15 is in key position only in the directed network and species #13 is important based only on CC (undirected, unweighted).

But species #14 has highest centrality based on both directed (K_{dir}) and undirected (BC) as well as both binary (TI^1) and weighted (WI^1) measures. All in all, species #14 can be clearly suggested to be the most critical node in this network.

Figure 4 shows the species-specific answers of single-species and pairwise perturbations (the average for several simulations shown in Figure 4a). Some perturbations have predominantly positive effects on others (like [9 15], the pairwise perturbation of species #9 and #15), this is indicated by a larger number of green cells in the corresponding row of Figure 4a. Some species are typically positively influenced by perturbations (like species #11), this is indicated by the larger number of green cells in the corresponding column of Figure 4a. Symmetrically, mostly negative effects are caused by perturbing [4 5] and the impacts are mostly negative on species #7. This detailed information is useful for better understanding the mechanistic details of community dynamics but the community response function we used does not consider the sign, only the strength of responses (otherwise strong positive and strong negative effects extinct each other and show weak community answer). The summarized community responses are shown in Figure 4c and the statistical analysis concerns these community responses, not the species-specific responses on Figure 4a.

The consistency of the previous results can be calculated by the standard deviation of individual responses during the simulations. Figures 4b and 4d show this information for the species-specific and for the community responses, respectively. Some perturbations have quite consistent effects on others (like [5 14]), with predictable results (mostly white cells in the corresponding row of Figure 4b), and some species are quite consistently impacted (like species #3, see the white cells in the corresponding column of Figure 4b). Similarly, some perturbations give quite inconsistent results (like [3 9]) and some species are quite inconsistently impacted (like species #4).

The numerical values of community responses generated by single-species perturbations are presented in Table 1 (CR_j). Here we see only 12 values since producers (species #1, #2 and #8) have not been perturbed. For visualization, see Figure 1. It can be seen that perturbing species #7 generates the largest community answer (note that $D_7 = 2$, so this species cannot be considered a hub species, and it does not belong to the highest-centrality nodes according to any index).

Correlation coefficients between community importance quantified by the various topological indices and community importance quantified by the effects of single-species perturbations are given in Table 2. Interestingly, no structural index shows significant correlation with dynamical importance. The highest (still non-significant) and lowest *p*-values characterize the K_{indir} and the *D* indices, respectively.

Pairwise species combinations are ranked according to the non-additivity of their effects (Table 3). The existence of non-additive effects is not surprising (e.g. Kareiva 1994; Wootton 1994) but their network-based, quantitative understanding is incomplete. The top of the ranking shows the least additive effects of perturbing a [*j k*] pair versus perturbing them separately ([*j*] + [*k*]). Combinations [7 15] and [7 11] give the least additive results, while combinations [6 7] and [3 10] give the most additive answers. The single-species perturbation of species #7 gives the largest community response (see Table 1) and this species is a member of most of the pairwise combinations generating the least additive effects. Without species #7, [12 15] gives the least additive effect and [6 7] gives the most additive effect with species #7.

The summed community responses to perturbing species [*j*] and [*k*] do not necessarily predict the community response to [*j k*] perturbations. In Figure 5, we can see how pairwise effects and single effects are related to each other for particular pairs of species. On the *y* axis, we see the pairwise community response values (CR_{jk}), while on the *x* axis we see the sum of the single-species community response values ($CR_j + CR_k$). Points on the $x = y$ line show combinations where it does not matter whether the two species are perturbed separately or in combinations (high additivity). Below the line, we have non-additive, dumping effects (e.g. [7 15], [7 11]) and above the line we have non-additive, escalating effects (only [3 9]). We can say that additivity is generally quite high.

If we look at the rank positions of the 25 different categories of species combinations, we find that 2 of them differ significantly from the rest (Table 4). Non-additivity of pairwise perturbations is higher if the species pair has high Δs-values or if they are (exploitative) competitors. Finally, we note that higher non-additivity values are generally accompanied with a larger variability of the pairwise community response values (Figure 6). This means that if the perturbation of species *i* and *j* produces more additive effects, the community response to their pairwise perturbation will be also more predictable (Spearman's rho = -0,094).

Conclusions and future directions

We have found significant effects of network topology on the additivity of pairwise perturbations. However, for single-species perturbations, we have found no significant relationships between food web position and community response.

We determined the trophic components of highest positional importance, the dynamical effects of single-species and pairwise perturbations and the additivity of pairwise species perturbations in a food web simulation model. We emphasize that the response function we have chosen does not provide information about positive and negative effects (increase or decrease of population size), only about large and small effects (the change in population size). This is supported by a conservation philosophy suggesting that minimizing the human impact (size of change) might be preferred over trying to help natural systems (direction of change).

We found that, according to the dynamical model we used, food web structure is a poor predictor of dynamics. The effects of single-species perturbations show no correlation with the position of the species in the food web. Yet, we can find that weighted measures perform better than unweighted ones (WI^n better than TI^n and wD better than D). Also, indirect measures almost always perform better than direct ones (TI^n and WI^n better than wD and D, the exception is TI^{10}). These support earlier findings of the poor predictive power of a local and binary view on networks (Jordán et al. 2008; Livi et al. 2011). Based on our results, we can state that pairwise species perturbations have non-additive and almost always dampening effects if the two perturbed species are competitors or if they have high net status values (Δs).

Better understanding the topological effects on additivity can be useful for systems-based conservation (e.g. multi-species fisheries management). Clearly, the sustainability of fisheries is a much more complicated issue: predicting interaction strength between trophic groups (or species) is not easy even in small systems of just a few species but there are recent developments for multi-species systems (based on a large number of attributes, including simplistic food web properties like degree, Berlow et al. 2009). Apart from better understanding the topological basis of sustainable ecosystems, it is clear that several other factors need to be addressed for sustainability research: these include economic aspects (like profitability, see Norrström et al. 2017) and fisheries management issues (like focusing on stock size versus fishing pressure, see Farcas and Rossberg 2016). Clarifying topological constraints can only be possible without considering all other aspects but these mathematical constraints must then be integrated with additional knowledge. Assessing MSY in a multi-species context may use information provided by this kind of analysis: the maximum yield values determined for a particular pair of species might be changed as a function of their topological relationship. This makes MSY assessment more complicated but also more system-based and holistic. Our purpose was to demonstrate how network analysis can be used for quantifying these constraints.

One of the key future extensions of this study is to investigate the generality of the results (same analysis is under investigation for 100 networks). General results on favourable topologies for dampening pairwise perturbations could really serve the basis of system-based conservation. Given that some general rules will emerge, these can be applied to real databases: in the case of fisheries on species *x*, we should be able to determine which other species *y* could also be fished, in combination with *x*, such that the combined impact is non-additive and favourable for the system (minimizing the impact). Topological analyses do not solve ecological problems themselves but they can help better understanding some basic constraints on ecosystem dynamics. Several additional factors can then be added and combined with it.

Here we addressed only the community-wide effects of heavy perturbations (e.g. fishing) on a single species or their pairwise combinations. But we think this is quite an important component of MSY, especially since our model provides a multi-species context for the problem. Understanding the relationship between single-species and multi-species perturbations (fisheries) is a major step towards better understanding additivity. If pairwise perturbations are more additive, the predictive value of single-species MSY-assessments is clearly higher (Walters et al. 2005). We have presented topological constraints on additivity: based on the network position of two species we can try to predict whether their pairwise perturbation will result in summed or dampened effects.

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Figure legends

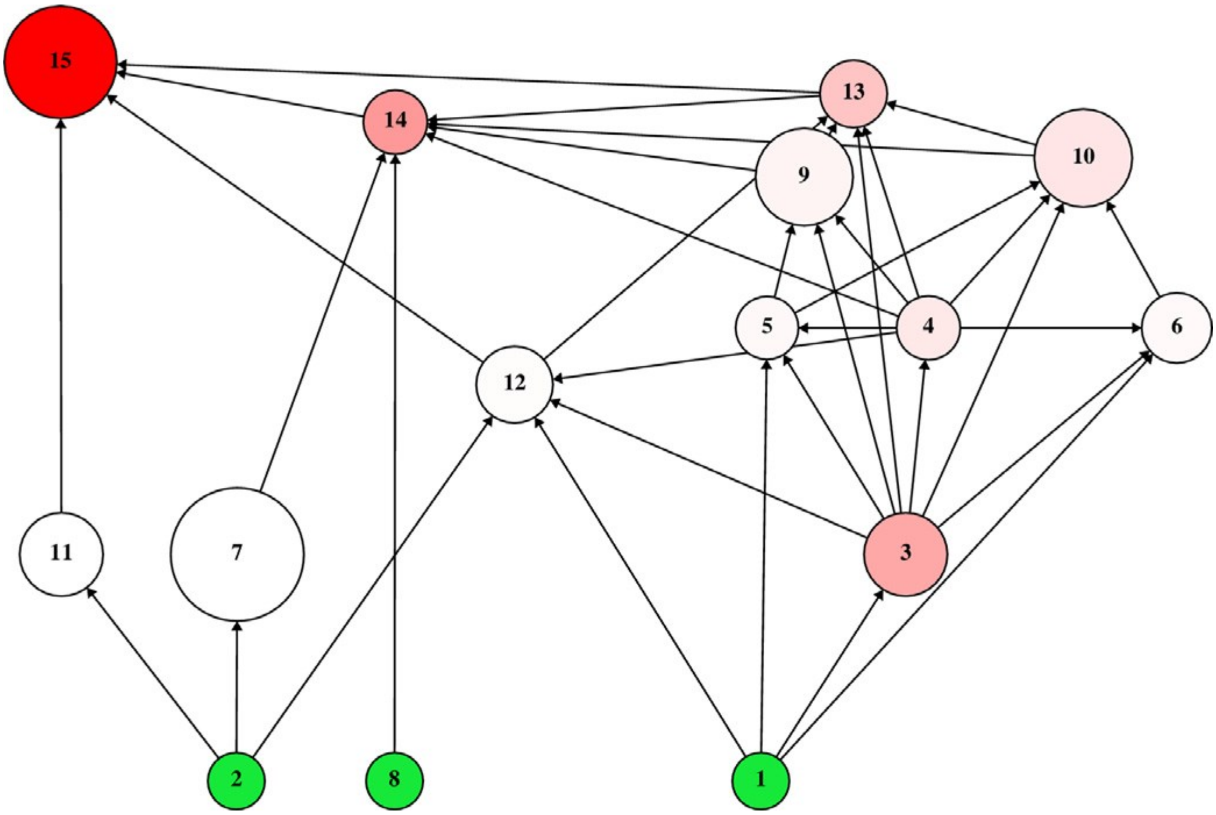
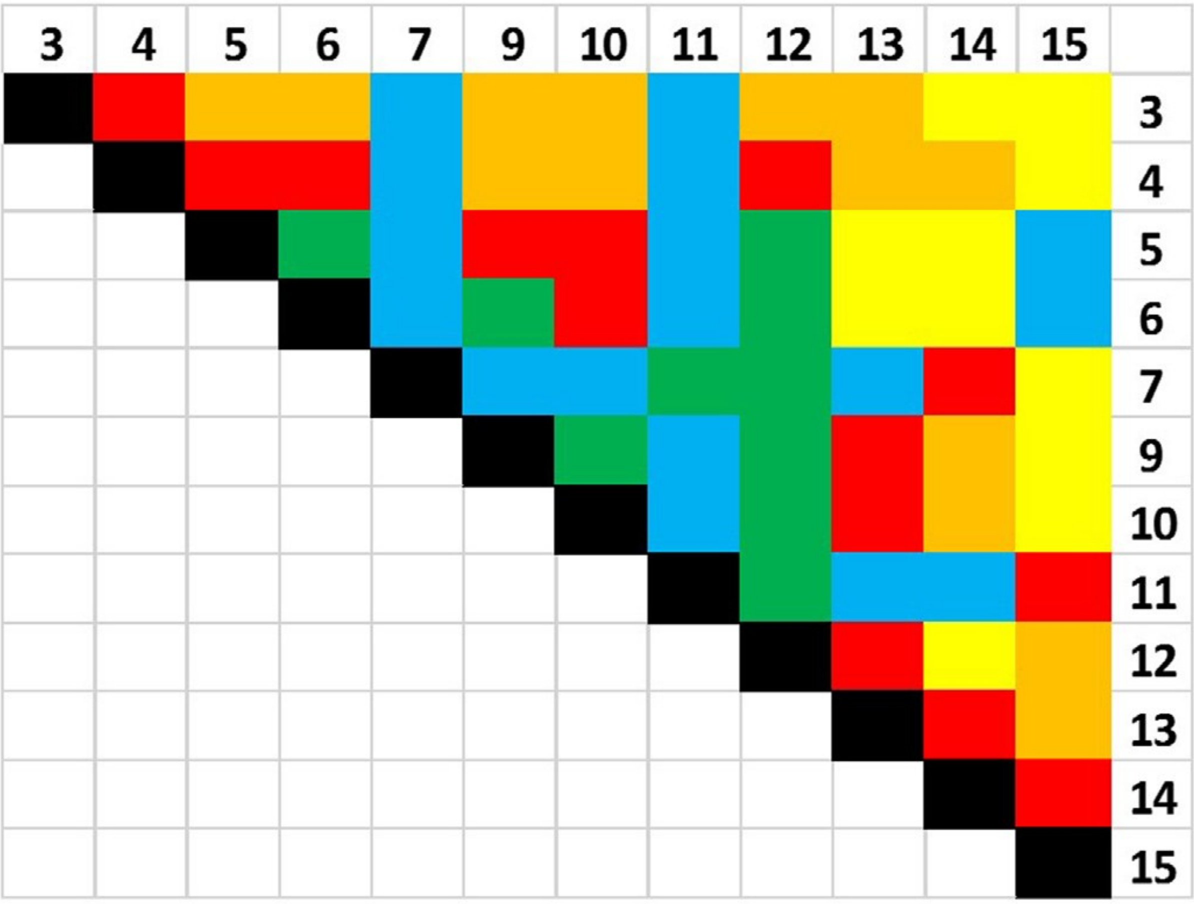


Figure 1. The studied food web. Arrows show carbon flows from resources to consumers. Producers (species #1, #2 and #8) are marked green, these are not perturbed in our study. Their size is arbitrary but the size of other nodes is proportional to the community response generated by their single-species perturbations (CR_j; species #7 is the largest one). The red shading of nodes is proportional to their indirect keystone index (K_{indir}; species #15 is of the deepest red colour). See Table 1 for numerical results.



	3	4	5	6	7	9	10	11	12	13	14	15
3	⬛	🟥	🟧	🟧	🟦	🟧	🟧	🟦	🟧	🟧	🟨	🟨
4		⬛	🟥	🟥	🟦	🟧	🟧	🟦	🟥	🟧	🟧	🟨
5			⬛	🟩	🟦	🟥	🟥	🟦	🟩	🟨	🟨	🟦
6				⬛	🟦	🟩	🟥	🟦	🟩	🟨	🟨	🟦
7					⬛	🟦	🟦	🟩	🟩	🟦	🟥	🟨
9						⬛	🟩	🟦	🟩	🟥	🟧	🟨
10							⬛	🟦	🟩	🟥	🟧	🟨
11								⬛	🟩	🟦	🟦	🟥
12									⬛	🟥	🟨	🟧
13										⬛	🟥	🟧
14											⬛	🟥
15												⬛

Figure 2. Community matrix showing different kinds of pairwise ecological relationships between pairs of species *j* and *k*: predation (red), intra-guild predation (orange), trophic cascade (yellow), exploitative competition (green) and none of these (blue). The rows and columns of unperturbed producers (species #1, #2 and #8) are not shown, while the main diagonal corresponding to single-species perturbations is black. The half-matrix representation indicates that the pairs of species are symmetrical (predator-prey and prey-predator is the same pair).

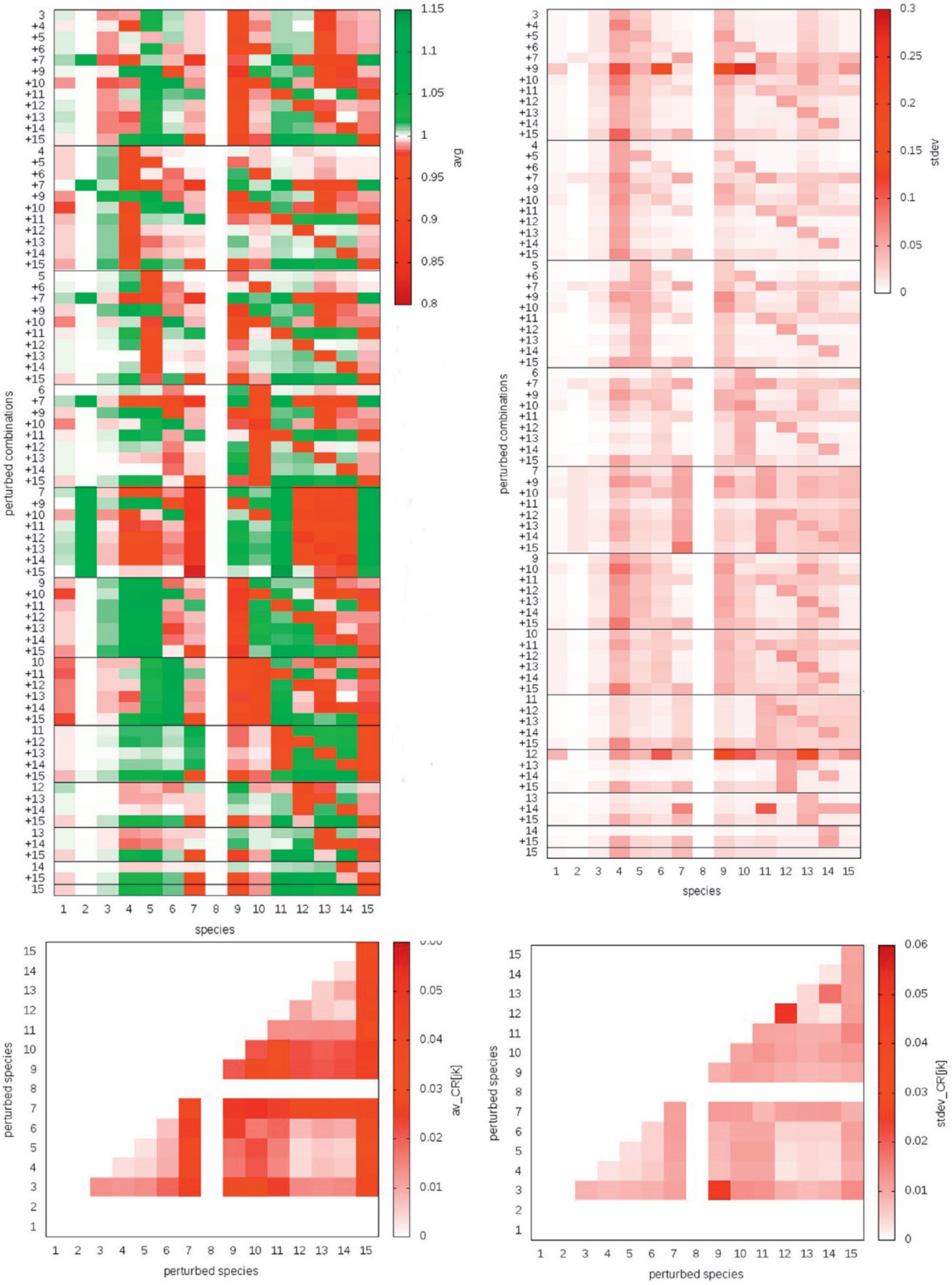


Figure 3. Heatmaps showing the effects of single-species and pairwise perturbations. In a, the species perturbed are shown in the rows: „5" corresponds to the single-species perturbation of species #5, while „+6" just below it corresponds to the pairwise perturbation of species #5 and #6. The species responding to perturbations are shown in columns. Green and red effects refer

to population increase and decrease, respectively, while deeper shades of both colours refer to stronger effects (see the scale on the right). We plot here the average effects measured over the simulations. In b, we show the standard deviation of the simulation outcome, i.e. the consistency of the previous results. The scale on the right shows how colour shade corresponds to standard deviation: for example, the effect of perturbing species #3 and #9 on species #10 is deep red, suggesting high standard deviation measured in the simulations, i.e. high inconsistency of the results. In the bottom heatmaps, the colour of the *ij* cells shows the average (c) and the standard deviation (d) of community response values, calculated by the response function, based on the simulation outcome shown in a and b (see colour scale for shade codes). In c and d, the rows and columns of the unperturbed producer species are white. For example, the pairwise perturbations of species #7 and #10 give strong results (deep red in c; large effects), and the pairwise perturbations of species #3 and #9 give inconsistent results (deep red in d; effects of various size).

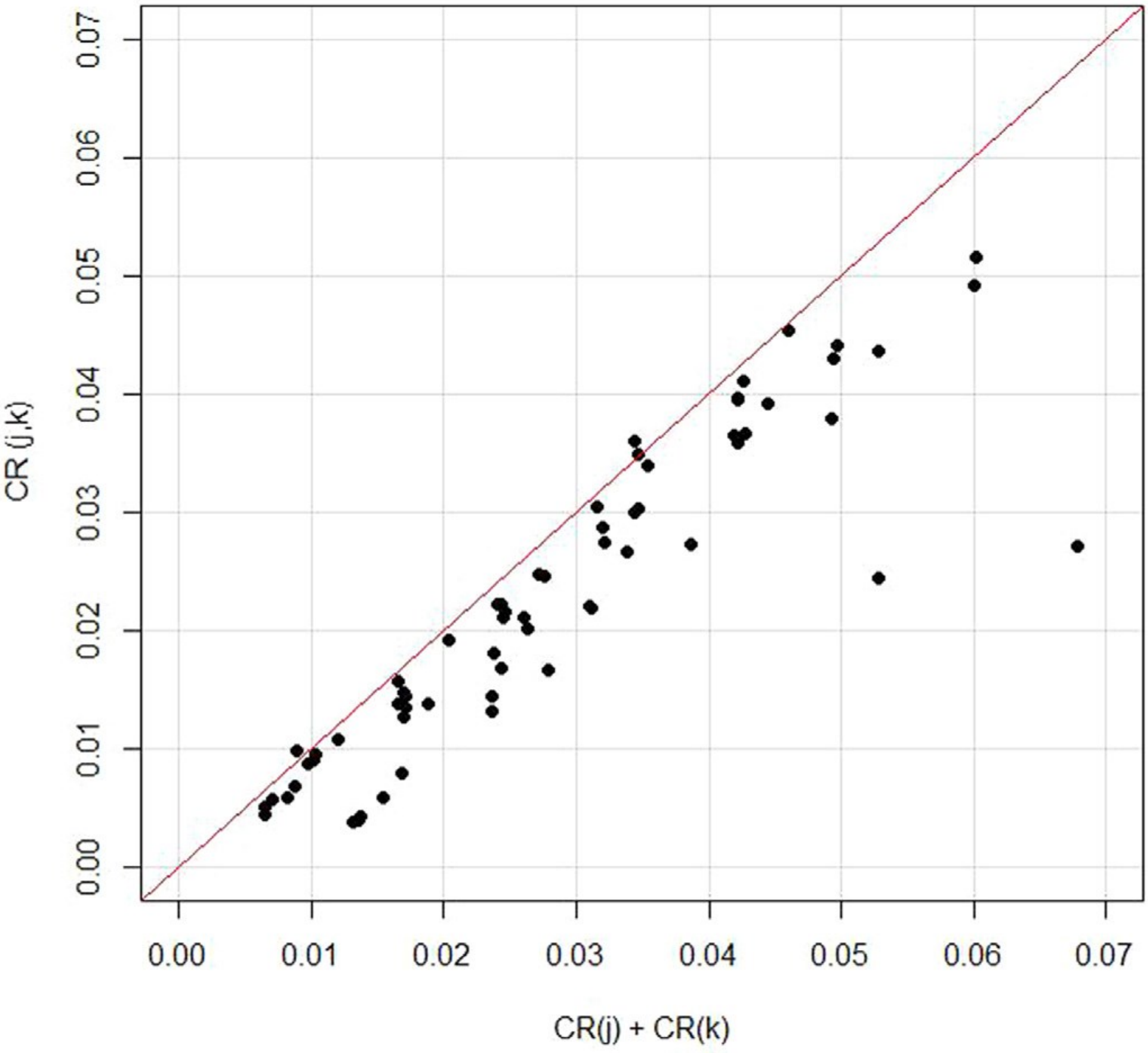


Figure 4. Plots showing the relationship between the community responses of pairwise [j k] perturbations (*CR(jk)*) and the sum of single [*j*] and [*k*] perturbations (*CR(j)* + *CR(k)*). Dots being on the $x = y$ line mark the additive node pairs, dots above the line mark pairwise perturbations that escalate single effects (only [3 9]) and dots below the line mark pairwise perturbations that dampen single effects (mostly [7 11] and [7 15]).

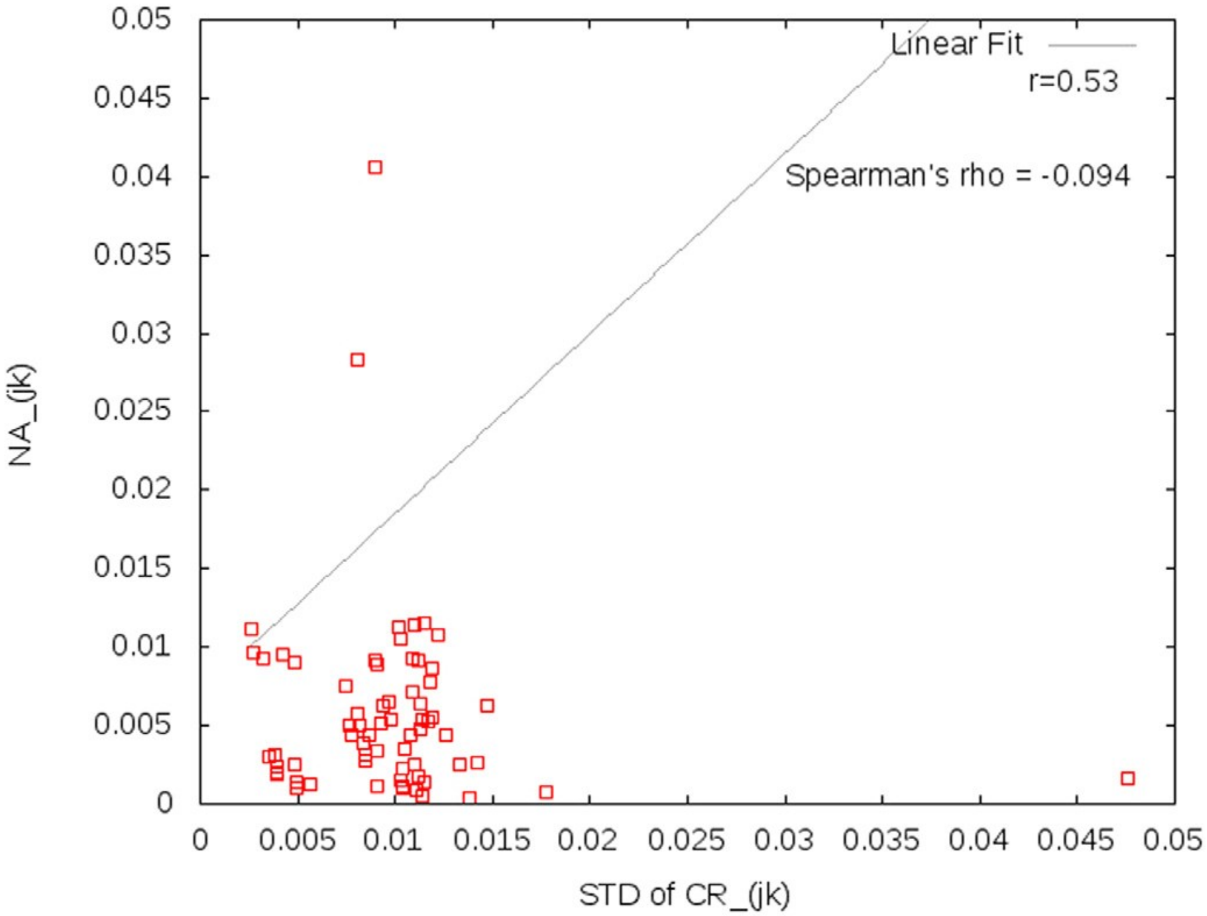


Figure 5. Correlation plot between the non-additivity (NA_{jk}) of pairwise [*j k*] perturbations and the inconsistency of their results (std of CR_{jk}).

Table 1. The relative importance of species based on 18 structural network indices (D, wD, BC, CC, TI^1, TI^3, TI^{10}, WI^1, WI^3, WI^{10}, s, $s`$, Δs, K, K_{bu}, K_{td}, K_{dir}, K_{indir}) and the community response to their single-species perturbations (CR_j). For each index, species are ranked according to the index value (see species codes in bold). Species #7 is marked by grey background for easier comparison.

	D		wD		BC		CC		TI1		TI3		TI10		WI1		WI3		WI10
3	8	**4**	2,06	**14**	25,05	**4**	66,67	**14**	2,38	**14**	1,81	**4**	1,6	**14**	2,47	**4**	1,88	**4**	2,06
4	8	**3**	1,89	**12**	16,13	**13**	66,67	**3**	1,50	**4**	1,5	**3**	1,58	**4**	1,88	**14**	1,79	**3**	1,89
13	7	**13**	1,33	**4**	9,91	**14**	63,64	**4**	1,39	**3**	1,48	**14**	1,57	**3**	1,66	**3**	1,7	**14**	1,46
14	7	**14**	1,19	**15**	9,75	**3**	60,87	**12**	1,23	**13**	1,36	**13**	1,43	**12**	1,14	**12**	1,29	**13**	1,32
10	6	**12**	1,18	**13**	7,84	**12**	60,87	**13**	1,18	**12**	1,27	**12**	1,27	**15**	1,13	**15**	1,16	**12**	1,31
12	6	**9**	1,09	**3**	7,24	**10**	58,33	**10**	0,99	**10**	1,1	**10**	1,19	**9**	0,89	**9**	1,13	**9**	1,17
5	5	**15**	1,00	**10**	5,32	**9**	56,00	**15**	0,95	**15**	0,96	**9**	0,99	**13**	0,87	**13**	1,13	**15**	1,12
9	5	**5**	0,52	**9**	2,64	**15**	53,85	**5**	0,87	**5**	0,9	**5**	0,97	**7**	0,59	**7**	0,69	**7**	0,59
6	4	**6**	0,50	**7**	2,50	**5**	48,28	**9**	0,74	**9**	0,9	**15**	0,9	**6**	0,40	**5**	0,46	**5**	0,52
15	4	**7**	0,43	**5**	1,78	**6**	46,67	**6**	0,67	**6**	0,71	**6**	0,78	**5**	0,38	**6**	0,45	**6**	0,5
7	2	**10**	0,43	**6**	0,92	**7**	46,67	**11**	0,58	**11**	0,57	**11**	0,49	**10**	0,36	**10**	0,45	**10**	0,46
11	2	**11**	0,25	**11**	0,50	**11**	38,89	**7**	0,48	**7**	0,54	**7**	0,48	**11**	0,34	**11**	0,37	**11**	0,33

	s		s'		Δs		K		Kbu		Ktd		Kdir		Kindir		CR(j)
3	11	**15**	26	**3**	10	**15**	14,00	**3**	6,48	**15**	14,00	**14**	3,89	**15**	11,00	**7**	0,039
4	9	**14**	19	**4**	6	**14**	8,32	**4**	2,84	**14**	8,07	**15**	3,00	**14**	4,43	**15**	0,029
5	9	**13**	13	**5**	6	**3**	6,73	**5**	0,88	**13**	4,26	**3**	2,95	**3**	3,78	**10**	0,021
6	8	**10**	6	**6**	5	**13**	4,71	**12**	0,54	**10**	2,74	**13**	2,20	**13**	2,51	**9**	0,021
9	4	**9**	5	**7**	2	**10**	3,24	**9**	0,50	**9**	1,15	**10**	2,15	**10**	1,09	**3**	0,014
10	4	**12**	4	**11**	0	**4**	3,02	**10**	0,50	**12**	0,93	**4**	2,01	**4**	1,01	**11**	0,014
12	4	**4**	3	**12**	0	**9**	1,65	**13**	0,46	**5**	0,60	**12**	1,32	**9**	0,49	**12**	0,010
7	3	**5**	3	**9**	-1	**5**	1,47	**6**	0,38	**6**	0,60	**9**	1,15	**5**	0,35	**6**	0,007
13	2	**6**	3	**10**	-2	**12**	1,47	**11**	0,25	**7**	0,33	**5**	1,12	**6**	0,19	**13**	0,005
11	1	**3**	1	**13**	-11	**6**	0,97	**14**	0,25	**11**	0,33	**6**	0,79	**12**	0,15	**14**	0,004
14	1	**7**	1	**14**	-18	**11**	0,58	**7**	0,21	**3**	0,25	**11**	0,58	**7**	0,04	**4**	0,003
15	0	**11**	1	**15**	-26	**7**	0,54	**15**	0,00	**4**	0,18	**7**	0,50	**11**	0,00	**5**	0,003

Table 2. The correlation between the 18 structural network indices and the community response quantified by single-species perturbations. Indices are ranked according to *p*-values (K_{indir} has the largest, while *D* has the smallest *p*-value) but none of the correlations are significant.

index	**rho**	**p**
Kindir	-0,028	0,9387
s'	-0,0284	0,9303
K	-0,0385	0,9054
Kdir	-0,0979	0,7663
Ktd	0,1368	0,6715
BC	-0,1748	0,5883
WI1	-0,2098	0,5135
WI3	-0,2456	0,4416
Δs	-0,2807	0,3768
WI10	-0,3217	0,3083
s	-0,3357	0,2861
CC	-0,3972	0,2011
TI1	-0,4126	0,1845
TI3	-0,4413	0,1509
Kbu	-0,4456	0,1465
WD	-0,4483	0,1438
TI10	-0,4685	0,1275
D	-0,4665	0,1264

Table 3. Pairwise species combinations are ranked according to the non-additivity of their combined perturbation (*NA_{jk}*). The topology of species pairs is categorized in 25 ways: black squares visualize group assignment. Based on *REGE* (see Figure 2), we can have species pairs in similar (*$REGE^s$*) and different (*$REGE^d$*) network positions. Based on ecological interactions (see Figure 3), we can have species pairs in prey-predator relationship („pred"), intra-giuld predation relationship („IGP"), trophic cascade relationship („tr casc"), exploitative competition relationship („expl comp") or none of these („none"). Finally, based on the 18 structural indices, we selected the 10 combinations of the 5 highest-centrality nodes, for each. For example, the combination of species #6 and #10 belongs to two categories: there is predator-prey relationship between them (pred) and both nodes belong the most central 5 nodes based on status (s).

Nodes	NA_{jk}	REGEs	REGEd	pred	IGP	tr casc	expl comp	none	D	K	Kbu	Ktd	Kdir	Kindir	wD	BC	CC	s	s'	ΔS	TI1	TI3	TI10	WI1	WI3	WI10
7+15	0,041		■			■																				
7+11	0,028						■																			
12+15	0,011		■		■											■								■	■	
7+12	0,011						■																			
6+10	0,011			■														■								
12+14	0,011					■			■						■	■	■				■	■	■	■	■	■
7+9	0,011							■																		
11+12	0,011						■																			
4+12	0,010			■					■		■				■	■	■	■			■	■	■	■	■	■
12+13	0,009			■					■						■	■	■				■	■	■			■
10+12	0,009						■		■		■							■								
5+12	0,009						■				■							■								
3+12	0,009				■				■		■				■		■	■			■	■	■	■	■	■
3+7	0,009							■												■						
6+12	0,009						■											■								
9+12	0,009						■				■							■								
7+10	0,009							■																		
7+14	0,008			■																						
4+9	0,008	■					■				■							■								
13+15	0,007		■		■					■		■	■	■		■			■							
9+15	0,006		■			■						■							■							
14+15	0,006		■	■						■		■	■	■		■			■					■	■	
11+15	0,006		■	■																						
10+13	0,006			■					■	■		■	■	■					■							
5+9	0,006			■							■							■								
10+15	0,005		■			■				■		■	■	■					■							
9+10	0,005	■					■				■	■						■	■							
11+14	0,005							■																		
7+13	0,005							■																		
11+13	0,005							■																		
9+13	0,005			■								■							■							
3+13	0,005				■				■	■			■	■	■		■				■	■	■			■
10+14	0,005				■				■	■		■	■	■					■							
10+11	0,004							■																		
3+4	0,004			■					■		■				■		■	■		■	■	■	■	■	■	■

3+14	**0,004**					■			■	■			■	■	■		■				■	■	■	■	■	■
9+11	**0,004**							■																		
9+14	**0,004**				■							■							■							
4+10	**0,003**	■			■				■		■							■								
4+15	**0,003**		■			■										■								■	■	
5+14	**0,003**					■																				
6+9	**0,003**						■											■								
4+14	**0,003**				■				■						■	■	■				■	■	■	■	■	■
3+5	**0,003**				■						■							■		■						
3+15	**0,003**		■			■				■			■	■										■	■	
6+14	**0,003**					■																				
5+7	**0,002**							■												■						
3+11	**0,002**							■																		
5+13	**0,002**					■																				
4+11	**0,002**							■																		
4+5	**0,002**			■							■							■		■						
4+13	**0,002**				■				■						■	■	■				■	■	■			■
5+10	**0,002**			■							■							■								
3+9	**0,002**				■						■							■								
4+7	**0,002**							■												■						
6+15	**0,001**		■					■																		
6+13	**0,001**					■																				
4+6	**0,001**			■														■		■						
3+6	**0,001**				■													■		■						
6+11	**0,001**							■																		
5+6	**0,001**	■					■											■		■						
5+15	**0,001**		■					■																		
5+11	**0,001**							■																		
13+14	**0,001**			■					■	■		■	■	■	■	■	■		■		■	■	■			■
6+7	**0,000**							■												■						
3+10	**0,000**				■				■	■	■		■	■				■								

Table 4. The statistical significance of the rank difference between node pairs belonging to particular categories (see Table 3) and the rest of the pairs, based on the non-additivity of effects (NA_{jk}). Indices are ranked based on *p*-values, and significant differences are bold.

index	p
Δs	**0,027**
expl comp	**0,030**
none	0,142
WI1	0,197
WI3	0,197
BC	0,303
IGP	0,447
REGEd	0,471
wD	0,549
CC	0,549
TI1	0,549
TI3	0,549
TI10	0,549
WI10	0,549
pred	0,577
Ktd	0,639
s'	0,639
K	0,661
Kdir	0,661
Kindir	0,661
D	0,679
Kbu	0,720
REGEs	0,781
s	0,941
tr casc	1,000